Ann. Rev. Psychol. 1982. 33:41–85

COLOR VISION

J. D. Mollon

Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, United Kingdom

CONTENTS

INTRODUCTION 42
Trichromacy and the Trichromatic Theory 42
Psychophysical Estimates of the Cone Sensitivities 44
The Two-Color Procedure and the π Mechanisms 45
Postreceptoral Processes 48
Color Deficiency 49
RECENT REVIEWS AND BIBLIOGRAPHIC SOURCES, TESTS, PERSONALIA 49
Books 49
Journals 50
Reviews and Specialist Bibliographies 50
New Tests and Other Materials 51
Necrology 51
THE FUNDAMENTAL SENSITIVITIES 52
Psychophysical Estimates 52
Microspectrophotometry 57
Concordance of Estimates of the Human Fundamentals 59
Individual Differences 61
THE ANOMALIES OF THE SHORTWAVE SYSTEM 63
Group A: Sensitivity of Short-Wavelength System 63
Group B: Adaptational Anomalies 66
Two Explanatory Principles 67
COLOR-OPPONENT CHANNELS 68
Primate Electrophysiology 68
Psychophysical Techniques for Isolating Color-Opponent Channels 68
Chromatically Opponent Processes Manifested in Threshold Measurements 70
Possible Identity of Opponent Mechanisms Revealed by Changes in Sensitivity, by Phenomenological Cancellation, and by Chromaticity Discrimination 72
DO STILES'S π MECHANISMS CORRESPOND TO CONE FUNDAMENTALS? 73
Experimental Tests 73
A Theory of π_1 and π_3 75
Self-Screening 75
Conclusions 76

0066-4308/82/0201-0041$02.00

SILENT SUBSTITUTION FOR POSTRECEPTORAL CHANNELS? THE REIFICATION OF LUMINANCE 76
TO WHAT EXTENT IS COLOR ANALYZED INDEPENDENTLY OF OTHER ATTRIBUTES OF THE RETINAL IMAGE? 78
Cortical Electrophysiology 78
Color-Contingent Aftereffects 79
Pathology 79
The Problem of Perceptual Synthesis 80

This review is dedicated to Dr. W. S. Stiles on the occasion of his eightieth birthday. It concentrates on human psychophysics and primate electrophysiology. While remembering those who use chapters in the *Annual Review of Psychology* as bibliographic instruments, I have tried also to write for the student reader who knows something of visual psychology but has not yet been initiated in the delicious mysteries of color. To this end I have corralled most of the general references into the second section and have attempted in the first to introduce the basic concepts needed later. For less compressed introductions, try Cornsweet (1970), Rushton (1972), or Mollon (1979, 1982a). For a *coup d'oeil* of the last 50 years of visual research try Rushton (1977a). The most recent survey of color vision in the *Annual Review of Psychology* was that by Jacobs (1976), which remains a most profitable source.

INTRODUCTION

Trichromacy and the Trichromatic Theory

The most fundamental property of human color vision remains that of trichromacy. Consider a circular matching field subtending two degrees of visual angle and divided into two halves. Suppose that we illuminate the left half of the field with three fixed wavelengths, and the right half with any other wavelength or spectral mixture. The three fixed wavelengths, by an unhappy convention, are called primaries, but the actual wavelengths chosen are arbitrary, provided only that no one of them can be matched by mixing the other two. Now, by adjusting only the intensities of the three primaries, the observer will be able to achieve a color match between the two sides of the field, although sometimes he will have to move one of the primaries to the right-hand side of the field. This is what is meant experimentally by saying that human foveal vision is trichromatic. By systematic experiments of this kind we can derive *color matching functions,* which give the amounts of our three primaries required to match each wavelength in the visible spectrum.

Trichromacy arises because there are just three types of cone photoreceptor in the normal retina, each type containing a different photosensitive pigment (Figure 1). The three pigments are maximally sensitive in different

parts of the spectrum, but their sensitivities overlap. Because of this overlap, no one of the primaries in a color-matching experiment will uniquely stimulate a single class of cone, and thus psychophysical color-matching functions cannot tell us directly how the sensitivities of the cones vary with wavelength.

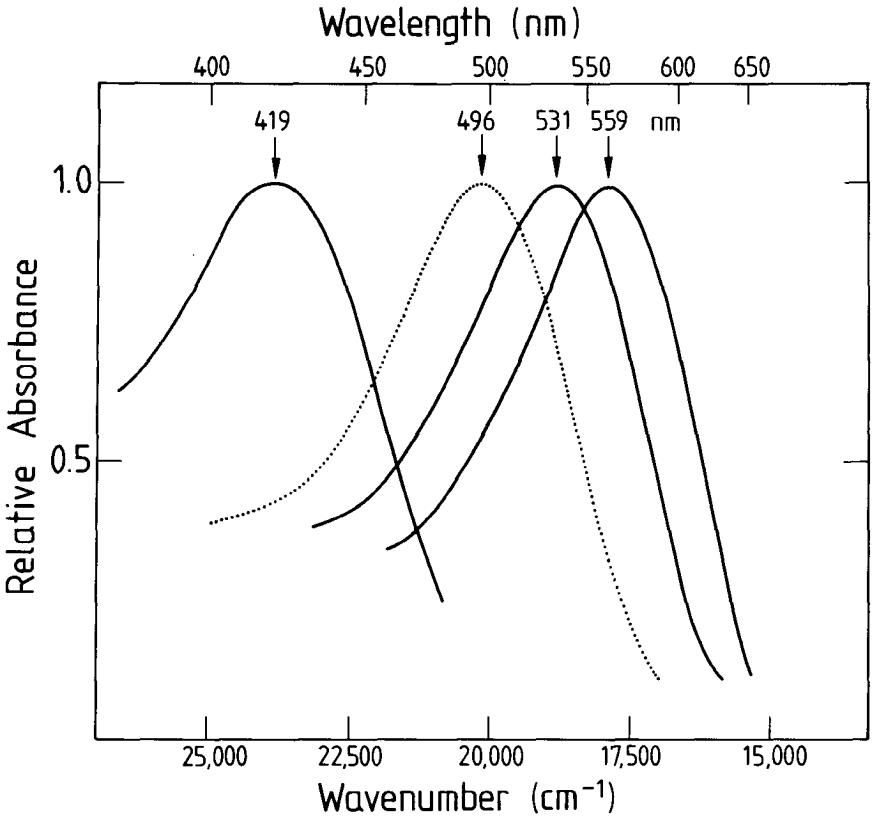

Figure 1 The absorbance spectra of the four photopigments of the normal human retina; the solid curves are for the three kinds of cone, the dotted curve for the rods. The quantity plotted is *absorbance,* i.e. log (intensity of incident light/intensity of transmitted light), expressed as a percentage of its maximum value; when "normalized" in this way, absorbance spectra have the useful property that their shape is independent of the concentration of the pigment (Knowles & Dartnall 1977, Chap. 3). It has become customary to plot absorbance spectra not against wavelength, but against its reciprocal, wavenumber, in part because it was once thought that photopigment spectra were of constant shape on such an abscissa, and in part because frequency (which is directly proportional to wavenumber) is independent of the medium.

These curves are based on microspectrophotometric measurements of 137 receptors from seven human retinae. The data will be published in detail elsewhere, and I am most grateful to Professor H. J. A. Dartnall and Dr. J. Bowmaker for permission to reproduce the absorbance spectra shown here.

The curves plotted in Figure 1 are *absorbance spectra,* which show for a given pigment how the quantity log (incident light/transmitted light) varies with wavelength. Also shown is the absorbance spectrum for the rods, which subserve our colorless vision at low levels of illumination; notice the essential similarity of shape of the four curves. All four photopigments, it is thought, consist of a protein molecule (called the "opsin") to which is bound a derivative of vitamin A_1, 11-*cis*-retinal (called the "chromophoric group"). The same chromophoric group is common to all the pigments but absorbs maximally at different wavelengths according to the protein to which it is bound.

The peak sensitivities of the cones lie in the violet (at a wavelength of approximately 420 nanometers), in the green (ca 530 nm) and in the yellow-green (ca 560 nm). The effect of selective absorption by the lens of the eye is to shift the peak sensitivity of the short-wavelength (violet-sensitive) cones to 440 nm when measurements are made in terms of the radiance incident at the cornea. It is traditional to speak of "blue," "green," and "red" cones, but this practice misleads equally the trusting student and the unguarded expert, and from now on I shall write of short-wavelength (S), middle-wavelength (M), and long-wavelength (L) cones.

In man and primates, any individual cone is thought to obey the *Principle of Univariance:* although the input to the cone can vary in wavelength and in intensity, the cone's electrical polarization increases simply with the rate at which photons are absorbed. All that varies as wavelength varies is the probability that an individual photon will be absorbed (the absorbance spectra of Figure 1 reflect this changing probability). Thus an individual class of cones is as color blind as are the rods. But whereas there is but one class of rod, there are three types of cone; and by comparing the rates of absorption in different classes of cone, the visual system becomes able to discriminate wavelength.

Psychophysical Estimates of the Cone Sensitivities

Reliable physical measurements of human absorbance spectra (Figure 1) have become available only in the last 2 years, and they certainly do not make redundant the many psychophysical estimates of the spectral sensitivities of the cones. For what we ultimately want to explain is seeing, and only psychophysical measurements can assure us that our physical measurements are relevant to color vision.

As we have seen, the overlap of the cone sensitivities means that we cannot discover the properties and spectral sensitivity of a class of cone simply by stimulating the retina with single colored lights. (There are many similar difficulties in other fields of experimental psychology. For example, we cannot study primary memory merely by asking our subject to report

back a list of words within a few seconds of presentation; some items may be recovered from primary memory, some from secondary memory.) To "isolate" one class of cone—to cause the subject's response to be determined by only that one class—typical psychophysical strategies have been to select observers who appear to lack either one or two of the three classes, to use temporal or spatial parameters to which some cones are thought to be insensitive, or to use colored adapting fields that selectively depress one or two classes of cone. Often two such devices are combined. I give below an account of one celebrated and easily understood technique, that of W. S. Stiles. There are two reasons for describing this in detail. First, it well illustrates some basic concepts and procedures, which are echoed in later methods. Second, although Stiles's system was set out more than 40 years ago, his work was curiously neglected for many years and has been more frequently cited in the last 6 years than during any previous period; so I shall have to refer to it frequently. In part, Stiles's papers may have gone unread earlier because they were obscurely published; this has been remedied by their recent republication in a single volume (Stiles 1978).

The Two-color Procedure and the π Mechanisms

Stiles typically presented a 200-msec foveal test flash of wavelength λ on a larger adapting field of wavelength μ (Figure 2a). For a given combination of λ and μ, the threshold intensity for detecting the incremental test flash is measured at a number of intensities of the field; this gives a "threshold-vs-intensity" (t.v.i.) curve (see Figure 2b).

To account for how t.v.i. curves change with variations in λ and μ, Stiles postulated that there exist, at a peripheral stage of the visual system, associations of cones (or π mechanisms) that obey two principles: first, the Principle of Univariance, and second, what I shall refer to as the *Principle of Adaptive Independence.* The latter specifies that the sensitivity of each π mechanism depends only on the rate at which photons are absorbed from the adapting field by that mechanism and is independent of the rates of absorption by other π mechanisms. It was from strictly psychophysical observations that Stiles inferred the existence of mechanisms with these two properties; so the π mechanisms are what psychologists call "hypothetical constructs." Since three of them are now known to have spectral sensitivities quite close to those of the cones, their status approaches that of the gene, which existed as a hypothetical construct for 50 years before it could, with qualifications, be identified with a section of a DNA molecule.

In the field sensitivity version of Stiles's method, λ is held constant and is chosen to favor one of the π mechanisms. T.v.i. curves are obtained for different values of μ. Two such curves are shown in Figure 2b. Provided detection remains dependent on a single π mechanism with the properties

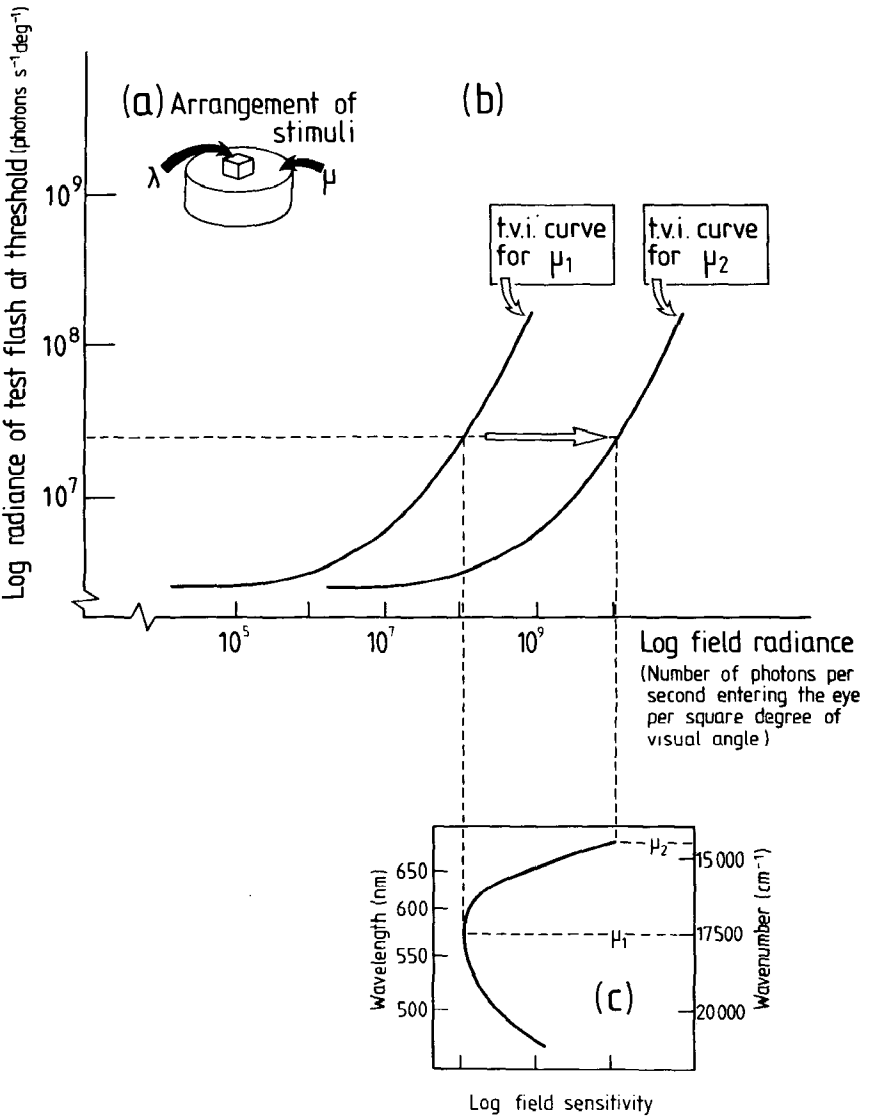

Figure 2 (a) The spatial arrangement of stimuli in Stiles's two-color experiments. (b) t.v.i. curves for two values of the field wavelength (μ_1 and μ_2). The horizontal broken line shows the criterion elevation of threshold (1 log unit) usually used by Stiles for deriving the "field sensitivity" of a π mechanism. (c) Derivation of field sensitivity.

defined above, then all that will happen as μ is varied is that the entire t.v.i. curve will move to and fro along the logarithmic abscissa without any other distortion. Stiles called this a *displacement rule;* in recent literature the same property of the t.v.i. curve is sometimes called *shape invariance.*

The "field sensitivity" of the π mechanism is directly given by the lateral movements of the t.v.i. curve as μ changes. A helpful way to look at it is this. If we could plot on the abscissa and ordinate of Figure 2b the actual rates at which photons are absorbed from the field and from the test flash, then the curve would always be the same (owing to the two defining properties of a π mechanism). But in fact we know only the rate at which photons are delivered to the observer's cornea. What the lateral movements of the curve show us is how the probability of absorption of an individual photon varies as we vary μ. Remember that a constant shift on a logarithmic axis is equivalent to multiplication by a constant factor. Figure 2c shows graphically the derivation of field sensitivity for the long-wave π mechanism. Fields of wavelength μ_2 need to be 100 times ("2 log units") more intense than for μ_1 to raise the threshold by the same criterion amount (Figure 2b); this means that the mechanism is 2 $\log_{10}$ units less sensitive to μ_2 than to μ_1 (Figure 2c). The spectral sensitivity curve derived in Figure 2c is called an action spectrum: it shows the intensity required at different wavelengths to achieve a criterion effect (in this case a rise of 1 $\log_{10}$ unit in the threshold). Its relation to the absorbance spectrum of the L cones will be a matter for discussion later in the review.

By holding μ constant and manipulating λ, Stiles derives a second measure, test sensitivity, from entirely analogous movements of the t.v.i. curve along the ordinate. Sooner or later, however, as λ and μ are varied, shape invariance will fail—the t.v.i. curve may, for example, break up into two branches that move independently. When this happens, Stiles's postulates require him to suppose that a different π mechanism has taken over detection. The three main π mechanisms so derived have peak sensitivities, measured at the cornea, of approximately 440 nm (π_3), 540 nm (π_4), and 570 nm (π_5). However, Stiles found more failures of shape invariance than were compatible with three independent cone systems and was led, for example, to postulate three blue-sensitive mechanisms (π_1, π_2, π_3), which all peak near 440 nm but differ in their sensitivity to longwave fields. Modern opinion attributes these additional failures of shape invariance to limited failures of adaptive independence, and I shall have much to say about this later. For a more detailed introduction to Stiles's method, see Marriott (1976). A brief history of the π mechanisms is given by Stiles (1980).

Postreceptoral Processes

Since individual classes of cone are color blind, there must exist neural machinery to compare the outputs of different classes. The way this comparison is made is thought to be analogous to the way local differences in retinal illumination are detected: some ganglion cells in the primate retina appear to receive excitatory inputs from one or two classes of cone and inhibitory signals from the remaining cones.

In the last two decades it has become very clear that the pattern of activation of the photoreceptor array is examined by a variety of postreceptoral pathways or "channels" that extract different attributes of the stimulus (for a review, see Lennie 1980). These channels, functionally parallel and anatomically intermingled, may correspond to morphologically distinct classes of fibers with perhaps different conduction speeds, different integrative properties, and different central destinations. Only a subset of these channels—the color-opponent channels—are concerned to extract information about wavelength. Accordingly, a dominant objective of color psychophysicists in recent years has been to find ways of isolating particular classes of postreceptoral channel, much as they earlier sought strategies that caused the response to depend on individual classes of cone.

The relative weightings of signals from the three cone types may be different for different postreceptoral channels and thus for different visual functions. If we ask subjects to equate lights of different wavelength for luminosity (e.g. by flicker photometry, in which a comparison light is alternated with a standard and the intensity of the comparison light is adjusted to minimize flicker), then we find that the spectral luminosity function thus obtained behaves as if it is dominated by the response of the L cones; the M cones apparently contribute less and the S cones possibly nothing at all. At any rate, this is the conclusion we must reach if we take modern estimates of the spectral sensitivities of the cones and if we adopt the common (though not entirely satisfactory) hypothesis that the spectral luminosity function represents the linear sum of signals from different classes of cone.

The contributions of the different cones to hue appear to be ordered in the opposite way. The S cones make a very large contribution to hue despite their low absolute sensitivity; and if—as many do—we wanted to suppose that L and M cones are making equal contributions to color-opponent channels when a light appears yellow, we should have to suppose that the M signal has been given a greater weighting before presentation to the opponent channel. However, another conclusion is clear from modern estimates of the cone sensitivities: it is quite impossible to maintain that the ratio of L to M cone signals is the same at the two points in the spectrum that appear neither reddish nor greenish ("unique yellow" and "unique

blue" ca 575 and 470 nm respectively). Given this, there is little firm ground for taking the ratio of signals to be unity at either of these wavelengths. To explain the spectral position of unique yellow we probably should look outside the observer: unique yellow is close to the wavelength that produces the same quantum catches in the L and M cones as does the average illumination from our world.

Color Deficiency

About 2% of men and 0.03% of women are dichromats, who require only two variables in a color-matching experiment and who (in this and other ways) behave as if they lack one of the three classes of cones of the normal. The terms protanope, deuteranope, and tritanope are used for observers who behave as if they lacked L, M, or S cones respectively. Protanopia and deuteranopia are inherited as recessive, sex-linked characteristics; inherited tritanopia is rare and is not sex-linked.

Against the idea that deuteranopia represents the simple absence of the M pigment (the "loss" or "reduction" hypothesis), the reader will often find it argued that the spectral luminosity curve of the deuteranope is little changed from that of normals. The curve for the protanope, on the other hand, does show a marked loss at long wavelengths, as would be expected if the L cone were absent. The considerations of the last section show why it is mistaken to advance this argument against the reduction hypothesis for deuteranopia: the spectral luminosity curve of the normal peaks at 555 nm and behaves as if it is dominated by the L cone, which the deuteranope retains.

A second major class of abnormal subjects are the anomalous trichromats, who require three primaries to make all possible color matches but whose matches are different from those of normal observers. All modern evidence is compatible with the hypothesis that the anomalous retina contains three cone photopigments, but at least one of them is abnormal in its spectral position. The term protanomaly is used to indicate the form of anomalous trichromacy in which the L pigment appears to be modified; deuteranomaly and tritanomaly correspond to analogous abnormalities of the M and S cones.

RECENT REVIEWS AND BIBLIOGRAPHIC SOURCES, TESTS, PERSONALIA

Books

A general textbook on color vision by Boynton (1979) is comprehensive and well balanced; with occasional exceptions it represents current orthodoxy. Those who enjoy a mild flirtation with heresy may turn to the text by

Wasserman (1978), which has some good expository passages and some mistaken ones. An authoritative handbook on photopigments has been published by Knowles & Dartnall (1977). Pokorny et al (1979a) have provided a very welcome survey of color deficiency, in which they attend equally to theoretical problems and to the details of clinical testing. A comparative review of vertebrate color vision is to be published by Jacobs (in press). A number of significant papers on color vision appear in a *Festschrift* for Lorrin Riggs (Armington et al 1978), in the proceedings of a conference held in Houston (Cool & Smith 1978), and in the proceedings of the Third AIC Congress (Billmeyer & Wyszecki 1978). The biennial proceedings of the International Research Group for Color Vision Deficiencies (e.g. Verriest 1980, 1982) are of mixed quality but always contain some papers of importance. A short, attractive introduction to colorimetry, *Measuring Colour* by R.R. Blakey (3rd ed., 1980), is available free from Tioxide, 10 Stratton Street, London W1A 4XP, UK. Troubling remarks on surface colors and on transparency will be found in Wittgenstein (1977). The curious, Joycean essay *On Being Blue* by Gass (1976) is a typographically exquisite collectors' item; it is certainly about color and is classified as psychology by the Widener Library.

Journals

A new interdisciplinary journal, *Color Research and Application* (J. Wiley), carries articles on vision as well as on industrial aspects of color. Well worth the $15 subscription is the running bibliography *Daltonia,* circulated by the International Research Group for Color Vision Deficiencies (available from: Dr. G. Verriest, Dienst Oogheelkunde, De Pintelaan 135, B-9000 Gent, Belgium); it concentrates on color deficiency but abstracts many straight papers on color vision. Tachistoscopically frozen glimpses of the latest state of the science will be found in the annual proceedings of the Association for Research in Vision and Ophthalmology, published as a supplement to *Investigative Ophthalmology and Visual Science.*

Reviews and Specialist Bibliographies

Much relevant background material will be found in a distinguished review of visual sensitivity by MacLeod (1978). A recommended review of colorimetry is that by Wyszecki (1978); for a gentle introductory treatment of chromaticity diagrams and color appearance systems try Padgham & Saunders (1975) or Sharpe (in press). Ronchi (1975) provides an annotated bibliography of papers on rods and cones, which is a useful guide to the literature on rod-cone interactions and on the possible role of rods in color vision. Serra (1980) has compiled an annotated bibliography on heterochromatic photometry (the matching of the brightness of lights that differ in color), with special reference to what is nowadays called the minimally

distinct border technique, in which the subject adjusts the intensity of a colored field until it forms a minimally distinct border with a juxtaposed reference field of a second color. Reviews by Verriest (1974) and Lyle (1974) are bibliographic sources for information on the many toxins, drugs, and diseases that can impair color vision. Hansen (1979) describes studies in which a perimetric form of the Stiles procedure was used to study cone mechanisms in visual disorders. Walraven (1981) reviews a series of studies on chromatic induction. Turn to Christ (1975) for a bibliography on color coding in visual search and identification tasks; see O'Neem (1981) for discussion of the use of color in street signs.

New Tests and Other Materials

The Okuma charts for detecting color deficiency (Okuma et al 1973) are constructed after the manner of classical pseudoisochromatic plates, such as the Ishihara, but the target is in the form of a Landolt C, a traditional test stimulus for measuring acuity, and thus the same card can be presented repeatedly to the patient in different orientations, if, say, one wishes to examine the effects of visual angle or position in the field. These plates are available from Amoriex Co., Kyodo Bldg., 5 Nihonbashi-Honcho 2 Chome, Chuo-ku, Tokyo, 103 Japan; a rough English translation of the instructions can be obtained from the present writer. The City University booklet test (Keeler Instruments, Windsor, Berks., SL4 4AA, UK) is intended to distinguish different types of deficiency, including the tritan type, which is not detected by most of the traditional booklet tests. A new microprocessor-controlled scorer for the Farnsworth-Munsell 100-hue test (Biophysic Medical S. A., 64 Saint-Jean, 6305 Clermont-Ferrand, France) should allow more use of this classical test when large numbers of subjects are to be screened.

The Optical Society of America has produced its own series of uniform color scales (the OSA UCS system), in which the perceptual separation of the colors is more even than in the Munsell system. These standards are available from OSA, 1816 Jefferson Place, N W, Washington DC 20036, USA.

Necrology

During the period of this review the death has occurred of H. Hartridge (1886–1976) and of his sometime pupil, W. A. H. Rushton (1901–1980). Rushton lived long enough to write two engaging obituaries of his former teacher (Rushton 1977b,c) and to recall that Hartridge, if not a Trinity man, was once a "sound Young-Helmholtz man" before he left Cambridge, entered "the most dangerous domain of color vision, the *appearance* of colors," and yielded to "the special pleading of each lovely color to make it legitimate by granting it a separate parent cone." Apostasy is unforgivable

in one who initiated you in the true faith. Many of the problems that exercised Hartridge during the 1940s—prereceptoral filters, chromatic aberration, the antichromatic response, Sloan's notch—are again to the fore, and it is worth returning to his papers. It is a pity that Rushton's bibliography of Hartridge omits his valuable book *Recent Advances in the Physiology of Vision* (1950), which contradicts any idea that Hartridge was preoccupied only with his polychromatic theory.

Rushton has left a brief, characteristically elegant autobiography—and an apology to colleagues for "the ungovernable sharpness of my scientific criticism" (Rushton 1975a). It is astonishing to remember that Rushton entered the field of vision only at the age of 50 and published over 100 papers on the subject before his death. He was especially attracted to color by the elegant manipulations that the trichromatic system allows (see next section), and he in turn has visibly influenced the style of several colleagues and pupils.

THE FUNDAMENTAL SENSITIVITIES

Psychophysical Estimates

There is a sophisticated history to psychophysical derivations of the "fundamentals," the spectral sensitivities of the receptors, and many contemporary discussions are addressed strictly to the cognoscenti. The clearest recent introduction I have come across is that by Sharpe (1980), who is especially concerned with the longwave fundamental. The serious student of this field should not fail to consult the monograph of Estévez (1979) and the recent paper of Wyszecki & Stiles (1980).

DERIVATIONS FROM COLOR-DEFECTIVE OBSERVERS Dichromats offer two classical routes to the fundamentals. Both start from the hypothesis that dichromats retain two of the normal pigments and have simply lost the third.

The first method is to measure directly the spectral luminosity function of a deuteranope or a protanope, eliminating the response of the S cones by using high spatial or temporal frequencies (see below) and thus securing the putative sensitivity of the L cones from the deuteranope and that of the M cones from the protanope (Smith & Pokorny 1975, Tansley & Glushko 1978). An interesting variation of this first method takes advantage of the fact that deuteranopes and protanopes are effectively monochromats in the red-green part of the spectrum: a shortwave "primary" light of fixed intensity and wavelength is mixed with a longwave light of variable wavelength (λ), and for each value of λ the dichromat is asked to adjust the intensity of the longwave component until the mixture matches a fixed white. This

"Maxwell-match" method was used to examine the L cones of deuteranopes by Alpern & Pugh (1977). At wavelengths greater than 530 nm the deuteranope was always able to complete the match with the one adjustment, and Alpern and Pugh infer that the adjustments needed at different values of λ are simply those required to yield a constant quantum catch in the L cones.

A second way of deriving fundamentals from dichromatic matches is to relate the confusions made by each kind of dichromat to the color-matching functions of the normal observer. Insofar as the normal observer can discriminate a set of lights that a certain dichromat confuses, he must be doing so with the single pigment that is lacked by that type of dichromat. Spectral sensitivities derived analytically in this way are called "König fundamentals." Needless to say, several slightly different sets of König fundamentals can be derived by taking different data for the dichromatic and normal color-matching functions. The set of König fundamentals most often adopted by modelers during the period of this review have been those of Smith & Pokorny (1975). The L and M functions of Smith and Pokorny are consistent with their direct measurements of deuteranopic and protanopic luminosities (see above). Two caveats may be helpful to anyone entering this literature. First, there is more than one set of "Smith-Pokorny fundamentals" in circulation: those tabulated by Boynton (1979) are the pure König fundamentals of Smith & Pokorny (1975), whereas those given by Ingling & Tsou (1977) were derived by a hybrid method (Smith et al 1976) in which the shortwave limbs of the L and M König fundamentals were slightly modified to make them more consistent with the absorbance spectrum of a known photopigment, iodopsin. The second caveat is that the formula given by Boynton (1979) for the Smith-Pokorny middlewave function has the wrong sign in front of the $\bar{z}$ term.

Another recent set of König fundamentals are those of Vos (1978), who like Smith and Pokorny, takes his normal color-matching functions from Judd's 1951 modification of the 1931 CIE "standard observer" but adopts different values for dichromatic confusions. Estévez (1979) has argued that König fundamentals are more appropriately derived from the 1955 color-matching functions of Stiles and Burch than from the CIE functions, because only the Stiles and Burch data were obtained directly using radiometrically calibrated primaries.

Some additional evidence for the reduction hypothesis—on which all the above derivations depend—is provided by a reflection densitometric study of 15 deuteranopes by Alpern & Wake (1977), who measured the reflectivity of the fovea at various wavelengths, first in the dark-adapted state and then after partial bleaching with red or green lights that were chosen to bleach approximately half of the L pigment. The measured changes in spectral

reflectivity, the difference spectra, were the same (within experimental error) whether red or green bleaching light was used. This result, which elaborates earlier measurements of Rushton, does not rule out the possibility of a small quantity of M pigment in the deuteranope—a quantity unmeasurable by this technique—but it does exclude forms of the classical "fusion" theory of deuteranopia in which it is supposed that L and M pigments are present in almost normal quantities but that pigments or neural signals are mixed to yield centrally a two-variable system. (Such hypotheses were traditionally supported by the deuteranope's luminosity function; see Introduction.) However, Alpern and Wake draw attention to differences in the anomaloscope settings made by different deuteranopes, and this raises a quite separate problem for derivations of the fundamentals from dichromatic data (see below).

SILENT SUBSTITUTION The Principle of Univariance (see Introduction) provides the theoretical basis for some new methods of experimentally isolating an individual class of cone. In these procedures, thresholds are measured not for simple increments, as in Stiles's method, but for a spatial or temporal transition between two lights that have been equated for their effect on one or two of the three classes of cone. If two different wavelengths or spectral mixtures are adjusted in intensity so that they lead to the same rates of quantum catch in, say, the M cones, then a "silent substitution" can be made between the two lights as far as the M cones are concerned. Detection of a transition from one light to the other must then depend on another class of cone—and if, say, measurements are confined to long wavelengths this will be the L cones. One can then use field-sensitivity measurements (see above) to derive the spectral sensitivity of the isolated cones: i.e. one finds for different values of μ the intensity of a background field needed to bring the transition to threshold. At this stage, one must, like Stiles, assume adaptive independence. The method may sound worryingly circular to the reader, for we seem to need to know the spectral sensitivity of at least one class of cone before we can set up the silent substitution in the first place. But in fact it is sufficient that one class of cone should be much more sensitive to the transition than the others; and by an iterative procedure it is possible to improve on an initially rough estimate of the spectral sensitivity of the silenced cones.

Rushton and his collaborators call their version of this technique the "exchange threshold method" (Rushton 1975b), and they obtain field sensitivities at only two field wavelengths (540 and 640 nm). Thereafter, to obtain sensitivities at intermediate wavelengths, they ask their subject to match a given monochromatic light (λ) with a mixture of the green (540 nm) and red (640 nm) lights, and they cunningly arrange that the latter

mixture, whatever proportion of red to green the subject requires, always produces the same total effect on the chosen cones. (They can do this because they know the field sensitivities for the red and the green lights and they implicitly assume adaptive independence). Having adjusted the red/green ratio to match the hue of λ, the subject completes his match by adjusting the intensity of λ to equate brightness. And now λ must be producing the same quantum catch in the chosen cones as does the mixture; and a spectral sensitivity can be obtained by repeating this operation for different values of λ. This procedure is complicatedly elegant and is marvelously characteristic of Rushton; I have attempted a less compressed exegesis in Mollon (1979).

Cavonius & Estévez (1975) use a more straightforward version of the silent substitution technique, calling it the "spectral compensation" method. They arrange that the spatiotemporal modulation of a grating should be invisible to two of the three cone types, and they measure field sensitivity throughout the spectrum for the isolated cones. Their three spectral sensitivities thus derived resemble the π_3, π_4, π_5 mechanisms of Stiles, although they find a systematic discrepancy at short wavelengths for the M cones. Piantanida et al (1976) used a similar method to obtain field sensitivities for normals, dichromats, and anomals. Silent-substitution methods are reviewed by Estévez & Spekreijse (in press).

A conceptually related method for securing the fundamentals is that of Williams & MacLeod (1979). Here the principle of silent substitution is used twice over, once in a spatial mode, once in a temporal mode. First, an afterimage is obtained of an intense, bipartite field, half of which is illuminated with green light (538 nm) and half with a longer wavelength, λ (which is different on different occasions). It is well known that afterimages, being perfectly stabilized on the retina, soon disappear if viewed against a homogeneous field but can be revived by a sudden lightening or darkening of the background field. Working in the longwave part of the spectrum, where only two mechanisms are in play, Williams and MacLeod set out to find combinations of (A) the ratio of the green light and λ in the original bleaching light, and (B) the ratio of two background fields, such that the afterimage appears homogeneous and not bipartite, when, after initial fading of the afterimage, a transition is made from one background field to the other. When such a combination is found it is assumed that *(a)* a spatially silent substitution has been achieved for one class of cone during the original bleach, and *(b)* a temporally silent substitution has been achieved for the second class of cone at the moment of transition between the two backgrounds. Only with both types of cone thus silenced does the bipartite division of the afterimage become invisible. By discovering the critical combinations of ratios A and B at different values of λ, Williams and

MacLeod derive spectral sensitivities similar to those obtained by inviting protanopes and deuteranopes to make brightness matches in the same apparatus. Their method depends on, and their results support, the assumption that the losses of sensitivity produced by bleaching are independent for different classes of cone.

COLOR NAMING A very different route to the fundamentals is described by Krauskopf (1978). If very brief (10 msec), very small (1.3′) flashes of liminal intensity and constant wavelength (say, 580 nm) are delivered to the central foveola, then from trial to trial their appearance varies strikingly: sometimes the 580-nm flash appears a saturated red, sometimes a saturated green, sometimes desaturated or white, and sometimes it is not seen. Krauskopf supposes that three statistically independent channels are available for detection, that the saturated colors are seen when only one channel is activated, and that desaturated sensations arise when more than one channel is activated. Now, as wavelength is varied, the probabilities of the different types of subjective report also vary. Of course, these probabilities cannot directly give spectral sensitivities for individual channels, since the probability of seeing, say, a saturated red flash at a given intensity and wavelength depends on the sensitivity of the M channel as well as that of the L channel. However, Krauskopf reasons as follows. Allow that the probability of seeing a saturated red flash is identical with the probability (P'_L) of the L channel being activated *in the absence of activation of any other channel.* (He gives evidence for this identity.) Then

$$P'_L = P_L\,(1-P_M)\,(1-P_S) \qquad 1.$$

where P_L, P_M, and P_S are the independent probabilities of detection by L, M, and S channels respectively. The probability of not activating any channel is the probability of not seeing anything at all (P_{ns}) and is given by

$$P_{ns} = (1-P_L)\,(1-P_M)\,(1-P_S) \qquad 2.$$

Dividing Equation 1 by Equation 2 we get

$$P'_L/P_{ns} = P_L/1-P_L \qquad 3.$$

So a constant value for the left-hand term of Equation 3 means a constant rate of activation of the L channel. Since both P'_L and P_{ns} are measured in the experiment, we can obtain an action spectrum for the L channel by finding at different wavelengths the flash intensity needed for a constant value of P'_L/P_{ns}. Krauskopf's general method of identifying sensory detec-

tors is at a special advantage when two sensory channels have closely similar sensitivities—and thus when other methods of isolation fail. In the paper cited, evidence is given that the psychophysically identified channels correspond to single classes of cone, but this is a separate assumption and not intrinsic to the method.

Microspectrophotometry

Ostensibly the most direct technique for discovering the fundamentals is microspectrophotometry, in which a very small beam (typically 2 μm wide) is passed through the outer segment of an individual photoreceptor and absorption is recorded at different wavelengths. In his 1976 review, G. H. Jacobs regretted that little had been done in primate microspectrophotometry since the classical reports of 1964. This has recently been remedied, and it is a happy turn of fate that Dr. Jacobs has become a collaborator in the new work.

Bowmaker et al (1978) published measurements for a large sample of rods and cones from Rhesus monkeys (*Macaca mulatta*); and results have followed for man (Bowmaker & Dartnall 1980), for the cynomolgus monkey *Macaca fascicularis* (Bowmaker et al 1980), and for the New World monkeys *Cebus apella* (Bowmaker & Mollon 1980) and *Saimiri sciureus* (Jacobs et al 1981). The measurements are made with a microspectrophotometer designed by P. Liebman; a description of the instrument is given by Knowles & Dartnall (1977, p. 564 ff.) Whereas the classical microspectrophotometric records were obtained by passing the measuring beam axially along the 30-μm length of the outer segment, in the newer measurements the beam passed transversely through the receptor; it turns out that the absorbance or "optical density" of the pigment is high enough (about 0.015 μm^{-1}) that a satisfactory signal can be obtained from this much shorter path length, and the advantage is that the experimenter, viewing through an infrared converter, can be confident that the beam is passing through only one outer segment.

Listed in Table 1 for the several species are the values of λ_{max} (= wavelength of peak sensitivity) and bandwidth for the different photopigments found. Figure 1 shows mean absorbance spectra for a large sample of cones from seven human eyes. The spectrum for the rods has been added to emphasize that the spectra for all four pigments are of approximately the same form when plotted, as here, against frequency (which is inversely proportional to wavelength). However, it has become very clear during the period of this review that the bandwidths of photopigment absorbance spectra are not constant in frequency units but increase systematically with increasing frequency. This is apparent from the exclusively primate data of Table 1, but a similar relationship has been shown to hold for a variety of

Table 1 Values of λ_{max} and bandwidth for primate photopigments[a]

Species	S cones		Rods		M cones		L cones	
	λ_{max} (nm)	half bandwidth (cm^{-1})	λ_{max} (nm)	half bandwidth (cm^{-1})	λ_{max} (nm)	half bandwidth (cm^{-1})	λ_{max} (nm)	half bandwidth (cm^{-1})
Man	419	2180	496	1770	531	1740	559	1680
Macaca mulatta (Rhesus)			503	1750	535	1720	566	1570
Macaca fascicularis (Cynomolgus)	419	2160	500	1720	535	1600	567	1420
Saimiri sciureus (Squirrel monkey)	429	2180	499	1830	535[b]	1730	552, 568[b]	1530, 1380
Cebus apella (Capuchin)			499	1680	535	1670		

[a] Data are taken from references cited in the text, except in the case of Man, where the values are taken from Figure 1. Absence of values for S cones should not be taken to indicate a tritan species, since these receptors are rare in all samples. The value given for the half-bandwidth is that for the half-bandwidth on the longwave limb (see Bowmaker et al 1980).

[b] The M cones were found only in a behaviorally protan specimen, the L cones in a deutan; the separation of the L cones into two classes is tentative.

nonprimate photopigments (Ebrey & Honig, 1977, Knowles & Dartnall 1977).

The most obvious way in which the new microspectrophotometric results differ from the 1964 data of Brown and Wald and of Marks, Dobelle, and MacNichol is in the value obtained for the λ_{max} of the S cones: as will be seen from Figure 1, these receptors are most sensitive at approximately 420 nm. The earlier reports and the newer ones do agree that the S cones are rare.

Concordance of Estimates of the Human Fundamentals

It is by no means a straightforward matter to compare psychophysical and microspectrophotometric estimates of the cone fundamentals. On the one hand, we have psychophysical action spectra expressed in terms of light incident at the cornea; on the other, we have physical measurements of absorption for a beam passed transversely through an outer segment. To reconstruct one type of sensitivity from the other, one must consider several factors:

(*a*) SELF-SCREENING It is necessary to allow for the fact that in vivo where the light passes axially along the outer segment, the photopigment in the anterior part will significantly screen the photopigment in the posterior part; this "self-screening," which is maximal at the λ_{max} of the pigment, has the effect of broadening the absorbance spectrum (see e.g. Knowles & Dartnall 1977, Chap. 3). Since current thought favors an axial absorbance in the range 0.3–0.5 for primate foveal photoreceptors, self-screening will be significant. Wyszecki & Stiles (1980) compare color matches made at moderate illuminances (ca 10^3 td) with those made at levels that would bleach most of the pigment (ca 10^5); they derive absorbances of 0.44 and 0.38 for the (unbleached) L and M cones respectively.

(*b*) RECEPTORAL OPTICS We must allow for any wavelength-dependent optical funneling that occurs for an axial beam. The magnitude of any such effect is still uncertain, and most recent calculations have ignored it.

(*c*) PRERECEPTORAL ABSORPTION Correction must be made for wavelength-dependent absorption by the media of the eye and the macular pigment. The latter is an inert yellow pigment in the central region of the retina; its peak absorption is at 460 nm, and it is thought to be concentrated in the outer plexiform layer, perhaps in the fibers of Henle (see Snodderly et al 1979). A small new complication is introduced by a distinct photostable violet-absorbing pigment in the inner segments of some primate photore-

ceptors (Mollon & Bowmaker 1979). This pigment, with peak absorption at 420 nm, could selectively screen individual outer segments. [In its morphological location and absorption spectrum, though not its absolute density, it resembles roughly the pigment of the "ellipsosomes" described in fish outer segments by MacNichol et al (1978).]

If factor *b* is taken to be negligible and if conventional values are assumed for factors *a* and *c,* the corneal sensitivities that are reconstructed from the microspectrophotometric results suggest that the converging psychophysical fundamentals are close to the truth. Equally, however, because of residual uncertainties about factors *a-c* and because the several psychophysical estimates are now very similar, it is unrealistic to try to use the microspectrophotometric measurements to choose among the psychophysical estimates. Thus Bowmaker et al (1978) and Bowmaker & Dartnall (1980), assuming an axial optical density of 0.525 and taking Wyszecki & Stiles's (1967) tabulated values for average prereceptoral absorption, showed that the reconstructed corneal sensitivities were in good first-order agreement with the mechanisms π_3, π_4, and π_5 of Stiles; but using lower values for the optical density and slightly different values for prereceptoral absorption, Estévez (1979) has shown good agreement between the microspectrophotometric spectra and his König fundamentals, and Sharpe (1980) has shown good agreement with the Smith-Pokorny (1975) fundamentals.

I should like to emphasize how similar are the psychophysical estimates now in play. It is remarkable that this agreement has gone almost unheralded, given the wide variety of candidate fundamentals that were available only 20 years ago, and given the badly mistaken sets of fundamentals that are reproduced in textbooks (e.g. Gregory 1977a, Hochberg 1978, Cotman & McGaugh 1980). From a casual reading of the specialist literature one would gain little impression of the convergence that has come about: it is a basic psychological law that small differences are harder to see than large ones, and so it is necessary to shout louder about small differences in order to attract attention to them.

Briefly, the residual differences between psychophysical fundamentals are as follows. In the range 400–500 nm, there is little dispute about the shortwave fundamental, and the discrepancies are no more than could be attributed to experimental error and to the known individual differences in prereceptoral absorption: thus there is reasonable agreement between Stiles's shortwave mechanisms (π_1 or π_3) and (*a*) the photopic sensitivity of rare monochromatic observers who appear to retain only rods and S cones (Alpern 1978, Figure 14) and (*b*) the König S fundamental of Estévez (1979). Stiles's π_4 is extremely similar in bandwidth and spectral position to the König M fundamental of Estévez (1979), but is rather broader than the M fundamental of Smith & Pokorny (1975). When normalized at their

peaks the different longwave fundamentals are similar in their longwave limbs, but the shortwave limb of π_5 is shallower than that of König fundamentals or deuteranopic luminosity functions, though the discrepancy is only slight in the case of Estévez's L fundamental. A set of useful plots comparing different estimates of the L fundamental will be found in Sharpe (1980); plots comparing π mechanisms with all three König fundamentals are given by Wyszecki & Stiles (1980). Further discussion of the status of the π mechanisms will be postponed until postreceptoral processes have been dealt with.

Individual Differences

Recent literature provides a further reason why we should not exaggerate the residual differences between psychophysical fundamentals: this is the unwelcome possibility that the absorbance spectra of the photopigments may vary slightly in their spectral positions from one "normal" observer to the next. Bowmaker et al (1975), in a study of frog retinae, reported an 8-nm (275-cm^{-1}) range between animals in the value obtained for the λ_{max} of the rod pigment; the variation appeared both in difference spectra for whole retinae and in mean absorbance spectra obtained microspectrophotometrically from samples of individual outer segments for a given retina.

Alpern & Pugh (1977) have suggested that the L pigment in a group of deuteranopes varied in spectral position over a total range of 7.4 nm (230-cm^{-1}). Their measurements were made psychophysically with the Maxwell-matching technique described above. Against the possibility that the inter-observer differences arose from differences in prereceptoral absorption, Alpern and Pugh offer (*a*) direct physical measurements of the spectral reflectivity of the bleached fovea, and (*b*) measurements of the ratio of two monochromatic primaries needed to match different spectral lights. Against the possibility of systematic differences in the axial density of outer segments they point to the coincidence of the individual action spectra when adjusted horizontally on a wavenumber abscissa. But this latter argument is question-begging, since the spectra have flat, indeterminate peaks, and the technique precludes much reliable measurement of the shortwave limb. If only vertical adjustment is allowed in their Figure 3, the discrepancies can be described as a broadening of the action spectrum and thus possibly attributed to self-screening; it all turns on a very few shortwave points. However, whether or not the differences in action spectra are due to density differences, further convincing evidence that they were real differences is given by Alpern & Moeller (1977), who show that two of the deuteranopes differed consistently on (*a*) Maxwell matches, (*b*) incremental test sensitivities (see Introduction), and (*c*) spectral luminosity functions made by matching lights of different wavelengths to be of the same brightness. For

further discussion of Alpern and Pugh's study see Estévez (1979), who suggests that the proposed spectral shifts of the L pigment cannot quantitatively account for the variation in color-matching functions independently found by these authors.

On the basis of color-matching functions for three deuteranomalous trichromats, Alpern & Moeller (1977) suggest that all deuteranomals cannot have the same three pigments. And contrary to what would be the common expectation, they report that a given deuteranope will not accept the color matches of all deuteranomals, while Alpern & Pugh (1977) similarly report that not all deuteranopes will accept the matches of a given normal. Since a trichromatic match requires that absorptions be equated in all three classes of cone, a dichromat ought to accept such matches if he merely lacks one of the normal's three classes of receptor. Alpern and his collaborators are led to suggest that there are not single L and M pigments that characterize normal observers; rather there is a range of possible L pigments and a range of M pigments. They additionally suggest that deuteranomals draw both their longwave pigments from the L range and that protanomals similarly draw two from the M range. Alpern and Moeller indeed found a deuteranomalous observer whose matches were accepted by two deuteranopes who would not accept each other's matches—a result to be expected if the deuteranomal's match is constrained by two L pigments, one common to each of the dichromats.

The microspectrophotometric results of Bowmaker et al (1978, 1980) are consistent with a limited variability of λ_{max} within each class of receptor; the variability is apparent both within and between retinae. In a study of 300 receptors (L and M cones and rods) from 17 Rhesus monkeys, Mollon & Bowmaker (1981) found a statistically significant variation among animals; standard deviations across monkeys for mean estimates of λ_{max} were 3.6 nm (L cones), 2.7 nm (M cones), and 1.7 nm (rods).

A limitation that faces the microspectrophotometric results, and some of the psychophysical ones, is that measurements are not made concurrently on all subjects, and we must rely on stability of experimental conditions. To assess instrumental error, what are clearly needed are independent psychophysical and microspectrophotometric measurements on the same subjects. Experiments of this kind have just begun. The species chosen is the squirrel monkey, *Saimiri sciureus,* for in this species Jacobs has recently found large behavioral differences between individuals in wavelength discrimination, in Rayleigh matches, and in incremental sensitivity at long wavelengths (Jacobs 1977, Jacobs & Blakeslee 1980). If categorized in human terms, some animals behave like mildly deuteranomalous trichromats and enjoy good wavelength discrimination in the red-green range, whereas some animals resemble severely protan observers. This is the first demonstration of

major individual differences in the color vision of a nonhuman primate. In a double-blind study, squirrel monkeys from Dr. Jacob's laboratory in Santa Barbara have been flown to London, where microspectrophotometric measurements are made. In a behaviorally protan animal, the cones were microspectrophotometrically found to cluster at 430 nm and 535 nm; in a deuteranomalous animal one shortwave receptor was recorded, no receptors with λ_{max} near 535 nm, and a range of receptors with λ_{max} values in the range 546 to 577 nm, possibly falling into two groups with means 552 and 568 nm (Jacobs et al 1981).

THE ANOMALIES OF THE SHORTWAVE SYSTEM

This is a topic that came to the fore at the beginning of the period of this review, but has moved so rapidly that some phenomena that were initially taken to be singularities of the shortwave system are now seen as general characteristics of color-opponent channels. Nevertheless there remains plenty that is odd about the shortwave mechanism. For the reader's convenience, the principal anomalies are listed summarily below and are arranged into two major subgroups, although the various phenomena are more interconnected than this superficial classification might at first suggest. By "anomalies of the shortwave mechanism" is meant "unusual features of our vision when detection or discrimination depends only on signals originating in the S receptors"; isolation has usually been achieved either by Stiles's method or by some form of silent substitution for L and M cones. For earlier lists and further discussion, see Willmer (1961), Mollon (1977a, 1982b), Gouras & Zrenner (1978), Pugh & Mollon (1979), Polden & Mollon (1980); a bibliography on tritanopia by Barca (1977) is very useful.

Group A: Sensitivity of Short-wavelength System

1. ABSOLUTE SENSITIVITY The quantum efficiency of the shortwave mechanism is much lower than that of the L and M mechanisms (Barlow 1958), although it is now clear that some part of this difference is due to lenticular and macular absorption (see above).

2. INCREMENTAL SENSITIVITY The Weber fraction ($\Delta I/I$) for Stiles's shortwave system is about 4.6 times that for π_4 and π_5. This is the value for Stiles's standard conditions of a 200-msec 1° flash (Stiles 1978) and corresponds, of course, to only one point on a temporal contrast-sensitivity-function (CSF) and one point on a spatial CSF (or more strictly, it represents a single point in a spatiotemporal contrast-sensitivity space). If we make the shortwave target very small or very brief, the Weber fraction and

the absolute threshold of the shortwave mechanism rise much more than those of π_4 and π_5 and we obtain the near-tritan states:

3. SMALL-FIELD TRITANOPIA, 4. TACHISTOSCOPIC TRITANOPIA,

5. SPACE CONSTANTS The reason that the Weber fraction is only 4.6 times poorer for the shortwave system under Stiles's conditions is that greater spatial and temporal integration compensate for the essential insensitivity of the shortwave mechanism. The penalty, of course, is poorer resolution. Thus Cavonius & Estévez (1975), using their silent-substitution technique described above, confirm earlier reports that the spatial CSF for the shortwave system peaks at $\sim$1 cycle.deg^{-1}, has a high-frequency cutoff at $\sim$10 cycles deg^{-1}, and shows a low absolute contrast sensitivity (see also Klingaman & Moskowitz-Cook 1979). A consequence of its spatial CSF is that the shortwave mechanism cannot contribute to the detection of sharp edges. Thus Tansley & Boynton (1978), having adjusted the relative intensity of two juxtaposed, differently colored fields until the boundary was minimally distinct, found that the rated distinctiveness of the residual border between any two colors could be represented by placing all colors on a continuous curved line rather than in the two-dimensional space normally needed to represent differences between equiluminant colors; and when the two colors constituted a tritan pair (i.e. were confusable by a tritan observer and thus probably provided a spatially silent substitution for L and M cones) the border dissolved completely. Similarly, Valberg & Tansley (1977) showed that when monochromatic lights were juxtaposed to a standard white light, the rated distinctiveness of the border, when plotted against the wavelength of the monochromatic light, resembled a tritanope's saturation function; and Boynton et al (1977) found (for some conditions and observers) that introducing a gap between two fields actually improved the chromaticity discrimination of tritan pairs.

6. TIME CONSTANTS Elegantly arranging a temporal silent substitution for L and M cones (by alternating between 439- and 492-nm lights, a tritan pair), Wisowaty & Boynton (1980) measured the temporal CSF for the shortwave mechanism without the use of the longwave field traditionally employed. They confirm earlier suggestions that the peak of the temporal CSF lies at low frequencies, in fact at 2 Hz under the conditions they examined. They also report that the addition of longwave adapting fields attenuate contrast sensitivity in a way that is frequency-selective, being greatest at low and high frequencies. But this latter finding is best taken only in the strictest operational sense: owing to the inverted-U shape of the CSF,

the magnitude of the loss of sensitivity is confounded with depth of modulation, and we do not know whether equal distances on the ordinate correspond to equal attenuations at the site where the longwave signal acts. Mollon & Polden (1976a) describe a subjective illusion resulting from the longer latency of the shortwave system.

7. TRITANOPIA OF THE CENTRAL FOVEOLA Williams et al (1981a) have tackled the vexed question of whether there is a tritanopia of the center of the foveola that is additional to the general insensitivity of the shortwave system to small targets. Measuring increment thresholds for the same wavelength but under conditions that isolate either M or S receptors, they show apparently complete absence of the shortwave mechanism in a central area of 20 min, a result that cannot be attributed to macular pigment, since the M mechanism is not concomitantly affected; and by using successive color matching (to exclude fading of a possible S-receptor signal and to avoid any spatial difficulty in discriminating two parts of a small bipartite field), they show that matches made with the center of the foveola are truly tritanopic. When viewed from a distance, Plate 6 of the City University color-deficiency test (see above) prettily demonstrates the tritanopia of the foveolar center. The common term for the phenomenon is foveal tritanopia, but this is unfortunate, because (contrary to the belief of many psychologists) the anatomical fovea corresponds to a visual angle of ca 5.0° and includes the annular zone of maximal S-receptor sensitivity that lies at an eccentricity of 1°.

8. ACQUIRED TRITANOPIA Although congential tritanopia may not be as rare as once thought (van Heel et al 1980), there is an interesting contrast between the genetic stability of the shortwave system and its disproportionate vulnerability to disease, both specifically ocular diseases such as retinitis pigmentosa (e.g. Wolf et al 1980) and systemic disorders such as diabetes mellitus (e.g. Birch et al 1980). What in older reports are described as "blue-yellow" defects are very likely to be tritanopia. Alpern et al (in press) give a particularly thorough demonstration of acquired unilateral tritanopia in a case of central serous chorio-retinopathy. There are two reports of a high incidence of tritan defects in women taking oral contraceptives (Marré et al 1974, Lagerlöf 1980).

9. NEONATAL TRITANOPIA? Preliminary measurements of increment thresholds on longwave fields suggest that some 2-month-old infants behave as if tritanopic (Pulos et al 1980).

Group B: Adaptational Anomalies

A second group of anomalies concerns the light and dark adaptation of the blue mechanism. It has become somewhat artificial to list these separately, since they are now seen to be interconnected. Moreover, it will be argued below that they represent general properties of opponent-color systems. Four examples are listed here and will be discussed further in later sections.

10. LIMITED CONDITIONING EFFECT Stiles found that the t.v.i. curve for violet flashes on a longwave field shows a plateau at field illuminances of 4–5 log td, before rising again at higher illuminances. He denoted the lower and upper branches of the curve π_1 and π_3 respectively (see Stiles 1978), but his original term for the plateau—the "limited conditioning effect"—now seems more appropriate, for reasons that will emerge below.

11. RESPONSE SATURATION Unlike the other cone mechanisms, but like the rod system, the shortwave system can be saturated by steady adapting fields: when violet targets are presented on violet or blue fields of increasing intensity—in the presence of a fixed longwave "auxiliary" field—the incremental threshold rises more quickly than is predicted by Weber's Law (Mollon & Polden 1977a). There is a further odd aspect to this "saturation": the state of insensitivity to violet increments is reached only after many seconds of adaptation and after the threshold has passed through a much lower value (Mollon & Polden 1978, 1980, Stromeyer et al 1979).

12. TRANSIENT TRITANOPIA If the eye is adapted for some time to light of long wavelength and the adapting field is then turned off, the threshold of the shortwave mechanism does not recover according to the normal dark adaptation curve but actually rises by as much as 2 $\log_{10}$ units; so a stimulus that is readily seen when the field is present becomes quite invisible for several seconds after the field is extinguished. This phenomenon, early described by Stiles, was named transient tritanopia by Mollon & Polden (1975). For detailed experimental results see Augenstein & Pugh (1977), Mollon & Polden (1977b), and Stiles (1977).

13. LIGHT ADAPTATION The adaptation of the shortwave mechanism to longwave fields has been known for some time to be unusually slow (see Augenstein & Pugh 1977), and in fact the time course of adaptation turns out to have a very curious structure to it: for 575-nm fields of intensities greater than $10^{10.8}$ quanta.sec^{-1}.deg^{-2} (which place the observer on the "π_3" plateau), the threshold for violet targets *rises* during the first 10 sec of exposure to the field and only thereafter recovers (unpublished results by Mollon, Polden & Stockman; Mollon 1980a).

Two Explanatory Principles

There is nothing grossly odd about the shape or size of individual S receptors when they are seen in the course of microspectrophotometry, but to explain the anomalies of the psychophysically defined shortwave mechanism we may turn to two hypotheses:

THE SHORT-WAVE CONES ARE RARE Evidence for this hypothesis is provided by microspectrophotometry (see above), by a histochemical staining technique (Marc & Sperling 1977), and by the histological damage produced by intense blue light (Sperling 1980). Although each of these methods may be open to unknown sampling biases, the last two gain credibility from the way in which the numerosity of the putative S cones in primate retinae parallels Brindley's (1954) psychophysical results for the variation of π_1 sensitivity with retinal eccentricity: the frequency of S cones is as low as 2–3% in the very center of the foveola, rises to a peak of approximately 16% in a zone equivalent to an eccentricity of 1°, and then falls to 8–10% in the parafovea. There is also evidence for a regular, widely spaced mosaic of S-receptors. Williams et al (1981b) offer convincing psychophysical evidence that the sensitivity of the shortwave mechanism in the foveola has a punctuate distribution. Electrophysiologically, primate ganglion cells receiving S-receptor input are found relatively rarely (Gouras & Zrenner 1978) and are reported to be most common at eccentricities between 2 and 5° (de Monasterio 1978a).

SIGNALS ORIGINATING IN THE S CONES HAVE ACCESS ONLY TO A CHROMATICALLY OPPONENT SUBSET OF POSTRECEPTORAL CHANNELS Whittle (1973) reported that suprathreshold flashes seen only by π_1 cannot be dichoptically matched in brightness to flashes seen by the longwave mechanisms, although their intensities can be discriminated by differences in phenomenal salience (Whittle 1974). Gouras & Zrenner (1978) state explicitly that S-cone inputs are detectable only in chromatically opponent ganglion cells of the primate retina; de Monasterio (1978a) basically agrees, but allows that a "fraction" of his nonopponent cells "received weak input" from S cones (the example he shows is somewhat ambiguous).

An agreed upon and interesting result is that it is very much more common to record blue ON-center ganglion cells than blue OFF-center units (Malpeli & Schiller 1978, de Monasterio 1978a, Gouras & Zrenner 1978). Also very suggestive is the finding that S-cone signals are virtually absent from fibers projecting to the superior colliculus (de Monasterio 1978a,c); this, rather than a difference between types of geniculo-striate

neurons, may account for the very marked slowness of simple reactions to liminal π_1 flashes (Mollon & Krauskopf 1973).

Hypotheses *a* and *b* might both in turn be related to the chromatic aberration of the eye, which ensures that the shortwave component of the retinal image is of little use for spatial discriminations when longer wavelengths are present.

COLOR-OPPONENT CHANNELS

Primate Electrophysiology

The color-opponent cells of the primate visual system differ from nonopponent cells in attributes other than wavelength selectivity; and this, of course, is of interest to psychophysicists seeking to isolate "color-opponent channels." Schiller & Malpeli (1977) confirm earlier reports that color-opponent retinal ganglion cells tend to be more sustained in their responses than do nonopponent cells. de Monasterio (1978a) essentially agrees, but reports that a more reliable distinction can be made on the basis of linearity of spatial summation within the receptive field—the classical basis for distinguishing X and Y cells. In a large sample of Rhesus ganglion cells, X cells had fully opponent responses, in that center and surround signals were drawn from different classes of cone. However, a less complete opponency was also seen in some Y cells: here the opponency arose because one of the types of cone mediating response in one part of the field made no contribution in the other. A second important difference between X and Y types of opponent cell is that the "surround" mechanism of the Y cell has a sensitivity that extends across the receptive field and indeed is maximal in the center, whereas the X cells have an annular input from a true surround (de Monasterio 1978b). Of the heterogeneous class of W cells, some have spatially coextensive, chromatically opponent inputs, and appear to deliver purely chromatic information to the geniculostriate pathway (de Monasterio 1978c). Color-opponent cells project predominantly to the parvocellular layers of the lateral geniculate nucleus and apparently not at all to the superior colliculus, either directly (Schiller & Malpeli 1977, de Monasterio 1978c) or indirectly (Schiller et al 1979).

Psychophysical Techniques for Isolating Color-Opponent Channels

Psychophysicists have recently developed a number of stratagems to try to ensure that detection depends on channels that receive antagonistic inputs from different classes of cone. However, as we leave the receptors and enter the jungle of nerves, we do not have the trusty parang of univariance with which to cut our passage; the techniques of isolation are thereby less secure. Moreover, there are several reasons for caution in identifying the psycho-

physicist's "opponent channels" with the electrophysiologist's "opponent cells." First, although the psychophysical literature often simplistically contraposes chromatic and achromatic channels, there are many different types of retinal ganglion cell and there are degrees of opponency. Second, the properties revealed psychophysically may be properties that emerge from a *population* of neurons and may not be properties of individual cells. Third, different psychophysical "channels" may correspond to the same class of cell operating in different modes; an example of this possibility comes from Gouras & Zrenner (1979), who show in Rhesus that "red-green" color-opponent ganglion cells are more sensitive to alternation between colored lights ("chromatic flicker") at low temporal frequencies but become more sensitive to achromatic, luminance flicker at high frequencies, the action spectrum shifting from one with two peaks to one resembling $V\lambda$.

Given the present state of knowledge, claims that detection "depends on color-opponent channels" should be taken (here and elsewhere) to mean only that detection depends on the comparison of absorptions in different classes of receptor. Nevertheless, detection by this mode is proving to have a clear signature: test spectral sensitivity shows multiple peaks (particularly characteristic is a depression ca 575 nm and a longwave peak ca 610 nm); and, as we shall see below, pairs of test flashes or pairs of adapting fields are often nonadditive in their effects.

The following techniques of isolation may be usefully listed:

USE OF INCREMENTAL TARGETS OF LOW SPATIAL AND TEMPORAL FREQUENCY Detection by chromatically opponent channels is thought to be favored when a colored, incremental target is large (say, 1°) and of long duration (say, 200 msec), whereas detection is held to be by achromatic channels when the target is small (0.05°) and brief (10 msec) (King-Smith & Carden 1976). Ingling (1978) has cautioned us against relating these suggestions directly to the integrative properties of individual neurons, since the color-opponent, X ganglion cells have *small* receptive fields. Here perhaps is a case where we must consider populations of cells: as one increases the area of a circular colored target, the number of color-opponent cells available for detection should be proportional to πr^2, since any such cell can compare local differences between signals from different types of cone; but the number of nonopponent cells available for detection may increase only as $2\pi r$, since such cells are more sensitive to spatial transients than to homogeneous illumination (cf Dain & King-Smith 1981).

ACHROMATIC ADAPTING FIELD Detection by opponent channels is thought to be favored when the field is neutral and bright (e.g. King-Smith & Carden 1976, King-Smith & Kranda 1981).

SPATIALLY COINCIDENT ADAPTING FIELD If monochromatic test flashes are delivered on a small, congruent "auxiliary" field and if field-sensitivity is measured with a larger, concentric "main" field, then the field sensitivities obtained with long and middlewave targets are not those of π_5 and π_4 but are spectrally narrower and have peaks at approximately 605 and 520 nm (Foster, in press). The effect is absent when the auxiliary field is presented dichoptically and is reduced when the target is small or brief. It appears that the presence of a contour coincident with that of the target masks a spatial transient that would otherwise allow detection by a nonopponent channel. Foster's configuration resembles that of the classical Dittmer-Westheimer effect (see Fry & Bartley 1935), which does occur for relatively large targets (e.g. Crawford 1940), and his results point to the interesting possibility that the Dittmer-Westheimer effect is absent or attenuated when detection depends on chromatic channels. This hypothesis, of course, becomes very plausible if you believe that the Dittmer-Westheimer effect arises because a spatial transient saturates edge-detecting cells that would otherwise respond to the circumference of the test flash.

TEMPORALLY COINCIDENT AUXILIARY FIELD No one seems to have tried systematically superimposing the chromatic target on a temporally coincident pedestal or on a randomly flickering field. These devices, which might eliminate detection by temporal transients, are listed here for completeness.

CONFINEMENT OF INPUT TO S CONES. EQUILUMINOUS TARGETS These last two strategies are discussed above and below respectively.

Chromatically Opponent Processes Manifested in Threshold Measurements.

One of the most remarkable features of the last 6 years has been the evidence for opponent processes that has come from applications of Stiles's two-color technique, which was originally introduced for the analysis of receptoral processes.

INTERACTION OF TEST FLASHES Earlier work on the interaction of test flashes of different wavelengths has been continued by Stromeyer et al (1978a), who show that the detectability of a large, long (1°, 200 msec) red flash on a bright yellow field is reduced if it is accompanied by a similar green flash. Red flashes similarly reduce the detectability of green targets. By now the reader will not be surprised to learn that the cancelative effect disappears if the flashes are very brief or very small.

INTERACTION OF ADAPTING FIELDS: COMBINATIVE EUCHROMATOPSIA If the threshold is found for violet (λ=423 nm) flashes on a steady blue (μ_1=473 nm) field and if enough yellow light is now added to the first field to produce a composite field that is brighter but achromatic, then the threshold actually falls by several tenths of a log unit (Mollon & Polden 1977c, Mollon 1979). The intensity of the yellow field required for maximum facilitation increases with the intensity of the blue field (Polden & Mollon 1980). Sternheim et al (1978) and Stromeyer & Sternheim (1981) have described a very similar phenomenon when detection depends on the L cones: a 633-nm grating of low spatial frequency (1 c.deg^{-1}) was presented on a 615-nm field of $10^{3.7}$td and the detection threshold was found to be reduced when a 565-nm field was added to the first field. The phenomenon was not observed when the grating was presented very briefly or was of higher spatial frequency, nor when detection was mediated by the M cones; but an analogous facilitation was obtained for both red and green targets when the task was to detect a sinusoidally flickering stimulus of low temporal frequency (Sternheim et al 1978). Similarly, Wandell & Pugh (1980b) have found facilitated detection of 200-msec 667-nm test flashes when a 540-nm field is added to a fixed, bright 650-nm field, a facilitation that is absent for 10-msec flashes (Wandell & Pugh 1980a). Particularly dramatic examples of such effects are seen for shortwave targets when flashed yellow fields are used to cancel the response saturation that is produced by flashed violet fields (Stromeyer et al 1978b, 1979).

The available evidence suggests some properties common to these phenomena: the facilitation occurs when the first colored field is of moderate to high intensity, and is absent if the second field is presented dichoptically; most important, it occurs under conditions that favor detection by chromatically opponent processes. Polden & Mollon (1980) propose the term *combinative euchromatopsia* for this facilitation of chromatic discrimination that occurs when certain adapting fields are combined. Combinative euchromatopsia points to a general hypothesis: a color-opponent channel is most sensitive to input perturbations when in the middle of its response range; sensitivity is lost if the channel is polarized, i.e. driven toward one or other extreme of its response range by large differences between the quantum catches of different classes of cone (Pugh & Mollon 1979, Polden & Mollon 1980).

THE DYNAMIC DYSCHROMATOPSIAS Transient tritanopia (see above) proved to have an analog in transient protanopia, a loss in sensitivity to longwave flashes after extinction of a dim cyan or a dim red field (Mollon & Polden 1977b, Reeves 1980); and indeed losses of sensitivity at the onsets and offsets of colored fields may prove to be the rule when detection is

mediated by chromatic channels (although, except in the case of the short-wave system, the availability of alternative channels will usually obscure the magnitude of the effects). A generic term is needed for this family of effects and I tentatively suggest that *dynamic dyschromatopsia* would capture their defining properties. It is particularly significant that transient tritanopia does not occur when a blue field is added to the usual yellow field so as to yield a composite field of neutral color (Augenstein & Pugh 1977); that transient tritanopia was not found in one of the rare patients, "blue cone monochromats," who appear to lack L and M cones (Hansen et al 1978); and that transient protanopia is absent when the adapting field is yellow (i.e. neither reddish nor greenish) and when the targets are small or brief (Reeves 1980). Transient tritanopia and transient protanopia are both reduced if the adapting field is flickered (Loomis 1980, Reeves 1980), and transient tritanopia is paradoxically absent if the longwave adapting field is too intense (Mollon & Polden 1976b).

An explanation of transient tritanopia has been proposed by Pugh & Mollon (1979). During initial adaptation to a longwave field, signals from L and M cones are thought to polarize an opponent site through which signals from the S cones must pass, but a restoring force acts to reduce the polarization. The restoring force depends on the input of a leaky integrator with a long time constant, and the input to the integrator is a function of the difference between the signal from the S cones and that from the L and M cones. When the adapting field is suddenly removed, the restoring force continues to act for some seconds and, being now unopposed, polarizes the opponent site and leads to a loss of sensitivity. The loss of sensitivity that accompanies polarization is the same as that postulated above to account for combinative euchromatopsia. Valeton & van Norren (1979) demonstrate transient tritanopia at the level of the b-wave of the local electroretinogram recorded from the fovea of a Rhesus monkey; this suggests that the chromatic interaction occurs at or before the level of the bipolar cells.

Possible Identity of Opponent Mechanisms Revealed by Changes in Sensitivity, by Phenomenological Cancellation, and by Chromaticity Discrimination

Are the opponent channels revealed by recent threshold measurements the same as those (Hurvich 1978) examined in classical studies of phenomenal cancellation? Using slightly different experimental techniques, Polden & Mollon (1980) and Pugh & Larimer (1980) have asked whether longwave lights of the radiance required to cancel the phenomenal blueness of a shortwave light are also lights that produce maximal facilitation under

conditions of combinative euchromatopsia; Pugh and Larimer give a positive answer, Polden and Mollon a negative one. Williams et al (1980) have asked whether the "cardinal directions" of color space, as revealed by selective alterations of sensitivity, are the same as those suggested by earlier phenomenological studies. They use a new colorimeter in which lasers provide the three primaries. The crucial idea of their technique is to adapt a putative channel by repeated brief excursions along a particular direction in an equiluminant color space and then to probe sensitivity to liminal excursions in this and other directions. Dynamic adaptation along a red-green axis produces maximal loss of sensitivity to liminal excursions along that axis, whereas thresholds are hardly changed for excursions along a tritan confusion line; conversely, adaptation along a tritan line produces maximum loss on that axis and little on the red-green axis. When adaptation is along other lines, the loss of sensitivity is much less selective; and in particular this is so when the adaptation is along a line connecting phenomenally pure blue and pure yellow, an axis that does not coincide with a tritan confusion line.

The hypothesis suggested by combinative euchromatopsia (see above) has an analog in a quite different literature, that concerned with predicting thresholds for chromaticity discrimination; the idea is explicit, for example, in the 1961 "line-element" of Friele (see Polden & Mollon 1980). Similarly, in reconstructing a tritan wavelength-discrimination function from π_4 and π_5, Cavonius & Estévez (1978) found that thresholds did not depend simply on the rate of change of the ratio of the two sensitivities; it was necessary to assume that the discrimination threshold rose with $r^{1.5}$, where r is the ratio of the adaptation levels of the two cone mechanisms.

DO STILES'S π MECHANISMS CORRESPOND TO CONE FUNDAMENTALS?

Ostensibly it looks as if Stiles settled on spatial and temporal parameters that would invite detection of his target by color-opponent channels. If this is so, then the sensitivity of postreceptoral channels will be varying as μ is varied in field-sensitivity measurements, and thus the measured sensitivity cannot be that of a single class of cone.

Experimental Tests

Recent literature offers several experimental tests of whether the π mechanisms satisfy the properties expected of individual classes of cone.

FIELD DISPLACEMENT RULE Sigel & Pugh (1980) report that "shape invariance" of the t.v.i. curve (see Introduction) does hold for a wide range

of values of μ under conditions that isolate the longwave mechanism, π_5. If, however, the t.v.i. curves for λ=667 nm are extended to higher field radiances, a single template will not fit the data for all values of μ (Wandell & Pugh 1980b); it was those discrepancies that led Stiles to postulate his "high-intensity" red-sensitive mechanism, π_5'. Shape invariance does hold for the full range of the t.v.i. curve if 10-msec flashes are used instead of the 200-msec flashes used by Stiles (Wandell & Pugh 1980a).

FIELD ADDITIVITY This test, like the previous one, depends on the Principles of Univariance and Adaptive Independence. It was introduced by de Vries (1949), although his characteristically elliptical account has enjoyed little credit in recent discussions. Suppose we measure t.v.i. curves for two different field wavelengths, μ_1 and μ_2. Knowing thereby, for a given π mechanism, the relative efficiencies of the two wavelengths, we can calculate what should be the effect of a given mixture of μ_1 and μ_2, if indeed the π mechanisms are adaptively independent and if, once absorbed, all photons are equal. The most thorough study of field additivity is that of Pugh (1976) who demonstrated that additivity held for π_1 if both μ_1 and μ_2 were $<$500 nm, but "superadditivity" held for $\mu_1<$500 nm and $\mu_2>$550 nm. Sigel & Pugh (1980) show that additivity holds for π_5 at the low field intensities used in Stiles's measurements.

SILENT SUBSTITUTION Can a transition be made between two fields of different wavelength without disturbing the sensitivity of a π mechanism, as is theoretically possible for a cone? No such case has yet been reported. *Failures* of silent substitution under conditions isolating π_1 and π_5' were found by Mollon & Polden (1975) and Sternheim et al (1977) respectively, but a failure of silent substitution is little argument against the independence of π mechanisms, for Stiles explicitly required that adaptation be at equilibrium.

COINCIDENCE OF TEST AND FIELD SENSITIVITIES If π mechanisms are adaptively independent, the relative spectral sensitivity obtained by manipulating λ (test sensitivity) should coincide with relative field sensitivity, in those parts of the spectrum where both can be measured. This test was central to Stiles's original discussions and he showed, for example, impressive agreement between test and field sensitivities for π_1 and π_3 in the range 400–500 nm (see Stiles 1978, p. 205). Now that we know more about how to reduce contamination by opponent processes, further application of this test to π_4 and π_5 might be valuable.

PREDICTION OF COLOR MATCHING If a subset of the π mechanisms has the sensitivities of cones, it is necessary, though not sufficient, that they

should be linear transformations of color-matching functions. With only minor discrepancies this condition has been shown to hold for π_3, π_4, and π_5 by Estévez & Cavonius (1977), who empirically obtained both types of measurement from the same observers, and by Pugh & Sigel (1978), who related Stiles's tabulated π mechanisms to the Stiles and Burch 1955 color-matching functions.

A Theory of π_1 and π_3

To explain the two-branched t.v.i. curve found when violet flashes are presented on longwave fields, Pugh & Mollon (1979) suppose that a signal originating in the S cones must pass through two successive sites, at each of which the signal may be attenuated. The first site probably corresponds to the outer segments of the S cones, and here the attenuation depends only on the rate at which photons are absorbed from the background by the S cones. At the second site, which is chromatically opponent, the attenuation depends on the magnitude of the difference between the signal from S cones and that from the L and M cones. For $\mu > 550$ nm, the lower (π_1) branch of the t.v.i. curve depends only on increasing polarization of the second site, since such fields produce negligible absorptions in the S cones. However, owing to bleaching and perhaps other processes of response compression, the signal from the L and M cones cannot grow indefinitely; hence the "limited conditioning effect" discussed earlier. Eventually, however, as the longwave field is made still more intense, it produces a significant level of direct absorptions in the S cones and then the π_3 branch is obtained. The "superadditivity" found by Pugh (1976) arises because long- and shortwave fields largely act at different sites. The "response saturation" described by Mollon & Polden (1977a) occurs when attenuation is increasing concomitantly at both sites as the intensity of a shortwave field is increased.

Self-Screening

Some part of the difference in shape between König fundamentals and the mechanisms π_4 and π_5 may arise because the former correspond to a 2° foveal field and the latter to a 1° field; the average length of outer segments will be higher for the smaller field and the absorbance spectrum should therefore be broader (see above).

It is interesting that a field sensitivity narrower than that of π_5 has been reported when the subject's task is to detect not a 200-msec flash but the flicker of a 10 Hz longwave target (Ingling & Tsou 1977, Sharpe 1980). To explain this result one might suppose that the use of a relatively high-frequency target reduces the contribution of opponent channels, but here again a change of self-screening may play a part. Baylor et al (1979), recording membrane current from individual toad rods and stimulating restricted parts of the outer segment, found that the time constant of

response was much shorter at the vitreal end of the outer segment; if this were so for mammalian cones, narrow field-sensitivity functions might arise because threshold flicker was always detected at the vitreal end of the receptor and the effective absorbance was low. This hypothesis assumes that adaptation is local within the outer segment.

Conclusions

The evidence suggests that π_5 corresponds closely to the L cones. Systematic tests for π_4 are not yet available, but its sensitivity is unlikely to be far from that of the M cones, except in the region of 475 nm, where the ratio of π_4 to π_5 does not well predict the color matches of a tritanope. The failures of adaptive independence seen for π_1 should be set in perspective: they affect only the longwave limb of the field-sensitivity function, and in the region 400–500 nm the (corneal) sensitivity of the S cones is almost certainly given by π_1.

Why did Stiles come so close to the cone fundamentals despite adopting what in retrospect seem to be unsuitable target parameters? One previously unappreciated strength of the two-color method is perhaps the polarization of chromatic channels that is caused by the monochromatic fields; for most values of μ, detection will depend on nonopponent channels that probably vary little in their sensitivity as μ is varied in a field-sensitivity experiment. It also now seems important that Stiles used a relatively low value for his criterion field intensity. The slight flattening of the peak of π_5 in the region of 575 nm may represent local contamination by red-green opponent channels left unpolarized by the yellow field. It might also represent absorption by the α band of oxyhemoglobin at 576 nm.

SILENT SUBSTITUTION FOR POSTRECEPTORAL CHANNELS? THE REIFICATION OF LUMINANCE

Many recent papers have proposed that chromatically opponent channels can be isolated by arranging a silent substitution for the putative nonopponent channel: the observer is required to respond to a temporal or spatial transition between stimuli that are of different wavelength but equal luminance. The technique is venerable: in its temporal form it was used by Piéron (1931), who explicitly postulated independent analysis of hue and brightness; and in its spatial form it was used by Lehmann (1904). In a spatiotemporal version of the method, Nissen & Pokorny (1977) have measured reaction time for stimuli presented in "hue-substitution" mode, and Bowen et al (1977) have similarly measured two-pulse discrimination: a monochromatic light is briefly substituted for the central area of an equiluminant white field, and it is found that latency is longest and two-pulse resolution poorest when the substituted light is yellowish (ca 570 nm),

whereas at longer and shorter wavelengths the subject's performance approaches that for luminance increments. A spatial form of the technique, in which a colored bar of variable luminance is set in a fixed white field, has been used to study color vision in infants (Teller et al 1978): in the case of some colored bars there was no luminance at which the bar did not significantly attract the infant's gaze, but for other colors, lying vaguely but not precisely on a tritan axis, such a luminance could be found. Lehmann (1904) found that the *verschobene Schachbrettfigur* of Münsterberg lost its distortion under "isoluminant" conditions whereas the Müller-Lyer illusion survived. Both these results have been rediscovered by Gregory (1977b), using similar apparatus, but one nice contradiction remains for someone to sort out: Lehmann writes "wenn Figur und Grund dieselbe Helligkeit haben, sind die Hauptlinien des Zöller'schen Musters vollständig parallel," whereas Gregory says the distortions of the Zöllner figure were "essentially unchanged."

Hue-substitution techniques, though they may throw up interesting phenomena, do not safely isolate chromatic channels. Suppose that a red field is briefly substituted for a white field of equal luminance. During the substitution an increment is presented to the L receptors and a decrement to the M receptors; transient responses will arise from both classes of receptor. In the spatial case, analogous transients will be present, if only as the result of eye movements. Those who intend to isolate chromatic channels must make the following assumptions: (*a*) the positive and negative transients are symmetrical in magnitude and waveform at the nonopponent site where they cancel; (*b*) the weightings of different cone inputs are identical for all nonopponent cells; and (*c*) linear summation occurs in the nonopponent channel for transient signals from different cones even though many nonopponent neurons (the Y cells) are known not to show linear summation for signals from different local areas. In short, we must reify luminance in the form of a single channel that has the spectral sensitivity of V_λ and obeys the Principle of Univariance. Given the variety of postreceptoral neurons and the biological significance of transients, it seems deeply implausible that assumptions *a*-*c* will always be valid. I am not saying that detection of "isoluminous" targets will invariably depend on nonchromatic channels; if the targets are at threshold and if one uses other devices that we believe favor chromatic channels (if e.g. the liminal target is large and blurred as in the study of duration thresholds by Pokorny et al 1979b), then isolation may be possible; but if the isoluminous target is well above threshold, as in studies cited earlier, then one has no guarantee that chromatic channels are isolated. Bowen et al (1980) cut away their own position by admitting that isolation will fail "at high luminances"; they offer no valid way of knowing when the safety margin has been crossed.

The receptor-transient hypothesis is very difficult to eliminate, because

the magnitude of transient responses and the phenomenal saturation of the substituted color both necessarily depend on how far the new quantum catches differ from those produced in the different cones by the white light. However, the properties of the shortwave system (see above) suggest one prediction: if the response depends on nonchromatic channels, its variation with wavelength should resemble the tritanope's saturation function, since only L and M cones will be involved (Mollon 1980b). Now, indeed, the poorest performance does occur when 570-nm light is substituted for white —these lights lie approximately on a tritan confusion line and their interchange should produce minimal transients in L and M cones—but 570-nm light is minimally saturated even for the normal, and more interesting would be a transition from white to the shortwave tritan neutral point, where the substituted light is very saturated. This has not been specifically tested. However, we know from other literature that a spatial tritan transition is extremely difficult to detect (see above); and similarly Boynton & Kaiser (1978) report that a "flickerless exchange" occurs when members of a tritan pair are alternated at low frequency. Is it likely that rapid reactions can be made to such exchanges?

The receptor-transient hypothesis offers an interesting interpretation of the results of Teller and her associates on neonatal tritanopia. Perhaps the infant is not tritanopic but indeed is effectively color blind, as might be expected if its visual behavior depended on the superior colliculus. Spatial transients detected by L and M cones could reach the colliculus and control eye movements.

TO WHAT EXTENT IS COLOR ANALYZED INDEPENDENTLY OF OTHER ATTRIBUTES OF THE RETINAL IMAGE?

There is space here only to indicate some recent papers that might be judged relevant to this celebrated question. For earlier evidence and further discussion, see Mollon (1977b).

Cortical Electrophysiology

Michael (1978a,b,c, 1979) reports a systematic study of the spatial properties of color-opponent cells in the striate cortex of the macaque. Color opponency, though present in only a subset of all cells, was associated with each of the receptive-field types classically distinguished by Hubel and Wiesel: concentric, simple, complex, hypercomplex. The first two types were concentrated in layer IV of the cortex and were almost always monocular, whereas complex and hypercomplex cells were most common in other layers and often could be driven from both eyes. The orientational and directional preferences of a given cell were independent of the wave-

length used for stimulation. Conversely, however, Krüger & Gouras (1980) report that the wavelength selectivity of a given cell increases with the length of a stimulating bar.

Bearing on our question in a distinct way is the work of Zeki (1978, 1980), who identifies two adjacent areas in the prestriate cortex of the Rhesus monkey that appear to be specialized for the analysis of color. The first of these ("V4") lies on the anterior bank of the lunate sulcus and the second in the lateral part of the posterior bank of the superior temporal sulcus. At least 56% of all cells in these areas were color opponent. Some color-opponent cells had an orientational preference, but most were not selective for either orientation or direction of motion. Krüger & Gouras (1980) have questioned whether spectral selectivity is in fact more common in V4 than in other areas; this controversy is not yet settled, but it may be significant that Krüger and Gouras confined themselves to foveal projection areas, and it is a pity they did not attempt one of Zeki's most striking comparisons, that between the lateral and medial regions of the posterior bank of the superior temporal sulcus, regions which Zeki reports to be specialized for color and movement respectively.

Color-Contingent Aftereffects

Color aftereffects have been reported that are contingent on the orientation or spatial frequency or direction of movement of a test stimulus. In each case the aftereffect is popularly attributed to the presence in our visual system of neurons specific to more than one stimulus attribute (although in several respects these phenomena resemble Pavlovian conditioning). A recommended review is given by Stromeyer (1978).

Pathology

After central damage, color vision may be lost completely with little or no loss of acuity. A disorder of this kind has been described by Young & Fishman (1980) in a 70-year-old patient who had suffered a cerebral infarct, and by Mollon et al (1980) in a younger man who had suffered a febrile illness, probably herpes encephalitis. By the technique of Stiles, it is possible to discover whether color-blind patients of this kind retain access to signals from more than one class of cone, since we can measure increment thresholds without asking anything about color. The patient of Mollon et al definitely retained both M and L cones but apparently lacked the machinery to compare their signals. In the light of current theories of the shortwave system, it is of special interest to know whether signals from the S cones can control the responses of such patients: increment-threshold measurements suggested that the short-wavelength mechanism was absent in the case of Young and Fishman and present in that of Mollon et al.

The Problem of Perceptual Synthesis

A priori considerations rule out complete independence and complete integration of the analyses of color and form. It would be no good having a system in which there were, say, single units specific to chartreuse-colored Volkswagens moving left at a distance of three meters, since we need to explain how the system recognizes a Volkswagen for what it is independently of its accidental features such as hue. But equally, we cannot postulate complete independence of analysis, since the subject, observing a complex scene, can quickly tell us that the Volkswagen is yellow and the Mini Metro is scarlet. Insofar as the analyses of different attributes are independent, there must be a mechanism for perceptual synthesis, for relating the outcomes of the separate analyses. Treisman & Gelade (1980), reviving a hypothesis of Exner, propose that selective attention provides the necessary mechanism and that indeed we carry out the synthesis for only one part of the field at once. They report that if a subject is required to scan an array for the presence of a single feature (e.g. a color or a form), reaction time varies little with the number of items in the array; but if he must identify a conjunction of features (e.g. pink O in a background of pink Ns and green Os), then reaction time increases with the number of items. The identification of a conjunction of hue and form requires the serial application of focal attention to individual items in our visual field.

ACKNOWLEDGMENTS

I am very grateful to the following friends who have commented on sections of the manuscript: M. Alpern, C. R. Cavonius, L. Fallowfield, M. Hayhoe, J. Krauskopf, D. MacLeod, A. Reeves, L. T. Sharpe, A. Stockman, and P. Whittle.

Literature Cited

Alpern, M. 1978. The eyes and vision. In *Handbook of Optics,* ed. W. G. Discoll, W. Vaughan, Sect. 12, pp. 1–37. New York: McGraw-Hill

Alpern, M., Kitahara, K., Krantz, D. H. 1981. Classical tritanopia. *J. Physiol.* In press

Alpern, M., Moeller, J. 1977. The red and green cone visual pigments of deuteranomalous trichromacy. *J. Physiol.* 266:647–75

Alpern, M., Pugh, E. N. 1977. Variation in the action spectrum of erythrolabe among deuteranopes. *J. Physiol.* 266:613–46

Alpern, M., Wake, T. 1977. Cone pigments in human deutan colour vision defects. *J. Physiol.* 266:595–612

Armington, J. C., Krauskopf, J., Wooten, B. R. 1978. *Visual Psychophysics and Physiology.* New York: Academic. 488 pp.

Augenstein, E. J., Pugh, E. N. 1977. The dynamics of the π_1 colour mechanism: further evidence for two sites of adaptation. *J. Physiol.* 272:247–81

Barca, L. 1977. *Sguardo Bibliografico al Problema della Tritanopia.* Firenze: Fond. 'Giorgio Ronchi' 67 pp. (In Italian).

Barlow, H. B. 1958. Intrinsic noise of cones. In *Visual Problems of Colour,* pp. 615–39. Natl. Phys. Lab. Symp. London: H. M. Stationery Off. 749 pp.

Baylor, D. A., Lamb, T. D., Yau, K.-W. 1979. The membrane current of single

rod outer segments. *J. Physiol.* 288:589–611
Billmeyer, F. W., Wyszecki, G. 1978. *Colour 77.* Proc. 3rd Congr. Int. Colour Assoc. Bristol: Hilger
Birch, J., Hamilton, A. M., Gould, E. S. 1980. Colour vision in relation to the clinical features and extent of field loss in diabetic retinopathy. See Verriest 1980, pp. 83–88
Bowen, R. W., Lindsey, D. T., Smith, V. C. 1977. Chromatic two-pulse resolution with and without luminance transients. *J. Opt. Soc. Am.* 67:1501–7
Bowen, R. W., Pokorny, J., Smith, V. C. 1980. Isolating colour vision mechanisms with hue substitution. *Nature* 285:440
Bowmaker, J. K., Dartnall, H. J. A. 1980. Visual pigments of rods and cones in a human retina. *J. Physiol.* 298:501–12
Bowmaker, J. K., Dartnall, H. J. A., Lythgoe, J. N., Mollon, J. D. 1978. The visual pigments of rods and cones in the rhesus monkey, *Macaca mulatta. J. Physiol.* 274:329–48
Bowmaker, J. K., Dartnall, H. J. A., Mollon, J. D. 1980. Microspectrophotometric demonstration of four classes of photoreceptor in an Old World primate, *Macaca fascicularis. J. Physiol.* 298: 131–43
Bowmaker, J. K., Loew, E. R., Liebman, P. A. 1975. Variation in the λ_{max} of rhodopsin from individual frogs. *Vision Res.* 15:997–1003
Bowmaker, J. K., Mollon, J. D. 1980. Primate microspectrophotometry and its implications for colour deficiency. See Verriest 1980, pp. 61–64
Boynton, R. M. 1979. *Human Color Vision.* New York: Holt, Rinehart & Winston, 438 pp.
Boynton, R. M., Hayhoe, M. M., MacLeod, D. I. A. 1977. The gap effect: chromatic and achromatic visual discrimination as affected by field separation. *Opt. Acta* 24:159–77
Boynton, R. M., Kaiser, P. K. 1978. Temporal analog of the minimally distinct border. *Vision Res.* 18:111–13
Brindley, G. S. 1954. The summation areas of human colour-receptive mechanisms at increment threshold. *J. Physiol.* 124: 400–8
Cavonius, C. R., Estévez, O. 1975. Contrast sensitivity of individual colour mechanisms of human vision. *J. Physiol.* 248:649–62
Cavonius, C. R., Estévez, O. 1978. π-mechanisms and cone fundamentals. See Armington et al 1978, pp. 221–31
Christ, R. E. 1975. Review and analysis of color coding research for visual displays. *Hum. Factors* 17:542–70
Cool, S. J., Smith, E. L. 1978. *Frontiers in Visual Science.* New York: Springer. 798 pp.
Cornsweet, T. N. 1970. *Visual Perception.* New York/London: Academic. 475 pp.
Cotman, C. W., McGaugh, J. L. 1980. *Behavioral Neuroscience.* New York: Academic. 838 pp.
Crawford, B. H. 1940. The effect of field size and pattern on the change of visual sensitivity with time. *Proc. R. Soc. London Ser. B* 129:94–106
Dain, S. J., King-Smith, P. E. 1981. Visual thresholds in dichromats and normals; the importance of *post*-receptoral processes. *Vision Res.* 21:573–80
de Monasterio, F. M. 1978a. Properties of concentrically organised X and Y ganglion cells of macaque retina. *J. Neurophysiol.* 41:1394–1417
de Monasterio, F. M. 1978b. Center and surround mechanisms of opponent-color X and Y ganglion cells of retina of macaques. *J. Neurophysiol.* 41:1418–23
de Monasterio, F. M. 1978c. Properties of ganglion cells with atypical receptive field organisation in retina of macaques. *J. Neurophysiol.* 41:1435–49
de Vries, H. 1949. An extension of Helmholtz's theory of colorvision. *Rev. Opt.* 28:91–100
Ebrey, G. T., Honig, B. 1977. New wavelength dependent visual pigment nomograms. *Vision Res.* 17:147–51
Estévez, O. 1979. *On the fundamental database of normal and dichromatic color vision.* PhD Thesis. Amsterdam Univ., The Netherlands. Amsterdam: Krips Repro. 147 pp.
Estévez, O., Cavonius, C. R. 1977. Human color perception and Stiles' π mechanisms. *Vision Res.* 17:417–22
Estévez, O., Spekreijse, H. 1982. The "silent substitution" method in visual research. *Vision Res.* In press
Foster, D. H. 1982. Changes in field spectral sensitivities of red-, green-, and blue-sensitive colour mechanisms obtained on small background fields. *Vision Res.* In press
Fry, G. A., Bartley, S. H. 1935. The effect of one border in the visual field upon the threshold of another. *Am. J. Physiol.* 112:414–21
Gass, W. 1976. *On Being Blue.* Boston: Godine. 91 pp.
Gouras, P., Zrenner, E. 1978. The blue sensitive cone system. In *XXIII Concilium Ophthalmologicum, Kyoto,* ed. K.

Shimizu, pp. 379–84. Amsterdam: Elsevier
Gouras, P., Zrenner, E. 1979. Enhancement of luminance flicker by color-opponent mechanisms. *Science* 205:587–89
Gregory, R. L. 1977a. *Eye and Brain.* London: Weidenfeld & Nicolson. 256 pp. 3rd ed.
Gregory, R. L. 1977b. Vision with isoluminant colour contrast: 1. A projection technique and observations. *Perception* 6:113–19
Hansen, E. 1979. *Selective chromatic adaptation studies with special reference to a method combining Stiles' two-colour threshold technique and static colour perimetry.* Oslo: Dept. Ophthalmol., Rikshospitalet
Hansen, E., Seim, T., Olsen, B. T. 1978. Transient tritanopia experiment in blue cone monochromacy. *Nature* 276: 390–91
Hartridge, H. 1950. *Recent Advances in the Physiology of Vision.* London: Churchill. 401 pp.
Hochberg, J. E. 1978. *Perception.* Englewood Cliffs NJ: Prentice-Hall. 280 pp. 2nd ed.
Hurvich, L. M. 1978. Two decades of opponent processes. See Billmeyer & Wyszecki 1978, pp. 33–61
Ingling, C. R. 1978. Luminance and opponent color contributions to visual detection and to temporal and spatial integration: Comment. *J. Opt. Soc. Am.* 68:1143–46
Ingling, C. R., Tsou, B.H-P. 1977. Orthogonal combination of the three visual channels. *Vision Res.* 17:1075–82
Jacobs, G. H. 1976. Color Vision. *Ann. Rev. Psychol.* 27:63–89
Jacobs, G. H. 1977. Visual sensitivity: significant within-species variations in a non-human primate. *Science* 197:499–500
Jacobs, G. H. 1982. *Comparative Color Vision.* New York: Academic. In press
Jacobs, G. H., Blakeslee, B. 1980. Within-species variations in color vision among New World monkeys. *Investig. Ophthalmol. Vis. Sci. Suppl.,* p. 136 (Abstr.)
Jacobs, G. H., Bowmaker, J. K., Mollon, J. D. 1981. Colour vision deficiencies in monkeys: behavioural and microspectrophotometric measurements on the same individuals. *Nature.* 292:541–43
King-Smith, P. E., Carden, D. 1976. Luminance and opponent-color contributions to visual detection and adaptation and to temporal and spatial integration. *J. Opt. Soc. Am.* 66:709–17
King-Smith, P. E., Kranda, K. 1981. Photopic adaptation in the red-green spectral range. *Vision Res.* 21:565–72
Klingaman, R. L., Moskowitz-Cook, A. 1979. Assessment of the visual acuity of human color mechanisms with the visually evoked cortical potential. *Invest. Ophthalmol. Vis. Sci.* 18:1273–77
Knowles, A., Dartnall, H. J. A. 1977. The photobiology of vision. In *The Eye,* ed. H. Davson, Vol. 2B. London/New York: Academic. 689 pp.
Krauskopf, J. 1978. On identifying receptors. See Armington et al 1978, pp. 283–95
Krüger, J., Gouras, P. 1980. Spectral sensitivity of cells and its dependence on slit length in monkey visual cortex. *J. Neurophysiol.* 43:1055–69
Lagerlöf, O. 1980. Drug-induced colour vision deficiencies. See Verriest 1980, pp. 317–19
Lehmann, A. 1904. Die Irradiation als Ursache geometrisch-optischer Täuschungen. *Pflugers Arch.* 103:84–106
Lennie, P. 1980. Parallel visual pathways: a review. *Vision Res.* 20:561–94
Loomis, J. M. 1980. Transient tritanopia: failure of time-intensity reciprocity in adaptation to long-wave light. *Vision Res.* 20:837–46
Lyle, W. M. 1974. Drugs and conditions which may affect color vision. *J. Am. Optom. Assoc.* 45:47–60, 173–82
MacLeod, D. I. A. 1978. Visual sensitivity. *Ann. Rev. Psychol.* 29:613–45
MacNichol, E. F., Kunz, Y. W., Levine, J. S., Harosi, F. I., Collins, B. A. 1978. Ellipsosomes: Organelles containing a cytochrome-like pigment in the retinal cones of certain fishes. *Science* 200:549–52
Malpeli, J. G., Schiller, P. H. 1978. Lack of blue OFF-center cells in the visual system of the monkey. *Brain Res.* 141:385–89.
Marc, R. E., Sperling, H. G. 1977. Chromatic organisation of primate cones. *Science* 196:454–56
Marré, M., Neubauer, O., Nemetz, U. 1974. Colour vision and the 'pill'. *Colour Vision Deficiencies II,* ed. G. Verriest. *Mod. Probl. Ophthalmol:* 13:345–48. Basel: Karger
Marriott, F. H. C. 1976. The two-colour threshold techniques of Stiles. In *The Eye,* ed. H. Davson, 2A:477–588. London: Academic. 616 pp.
Michael, C. R. 1978a. Color vision mechanisms in monkey striate cortex: dual-opponent cells with concentric receptive fields. *J. Neurophysiol.* 41:572–88
Michael, C. R. 1978b. Color vision mechanisms in monkey striate cortex: simple cells with dual opponent-color receptive fields. *J. Neurophysiol.* 41:1233–49

Michael, C. R. 1978c. Color-sensitive complex cells in monkey striate cortex. *J. Neurophysiol.* 41:1250–66
Michael, C. R. 1979. Color-sensitive hypercomplex cells in monkey striate cortex. *J. Neurophysiol.* 42:726–44
Mollon, J. D. 1977a. The oddity of blue. *Nature* 268:587–88
Mollon, J. D. 1977b. *The Perceptual World,* ed. K. von Fieandt, I. Moustgaard, pp. 45–97. London: Academic. 680 pp.
Mollon, J. D. 1979. The theory of colour vision. In *Psychology Survey No. 2,* ed. K. Connolly, pp. 128–50. London/Boston: Allen & Unwin
Mollon, J. D. 1980a. On the light adaptation of the 'blue' mechanism. In *Recent Advances in Vision.* Washington: Opt. Soc. Am. (Abstr.)
Mollon, J. D. 1980b. Isolating colour vision mechanisms with hue substitution: reply to Bowen, Pokorny and Smith. *Nature* 285:440
Mollon, J. D. 1982a. Colour vision and colour blindness. In *The Senses,* ed. H. B. Barlow, J. D. Mollon. Cambridge: Cambridge Univ. Press. In Press
Mollon, J. D. 1982b. A taxonomy of tritanopias. See Verriest 1982
Mollon, J. D., Bowmaker, J. K. 1979. Photostable violet-absorbing structures in primate retinae. *Investig. Ophthalmol. Vis. Sci. Suppl* 18:31 (Abstr.)
Mollon, J. D., Bowmaker, J. K. 1981. Distribution characteristics of a large microspectrophotometric sample of Rhesus photoreceptors. *Investig. Ophthalmol. Vis. Sci. Suppl.* 20:205 (Abstr.)
Mollon, J. D., Krauskopf, J. 1973. Reaction time as a measure of the temporal response properties of individual colour mechanisms. *Vision Res.* 13:27–40
Mollon, J. D., Newcombe, F., Polden, P. G., Ratcliff, G. 1980. On the presence of three cone mechanisms in a case of total achromatopsia. See Verriest 1980, pp. 130–35
Mollon, J. D., Polden, P. G. 1975. Colour illusion and evidence for interaction between colour mechanisms. *Nature* 258:421–22
Mollon, J. D., Polden, P. G. 1976a. Some properties of the blue cone mechanism of the eye. *J. Physiol.* 254:1–2P (Abstr.)
Mollon, J. D., Polden, P. G. 1976b. Absence of transient tritanopia after adaptation to very intense yellow light. *Nature* 259:570–72
Mollon, J. D., Polden, P. G. 1977a. Saturation of a retinal cone mechanism. *Nature* 265:243–46
Mollon, J. D., Polden, P. G. 1977b. An anomaly in the response of the eye to light of short wavelengths. *Philos. Trans. R. Soc. London Ser B* 278:207–40
Mollon, J. D., Polden, P. G. 1977c. Further anomalies of the blue mechanism. *Investig. Ophthalmol. Vis. Sci. Suppl.* 16:140 (Abstr.)
Mollon, J. D., Polden, P. G. 1978. An anomaly of light adaptation. *Investig. Ophthalmol. Visual Sci. Suppl.* 17:177 (Abstr.)
Mollon, J. D., Polden, P. G. 1980. A curiosity of light adaptation. *Nature* 286:59–62
Nissen, M. J., Pokorny, J. 1977. Wavelength effects on simple reaction time. *Percept. Psychophys.* 22:457–62
Okuma, T., Masuda, H., Kawada, C., Shinjo, U. 1973. Ishihara-Okuma's new testplates for colour defectives. *Acta Soc. Ophthalmol. Jpn.* 77:1359–65
O'Neem, E. P. 1981. Drei Abhandlungen zur Wegweiserfarbentheorie. *Z. Fussgängerforsch* 1:69–173 (In German)
Padgham, C. A., Saunders, J. E. 1975. *The Perception of Light and Colour.* London: Bell. 192 pp.
Piantanida, T. P., Bruch, T. A., Latch, M., Varner, D. 1976. Detection of quantum flux modulation by single photopigments in human observers. *Vision Res.* 16:1029–34
Piéron, H. 1931. La sensation chromatique. *Année Psychol.* 32:1–29 (In French)
Pokorny, J., Bowen, R. W., Lindsey, D. T., Smith, V. C. 1979a. Duration thresholds for chromatic stimuli. *J. Opt. Soc. Am.* 69:103–6
Pokorny, J., Smith, V. C., Verriest, G., Pinckers, A. J. L. G. 1979b. *Congenital and Acquired Color Vision Defects.* New York: Grune & Stratton. 409 pp.
Polden, P. G., Mollon, J. D. 1980. Reversed effect of adapting stimuli on visual sensitivity. *Proc. R. Soc. London Ser. B* 210:235–72
Pugh, E. N. 1976. The nature of the π_1 mechanism of W. S. Stiles. *J. Physiol* 257:713–47
Pugh, E. N., Larimer, J. 1980. Test of the identity of the site of blue/yellow hue cancellation and the site of chromatic antagonism in the π_1 pathway. *Vision Res.* 20:779–88
Pugh, E. N., Mollon, J. D. 1979. A theory of the π_1 and π_3 colour mechanisms of Stiles. *Vision Res.* 19:293–312
Pugh, E. N., Sigel, C. 1978. Evaluation of the candidacy of the π-mechanisms of

Stiles for color-matching fundamentals. *Vision Res.* 18:317–30
Pulos, E., Teller, D. Y., Buck, S. L. 1980. Infant color vision: a search for short-wavelength-sensitive mechanisms by means of chromatic adaptation. *Vision Res.* 20:485–93
Reeves, A. 1980. Transient protanopia results from desensitization of a red-green opponent process. *Invest. Ophthalmol. Vis. Sci. Suppl.* 19:135 (Abstr.)
Ronchi, L. 1975. *150 Years of Rods and Cones. An Annotated Bibliography* Firenze: Fond. 'Giorgio Ronchi'. 88 pp.
Rushton, W. A. H. 1972. Pigments and signals in colour vision. *J. Physiol.* 220:1–31P
Rushton, W. A. H. 1975a. From nerves to eyes. In *The Neurosciences: Paths of Discovery,* pp. 277–92. Cambridge, Mass: MIT Press
Rushton, W. A. H. 1975b. Visual pigments and color blindness. *Sci. Am.* 232 (3): 64–74
Rushton, W. A. H. 1977a. Some memories of visual research in the past 50 years. In *The Pursuit of Nature,* ed. Hodgkin et al, pp. 85–104. Cambridge: Cambridge Univ. Press.
Rushton, W. A. H. 1977b. H. Hartridge. *Vision Res.* 17:507–13
Rushton, W. A. H. 1977c. Hamilton Hartridge (1886–1976). *Biogr. Mem. Fellows R. Soc.* 23:193
Schiller, P. H., Malpeli, J. G. 1977. Properties and tectal projections of monkey retinal ganglion cells. *J. Neurophysiol.* 40:428–45
Schiller, P. H., Malpeli, J. G., Schein, S. J. 1979. Composition of geniculostriate input to superior colliculus of rhesus monkey. *J. Neurophysiol.* 42:1124–33
Serra, A. 1980. An annotated bibliography on MDB technique and related topics. *Atti Fond. Giorgio Ronchi* 35:664–76, 786–827
Sharpe, L. T. 1980. *The effect of test-flash duration upon long-wavelength cone mechanisms field sensitivity.* PhD thesis. Univ. Rochester, New York. 329 pp.
Sharpe, L. T. 1982. Colorimetry. In *Encyclopaedia of Physics in Medicine and Biology,* ed. T. F. McAnish. Oxford: Pergamon. In press
Sigel, C., Pugh, E. N. 1980. Stiles's π_5 color mechanism: tests of field displacement and field additivity properties. *J. Opt. Soc. Am.* 70:71–81
Smith, V. C., Pokorny, J. 1975. Spectral sensitivity of the foveal cone pigments between 400 and 500 nm. *Vision Res.* 15:161–71
Smith, V. C., Pokorny, J., Starr, S. J. 1976. Variability of color mixture data. I. Interobserver variability in the unit coordinates. *Vision Res.* 16:1087–94
Snodderly, D. M., Auran, J., Delori, F. C. 1979. Localization of the macular pigment. *Investig. Opthalmol. Vis. Sci. Suppl.* 18:80 (Abstr.)
Sperling, H. G. 1980. Blue receptor distribution in primates from intense light and histochemic studies. See Verriest 1980, pp. 30–44
Sternheim, C. E., Gorinson, R., Markovitz, N. 1977. Visual sensitivity during successive chromatic contrast: evidence for interactions between photopic mechanisms. *Vision Res.* 17:45–49
Sternheim, C. E., Stromeyer, C. F., Spillmann, L. 1978. Increment thresholds: sensitization produced by hue differences. See Armington et al 1978, pp. 209–20
Stiles, W. S. 1977. Early threshold observations of transient tritanopia. *Philos. Trans. R. Soc. London Ser. B* 278:233–38
Stiles, W. S. 1978. *Mechanisms of Colour Vision* London: Academic. 298 pp.
Stiles, W. S. 1980. The two-colour threshold and π mechanisms: historical note. See Verriest 1980, pp. 111–14
Stromeyer, C. F. 1978. Form-color aftereffects in human vision. In *Handbook of Sensory Physiology,* ed. R. Held, H. Leibowitz, 8:98–142. Berlin: Springer. 993 pp.
Stromeyer, C. F., Khoo, M. C. K., Muggeridge, D., Young, R. A. 1978a. Detection of red and green flashes: evidence for cancellation and facilitation. *Sens. Processes* 2:248–71
Stromeyer, C. F., Kronauer, R. E., Madsen, J. C. 1978b. Apparent saturation of blue-sensitive cones occurs at a color-opponent stage. *Science* 202:217–19
Stromeyer, C. F., Kronauer, R. E., Madsen, J. C. 1979. Response saturation of short-wavelength cone pathways controlled by color-opponent mechanisms. *Vision Res.* 19:1025–40
Stromeyer, C. F., Sternheim, C. E. 1981. Visibility of red and green spatial patterns upon spectrally mixed adapting fields. *Vision Res.* 21:397–407
Tansley, B. W., Boynton, R. M. 1978. Chromatic border perception: the role of red- and green-sensitive cones. *Vision Res.* 18:683–97
Tansley, B. W., Glushko, R. J. 1978. Spectral sensitivity of long-wavelength-sensitive

photoreceptors in dichromats determined by elimination of border percepts. *Vision Res.* 18:699–706
Teller, D. Y., Peeples, D. R., Sekel, M. 1978. Discrimination of chromatic from white light by two-month-old human infants. *Vision Res.* 18:41–48
Treisman, A. M., Gelade, G. 1980. A feature-integration theory of attention. *Cognit. Psychol.* 12:97–136
Valberg, A., Tansley, B. W. 1977. Tritanopic purity-difference function to describe the properties of minimally distinct borders. *J. Opt. Soc. Am.* 67:1330–35
Valeton, J. M., van Norren, D. 1979. Retinal site of transient tritanopia. *Nature* 208:488–90
van Heel, L., Went, L. N., van Norren, D. 1980. Frequency of tritan disturbances in a population study. See Verriest 1980, pp. 256–60
Verriest, G. 1974. *Recent Advances in the Study of the Acquired Deficiencies of Colour Vision.* Firenze: Fond. 'G. Ronchi'. 80 pp.
Verriest, G., ed. 1980. *Colour Vision Deficiencies V.* Bristol: Hilger. 410 pp.
Verriest, G., ed. 1982. *Colour Vision Deficiencies VI.* The Hague: Junk. In press
Vos, J. J. 1978. Colorimetric and photometric properties of a 2 deg fundamental observer. *Color Res. Appl.* 3:125–28
Walraven, J. 1981. *Chromatic Induction.* Utrecht: Elinkwijk
Wandell, B. A., Pugh, E. N. 1980a. A field-additive pathway detects brief-duration, long-wavelength incremental flashes. *Vision Res.* 20:613–24
Wandell, B. A., Pugh, E. N. 1980b. Detection of long-duration incremental flashes by a chromatically coded pathway. *Vision Res.* 20:625–35
Wasserman, G. S. 1978. *Color Vision.* New York: Wiley. 224 pp.
Whittle, P. 1973. The brightness of coloured flashes on backgrounds of various colours and luminances. *Vision Res.* 13:621–38
Whittle, P. 1974. Intensity discrimination between flashes which do not differ in brightness. Some new measurements on the "blue" cones. *Vision Res.* 14:599–602
Williams, D. R., Krauskopf, J., Heeley, D. W. 1980. In search of the cardinal directions of color space. *J. Opt. Soc. Am.* 70:1574 (Abstr.)
Williams, D. R., MacLeod, D. I. A. 1979. Interchangeable backgrounds for cone after-images. *Vision Res.* 19:867–77
Williams, D. R., MacLeod, D. I. A., Hayhoe, M. 1981a. Foveal tritanopia. *Vision Res.* 21:1341–56
Williams, D. R. MacLeod, D. I. A., Hayhoe, M. 1981b. Punctate sensitivity of the blue-sensitive mechanism. *Vision Res.* 21:1357–75
Willmer, E. N. 1961. Human colour vision and the perception of blue. *J. Theor. Biol.* 2:141–79
Wisowaty, J. J., Boynton, R. M. 1980. Temporal modulation sensitivity of the blue mechanism: measurements made without chromatic adaptation. *Vision Res.* 20:895–909
Wittgenstein, L. 1977. *Bemerkungen über die Farben.* Oxford: Blackwell. 63 pp. (In German and English)
Wolf, E., Scheibner, H., Pascke, G. 1980. Colour vision in a case of retinopathia pigmentosa. See Verriest 1980, pp. 280–84
Wyszecki, G. W. 1978. Colorimetry. In *Handbook of Optics,* ed. W. G. Driscoll, W. Vaughan, Sect. 9, pp. 1–40. New York: McGraw-Hill
Wyszecki, G. W., Stiles, W. S. 1967. *Color Science.* New York: Wiley. 628 pp.
Wyszecki, G. W., Stiles, W. S. 1980. High-level trichromatic color matching and the pigment-bleaching hypothesis. *Vision Res.* 20:23–27
Young, R. S. L., Fishman, G. A. 1980. Loss of color vision and Stiles' π_1 mechanism in a patient with cerebral infarction. *J. Opt. Soc. Am.* 70:1301–5
Zeki, S. M. 1978. Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *J. Physiol.* 277:273–90
Zeki, S. 1980. The representation of colours in the cerebral cortex. *Nature* 284:412–18

Annual Review of Psychology
Volume 33, 1982

CONTENTS

SOCIAL PSYCHOLOGY OF INTERGROUP RELATIONS, *Henri Tajfel* 1
COLOR VISION, *J. D. Mollon* 41
ENDORPHINS AND BEHAVIOR, *Robert C. Bolles and Michael S. Fanselow* 87
PSYCHOLOGY IN LATIN AMERICA TODAY, *Ruben Ardila* 103
SOCIAL MOTIVATION, *Janusz Reykowski* 123
TOUCH IN PRIMATES, *Ian Darian-Smith* 155
GROUP RESEARCH, *Joseph E. McGrath and David A. Kravitz* 195
ABNORMAL BEHAVIOR: SOCIAL APPROACHES, *Leonard D. Eron and Rolf A. Peterson* 231
BEHAVIORAL STUDIES OF ASSOCIATIVE LEARNING IN ANIMALS, *Robert A. Rescorla and Peter C. Holland* 265
MENTAL RETARDATION, *H. Carl Haywood, C. Edward Meyers, and Harvey N. Switzky* 309
ORGANIZATIONAL DEVELOPMENT AND CHANGE, *Claude Faucheux, Gilles Amado, and André Laurent* 343
BRAIN FUNCTION, SYNAPSE RENEWAL, AND PLASTICITY, *Carl W. Cotman and Manuel Nieto-Sampedro* 371
HUMAN BEHAVIOR GENETICS, *Norman D. Henderson* 403
THE PSYCHOLOGY OF LAW, *John Monahan and Elizabeth F. Loftus* 441
INFORMATION PROCESSING MODELS—IN SEARCH OF ELEMENTARY OPERATIONS, *Michael I. Posner and Peter McLeod* 477
LARGE GROUP AWARENESS TRAINING, *Peter Finkelstein, Brant Wenegrat, and Irvin Yalom* 515
ORGANIZATIONAL BEHAVIOR, *L. L. Cummings* 541
PERSONNEL SELECTION AND CLASSIFICATION, *Mary L. Tenopyr and Paul D. Oeltjen* 581

CONSUMER PSYCHOLOGY, *Harold H. Kassarjian* 619

ENVIRONMENTAL PSYCHOLOGY, *James A. Russell and Lawrence M. Ward* 651

CHAPTERS PLANNED FOR VOLUME 34 (1983) 689

INDEXES

Author Index 691

Subject Index 717

Cumulative Index of Contributing Authors, Volumes 29–33 739

Cumulative Index of Chapter Titles, Volumes 29–33 741