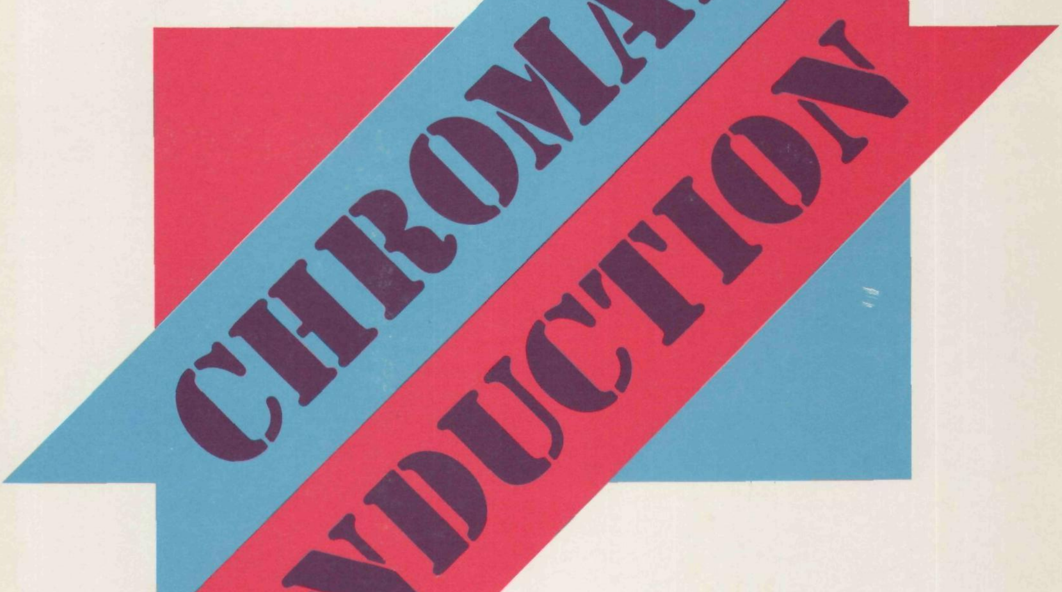

CHROMATIC INDUCTION

JAN WALRAVEN

The cover shows an example of (moderate) chromatic induction. The words "chromatic" and induction" are printed with the same ink but appear differently coloured due to contrast with the coloured bands.

CHROMATIC INDUCTION

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PSYCHOPHYSICAL STUDIES ON SIGNAL PROCESSING IN HUMAN COLOUR VISION

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN
DE WISKUNDE EN NATUURWETENSCHAPPEN AAN DE
RIJKSUNIVERSITEIT TE UTRECHT, OP GEZAG VAN
DE RECTOR MANIFICUS PROF. DR. M.A.BOUMAN,
VOLGENS BESLUIT VAN HET COLLEGE VAN DECANEN
IN HET OPENBAAR TE VERDEDIGEN OP WOENSDAG
1 JULI 1981 DES NAMIDDAGS TE 4.15 UUR

DOOR

JAN WALRAVEN

GEBOREN OP 10 SEPTEMBER 1937 TE BANDOENG

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PROMOTOR: PROF. DR. M.A. BOUMAN

Deze dissertatie werd bewerkt op de afdeling Visuologie, hoofd Dr. J.J. Vos, van het Instituut voor Zintuigfysiologie TNO te Soesterberg.

Research is to see what everybody else has seen
and to think what nobody else has thought.

Szent-Gyorgyi

Aan mijn Moeder
Aan de nagedachtenis van mijn Vader

VOORWOORD

Wetenschappelijk onderzoek is en blijft mensenwerk. Het kan zich daarom slechts dàn met vrucht ontwikkelen wanneer het plaats vindt binnen een structuur, waarin de mens de ruimte wordt gelaten zich vrijelijk te ontplooien. Binnen de Hoofdgroep Defensieonderzoek van TNO bestaat die ruimte, waarvan getuige het feit dat ik dit proefschrift heb mogen bewerken. Daarvoor wil ik hierbij nog mijn oprechte dank uitspreken jegens het bestuur.

Voor ontplooiing is niet alleen ruimte nodig, maar ook een vruchtbare voedingsbodem. Ik prijs mijzelf gelukkig die te hebben aangetroffen op het Instituut voor Zintuigfysiologie, en beschouw het als een voorrecht bij de grondlegger daarvan te mogen promoveren. Dat dit mogelijk is geworden is mede te danken aan mijn naamgenoot en mede-colorifiel, Pieter Walraven, onder wiens beleid de voorwaarden werden gecreëerd voor wetenschappelijk onderzoek op internationaal niveau.

In de benadering van mijn fundamenteel onderzoek heb ik wel eens teveel de neiging gehad dat te beschouwen als een privé-aangelegenheid tussen Moeder Natuur en mijzelve, daarbij de mogelijkheid van het bewerken van een proefschrift eerder als hinderlijk dan als stimulerend ervarend. Dat dit proefschrift er toch is gekomen is dan ook in niet geringe mate te danken aan de actieve begeleiding van Hans Vos. Hij heeft mij daarbij mijn eigen weg laten gaan, maar niet zonder nauwlettend toe te zien dat het werk altijd voldeed aan zijn eigen strenge normen van vorm en inhoud. Dat gebeurde echter altijd in een goede sfeer en ik zou mij dan ook geen sympathiekere personificatie van mijn wetenschappelijk geweten hebben kunnen wensen.

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Tot slot wil ik nog mijn dank betuigen aan mijn collega's, voor hun vriendschap en hun bijdrage tot mijn wetenschappelijke vorming. Dank ben ik ook verschuldigd aan al diegenen die hebben bijgedragen tot het onderzoek en de vormgeving daarvan. Vooral de blijmoedigheid en het geduld waarmee zij tegemoet kwamen aan mijn neiging tot eindeloos blijven verbeteren heb ik zeer gewaardeerd. Ik hoop in de toekomst dat geduld nog vaak op de proef te mogen stellen.

CONTENTS

"........ *the appearance of colours is profoundly affected by their juxtaposition with one another.*"

Aristotle, *Meteorologica*
c. 350 B.C.

I. INTRODUCTION

1.1 THE PHENOMENON OF INDUCED COLOUR

"All homogeneous Light has its proper Colour corresponding to its degree of Refrangibility ...," thus begins the second proposition of Newton's (1704) second theorem of the first book of his *Opticks*. This was a major breakthrough in a field of science which nowadays is called psychophysics, for it deals with phenomena that, like colour, result from the interaction of mind and matter. The true greatness of Newton's insight may be fully appreciated only when realizing that the prevailing theories on the nature of a colour in his time, were still based on the Aristotelian concept that colour results from the interaction of light and darkness. More than a century later, even an enlighted man like Goethe (1810) could not accept Newton's heresy and fought it bitterly in "das polemische Teil" of his massive *Farbenlehre*.

Although Newton's contribution to colour science was a giant leap forward, it only dealt with the physical aspect of colour. And even in that respect it left unexplained how colours could mysteriously change when put in juxtaposition with other colours, or conversely, remain constant despite large variations in the spectral composition of the illuminant. Such departures from the Newtonian principles are usually referred to, depending on the conditions that give rise to them, as simultaneous (colour) contrast, successive contrast, or chromatic adaptation. These are different processes but they affect (perceived) colour in the same way, and thus reinforce each others effect if not carefully isolated in the experiment. This has often been neglected, even by prominent investigators in this field. Consider, for example, the following typical laboratory experiment in which a circular patch of white light is surrounded by an inducing field consisting of, say, red light. Immediately on presentation of the red inducing field, the achromatic central test field will appear tinged with bluish green. This virtually instantaneous effect, which only can be attributed to lateral interactions in the physiological substrate, is called simultaneous contrast. This term was first introduced by Chevreul (1838), director of the Gobelins tapestry works and one of the first investigators who did systematic research in this field*).

If, in the above experiment, the surround is presented continuously and the observer is allowed to let his gaze dwell freely over the stimulus pattern (as is necessary for maintaining a clear visual perception), the induced colour will gradually become more prominent and finally appear as an intense, fully saturated bluish green. This is caused by both successive contrast and chromatic adaptation. Actually the distinction between these two phenomena is not that well defined. The term successive contrast is usually reserved for the condition in which the test stimulus is seen briefly after the presentation of the inducing stimulus. If, for example, one views a (slowly) rotating disc with alternating red and white sectors, the white sectors will be perceived as a vivid green, due to the after-effect caused by the intermittent pre-exposures to the preceding red light. The same effect may be expected to occur in the experiment discussed here, since scanning movements of the eye across the boundary between red surround and white centre field, causes the photoreceptors in the retina to be stimulated by a similar sequence of alternating red and white light. The effect may possibly be attributed to a neural "rebound" effect, that is, an after-discharge of green-encoding cells after being released from inhibition by antagonistic red-encoding cells (see later).

Eye movements will also cause the photoreceptors (and other neural stations) to selectively adapt to the red light from the surround. The resulting desensitisation of the red-encoding neural structures will be attended by a shift of the "colour balance" in the direction of green, thus reinforcing the effects of simultaneous and successive contrast. So, as mentioned before, the analysis of the induced response is complicated because of the confounding of effects from different mechanisms acting in concert.

Those not acquainted with this specialized area of colour vision may ask why the induced colour produced by the red surround in the experiment discussed above, is bluish-green rather than, for example, yellow or violet.

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*) Chevreul was more or less forced to do so in order to cope with complaints about the quality of the (induced) colours in the tapestry.

To answer that question we shall first have to discuss some of the basic principles that have emerged over the first two centuries of systematic colour research that have passed since Newton placed a glass prism "... at a round Hole, about one third of an Inch broad, made in the Shut of a Window ...".

1.2 FOUNDATIONS

One of the most celebrated findings in colour science is the trivariance of colour mixture. It attests to the fact that the colour evoked by any given light can be matched by mixing no more than three appropriately chosen standard lights (primaries). This implies that, from a physical point of view, our colour sense is quite inadequate; we cannot discriminate, for example, between the broad-band light from the sun and an infinite number of light mixtures consisting of only two wavelengths. The theoretical base for the trichromacy of colour is usually attributed to Young (1802)*), but it did not become very well known until it was resuscitated and elaborated by Helmholtz (1866), more than half a century later. The Young-Helmholtz theory postulates that the light entering the eye stimulates three sets of "nervous fibres" (with overlapping spectral sensitivities), that respectively produce the sensations of violet, green and red. We know now that these three different sets of nervous fibres are the three types of photoreceptors (cones), filled with pigments with broad absorption spectra peaking at wavelengths of respectively 440, 540 and 570 nm.

The notion that colour sensations would be subserved by the three "primary sensations" of the Young-Helmholtz theory has been abandoned, however. Instead, most modern theories, like that proposed by (P.L.) Walraven (1962), for example, assume an additional (antagonistic) stage of colour processing, in accordance with the concepts proposed by Hering (1878). The latter, which have been elaborated and put on a quantitative basis by Hurvich & Jameson (1955), incorporate the assumption that colour signals are processed by antagonistically coupled channels. That is, a red-green balance that either signals redness or greenness, depending on the sign of the difference signal from the middle-wave ("green") and long-wave ("red") photoreceptors, and a blue-yellow balance that, upon receiving difference signals from short-wave ("blue") and summed middle and long-wave receptors, similarly produces the

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*) See however MacAdam (1970, 1975) for a fascinating account of the genesis of trichromatic colour theory.

other pair of primary (or unique) colour sensations, blue and yellow. In addition an achromatic channel is assumed, which integrates the outputs of the three cone types, thus encoding luminance contrast in terms of blackness, whiteness and the intermediate grey sensations.

Turning now to the theory of induced colours, the general consensus is that these result from a selective suppression and/or reduced responsiveness of the colour-mediating structures (which includes the photoreceptors) that are most sensitive to the light from the inducing field. Thus, a red surround will mainly reduce the activity of the red and yellow-encoding channels (which both receive inputs from the "red" photoreceptor), and hence, cause the red-green and yellow-blue balance to signal respectively greenness and blueness, as is consistent with the observed induced colour of the test field (bluish green).

There exists a vast literature on chromatic induction (which comprises chromatic adaptation and colour contrast), for which the interested reader may be referred to reviews by Tschermak (1903), Parsons (1924), Graham & Brown (1965), Terstiege (1972) and Bartleson (1977). Most of the older studies are of a qualitative nature, which by no means implies, however, that they should be considered as inferior to modern quantitative studies. In particular Helmholtz (1911) has magnificent chapters on contrast, that are unsurpassed in the handling of the phenomology, and in which the foundation has been laid for much of the modern theoretical work. He already warned for the danger that simultaneous contrast effects may be confounded with selective sensitivity changes due to chromatic adaptation produced by eye excursions over the inducing field. His views on simultaneous contrast were probably too one-sided, however.

Helmholtz conceived of simultaneous contrast as an "error of judgement", a rather poor choice of terminology for it suggests some kind of cognitive act, something he definitely had not in mind. By "error" he meant a reflex-like subconscious rescaling of some internal standard for white. For example, a grey disc surrounded by a yellow field would appear blue because in the absence of an absolute standard, the yellow light sets a new standard - which should be more yellowish - and consequently, what originally was considered to be white is now perceived as blue. According to Helmholtz the principle is analogous to that which makes a medium-sized man look small when seen by the side of a tall person; here the judgement of normal size is biassed towards larger sizes because now, with the evidence of smaller sizes lacking, "medium" has become the lower limit. Helmholtz also assumed that the visual system was somehow able to evaluate the colour of the illuminant, but left unexplained how this might be achieved. Hering already pointed out that this is not that easy since the light entering the eye is always the product of reflectance times illumination, so these two variables are always confounded.

Hering postulated the for his time modern concept of lateral interaction in order to account for simultaneous contrast. Thus he assumed that any activity in a given area of the retina would evoke opposed activity in adjacent regions. This notion of opponent interaction is basic to Hering's whole theoretical approach of the visual system. Unfortunately, he interpreted his opponent mechanisms in terms of assimilation and dissimilation, biological processing relating to constructive (energy requiring) and destructive (energy releasing) biochemical reactions, that seemed rather out of place in the context of sensory physiology. This was the main reason for the initial unpopularity of his concepts. Today, however, the lateral inhibitory processes that have been discovered in the visual pathway may easily accommodate Hering's ideas.

1.3 THE "TWO-PROCESS" EXPLANATION

The main difference between the approach of Helmholtz and Hering with respect to the phenomenon of induced colour, is that Helmholtz stressed interpretations in terms of multiplicative operations (attenuation or scaling), whereas Hering focussed on differential processes. These different concepts have been reconciled in the chromatic induction theory of Jameson & Hurvich (1961). They assume Helmholtzian sensitivity controls (at the receptor level) in combination with a differential process (the inducing mechanism proper) situated at the level of Hering's colour-opponent channels. They called this the "two-process" interpretation (Jameson & Hurvich, 1959, 1972).

The first process of the two-process theory, the sensitivity control, derives from the adaptation principle proposed by Helmholtz, as worked out by von Kries (1878, 1905) who designated it as the Coefficient Law. This law states, broadly speaking, that chromatic adaptation can be described in terms of (three) receptor-specific attenuation factors (or coefficients between 0 and 1). This does not necessarily imply that the adaptation mechanism is situated in the cones themselves, but it rules out the possibility, that chromatic adaptation is governed at a level where, for example, neurons are tuned to just a narrow band of the spectrum. Such neurons do exist, so the coefficient rule is not that self-evident, as it might seem at first.

The validity of the coefficient rule has sometimes been assumed to be implied in the validity of what von Kries (1905) has called the Persistence Law. The latter attests to the fact that metameric colours, i.e. colours that despite a difference in spectral composition are indistinguishable for the eye (because they produce equal quantum absorptions in the photopigments), remain metamers under conditions of (moderate) chromatic adaptation. The persistence law breaks down at very high light levels, where loss of pigment density causes a narrowing of the spectral absorption functions, and also at very low light levels where the rods, the photoreceptors subserving night vision, come into play. Still, this does not invalidate the *principle* underlying the coefficient rule. Neither, however, does validity of the persistence rule proof the validity of the coefficient rule. It only attests to unaltered (relative) spectral absorption functions of the photopigments. It does not tell us anything about what kind of operations the visual system may perform on the receptor outputs.

Valid evidence for the coefficient rule only can be provided by chromatic adaptation experiments showing that adaptive hue shifts indeed can be described by a von Kries transformation. So far, however, there are more studies showing the invalidity than the validity of the coefficient scheme. In particular a corollary of the coefficient law, the so-called Proportionality Rule has a long record of proven failures. This "rule" states that, for a given state of adaptation (implying fixed coefficients) dim and bright test stimuli should be attenuated in the same proportion. The general finding is, however, that increasing the intensity of the test light is attended by a reduction in the (presumed) attenuation factors.

Invalidity of the proportionality prediction can only mean that either the coefficient rule does not apply, or that more than one mechanism is involved in determining the induced response. The latter possibility was proposed by Hurvich & Jameson (1959, 1972), who assumed a subtractive "second process", which can be described in terms of removing a fixed amount of (coloured) light from the test stimulus (for a given background condition). The model will thus predict deviations from the proportionality rule since the induced hue change due to this second process, will come less to the fore when the intensity of the test light is raised. This is indeed consistent with the general finding that the size of the adaptative hue shift of the test stimulus decreases with stimulus intensity.

The two-process model has been evaluated in various studies, but always over rather restricted ranges of the stimulus parameters. Also, in the theoretical treatment of the data it was not always clear what part of the induced response was due to one or the other process. The most thorough test of the model has been performed by Wooten (1970) who measured the effects of successive and simultaneous contrast as produced by (unique) blue, green, yellow and red inducing fields on test stimuli throughout the whole spectrum. He confirmed the necessity of employing a two-process model, but did not try to present a quantitative account of the data based on such a model. The general impression from his extensive studies is that some important predictions of the opponent-induction concept were not corroborated, in particular with respect to induced responses evoked by blue and yellow surrounds.

The two-process approach seems quite sound, however, and is also attractive in view of established physiological mechanisms. To wit, the subtractive (second) process is quite consistent with the action of lateral inhibitory networks (cf. Cornsweet, 1970), whereas the von Kries coefficient scheme may be easily implemented by the adaptation mechanisms that are found throughout the retina, from photoreceptor to ganglion cell (e.g. Werblin, 1970). Our own data, which are to be summarized in the synopsis presented hereafter, point in the same direction. They show that the subtractive process amounts to the extraction of signal transients in the retinal image and thus demonstrate the functional significance of the mechanism that is responsible for what Helmholtz called an error of judgement. They also show the validity of the von Kries coefficient scheme, and moreover, provide the basis for a mechanistic model for describing the behaviour of the coefficients as a function of the luminance and chromaticity of the adapting light.

1.4 PREVIEW

In the following we shall present a brief overview of the studies comprising this dissertation, starting with the method employed. This was essentially a null-response method, that is, maintaining a constant (yellow or white) hue of the test stimulus. The latter consisted of a mixture of two coloured lights the ratio of which could be varied by the observer in order to cancel the hue shift resulting from the interaction with the inducing field. These compensatory changes in the ratio of the two test primaries provided the measure for the induced response.

In the first study (Walraven, 1973) the "second" process, which may be assumed to underly the phenomenon of simultaneous contrast, was studied in isolation. This was achieved by presenting the whole stimulus pattern as a short flash, thus preventing artificial lateral effects due to eye movements.

It thus could be shown that the main mechanism involved operates over very short distances only, which suggests that it is mediated by colour-coded edge detectors.

The results from this study were corrected for straylight artefacts, a necessary precaution in view of the results of many so-called glare studies showing that light scatter in the ocular media may be the sole cause of alleged neural interactions across the retina (cf. Vos, 1963). A useful offshoot of the evaluation of the straylight factor was an extension of the expression describing the foveal intensity profile produced by a point source. That is, it was possible, as described in the paper by Vos, Walraven & van Meeteren (1976), to bridge the (angular) data gap between 5' of arc (up to which there are only data from fundus reflectometry) and 1° (beyond which the data come from glare studies), and thus map the complete point-spread function.

In the next study (Walraven, 1976), a new experimental paradigm was introduced. Rather than using the classical configuration in which the test stimulus is presented in a hole in the centre of the inducing field (annular field), the test light was presented as in increment superimposed on a (steady) background. The results obtained with this new stimulus arrangement invited and, more importantly perhaps, *enabled* a completely different type of data analysis. The test field was no longer treated as a field in the centre of a *surround*, but rather as an increment on a *background*, conform the way it was produced. The data suggested that the visual system may actually perform the same type of analysis. This was evidenced by the finding that, for a fixed background level, decreasing the luminance of the test field, all the way down to the contrast threshold, was not attended by a change in hue, despite the tremendous change in the spectral composition of the mixture of test and background light. Apparently the light from the background, although mixing physically with the test flash, was somehow unmixed at the response level. This phenomenon, which might be considered as a form of AC-coupled signal processing was called "discounting the background".

When the discounting principle is applied to the classical centre-surround stimulus configuration it predicts that the light that the test field has in common with the surround id nullified. Thus, for example, a red surround will cause an effect similar to extracting redness from the test field. Due to the antagonistic processing of colour, this is tantamount to biassing the hue response in the direction of green, or inducing a green colour. Here we may have found, then, the nature of the mechanism underlying the "second" process in the model of Hurvich & Jameson.

In the above study we only considered stimuli that were brighter than the inducing field, that is, incremental test fields. In the next study (Walraven, 1977) we addressed the question as to what would happen if the test field was presented as a decrement. Thereto, we used the same stimulus arrangement as before, but now the red component (ΔR) of the test field was no longer presented as an increment superimposed on the background R (which consisted of the same red light), but as a decrement, thus causing a dip in the luminance profile of the background. The green stimulus component (ΔG) was adjusted until the test mixture looked neither reddish nor greenish, and thus served as a measure for the strength of the red hue signal at the test field locus.

The interesting result of that experiment was that we measured no (decremental) redness signal at all. The slightest amount of ΔG (about twice the amount required for threshold) was always sufficient to cancel the redness of the test field, whatever the size of the decremental step. So, having concluded already that colour vision is subserved by transient signals, we could now add that the transients, within the colour channel in question, must be of positive sign in order to affect the (antagonistic) colour balance.

To demonstrate further the dependence of colour signals on transients (i.e. discontinuities in the retinal image) we showed that a uniform red background which, as we have discussed above, normally is "discounted" at the test field locus, can be "activated" by surrounding that locus with a thin dark border. Such an encircled portion of the background, which was called a pseudo-increment (it was only incremental with respect to the dark border), was found to generate a redness signal in proportion with the depth of the decremental border. In other words, the background which first did not seem to add to the test field, now did produce an additive effect, apparently because it was now provided with a contour that could no longer be "written over" by that of the test field.

Additive effects were also obtained by Shevell (1978), which led him to reject the discounting hypothesis. His criticism initiated the next paper (Walraven, 1979) in which we showed, using his own data, that non-additivity only obtained in those of Shevell's experiments in which temporal or spatial transients were more or less avoided. Actually, Shevell's results provide additional support for the transient processing concept, by showing that the amount of background discounting decreases when the (test) transients are relatively weak.

So far, we have discussed only the second process (the subtractive operation) of chromatic induction, and concluded that it might reflect the activity of a mechanism that separates differential from common information. From the experiments employing steady backgrounds we also obtained information regarding the "first" process (the multiplicative operation), the one responsible for the adaptation effect proper. That is, we found that, for a given background, varying the intensity of the incremental test field did not affect its hue. In other words, we confirmed the proportionality rule, which suggested that we were dealing with a well-behaved von Kries-type sensitivity control; provided, of course, that allowance was made for the second process, the discounting of the background.

Having isolated the effect due to chromatic adaptation proper, that is, free from the confounding effect of the second process, we started speculating about the possible mechanism(s) involved. In particular we were interested in the role that might be played by the stimulus-response or transducer function of the photoreceptor. The latter may already contain an element of sensitivity control, due to response compression at high stimulus intensities. Unfortunately, psychophysical data that enable a straightforward determination of such a transducer function are virtually non-existent. Probably the only exception in this respect might be found in the work of Alpern, Rushton & Torii (1970a, b). They used a technique that yielded data which directly seemted to trace the function we were looking for. However, the data analysis on which the derivation of that function was based started from an assumption that led to serious incongruities, as Wandell (1976) had already pointed out before. Apart from that, it can be shown that the mathematical treatment of the data is incorrect, and hence, the analysis. On the other hand, the data themselves seemed interesting enough, so we decided to subject them to a re-analysis, which resulted in the next paper (Walraven, 1980).

It turns out that these data can be described by a relatively simple model incorporating an intensity (I) - response (R) function in accordance with the familiar function $R = I/(I+c)$ for which there now exists such an overwhelming physiological evidence. In addition, however, we had to assume a gain control operating on the receptor output. The latter can be described as a resetting device: It scales the response in proportion with the steady-state response, including that attributed by the system's "dark" light (Eigengrau). Such a volume control produces the well-known Weber-Fechner relation, the function which describes the contrast threshold as a function of background intensity. The latter thus may be interpreted as reflecting the increasing attenuation of the photoresponse with increasing luminance level.

The concept of such gain controls, one for each receptor systems, seemed attractive for describing our own results. We knew already from Stiles' work on two-colour threshold (e.g. Stiles, 1959, 1978) that the threshold elevation of isolated colour systems, his so-called π mechanisms, can be described - like the results of Alpern et al. - by the Weber-Fechner relation. The latter, expressed as a gain characteristic (i.e. as its reciprocal), called $\zeta(x)$ by Stiles, has been tabulated by Wyszecki & Stiles (1967). The underlying mechanisms, which may be partly situated in the cones themselves, are not fully understood as yet, although ingeneous "Weber machines" have been developed by Bouman and his associated (e.g. Bouman, 1969; Koenderink, van de Grind & Bouman, 1971).

In the next study (Walraven, 1981) we tested the applicability of Stiles' function $\zeta(x)$ for describing a new set of data, covering a broad range of background intensities. Before we could do so, however, we had to make an assumption as to the spectral sensitivity distributions of the photoreceptors. We decided to use the functions derived by Vos and Walraven (1970), probably one of the best sets of receptor "fundamentals" available at present. We then tried to describe our findings by assuming receptor selective gain factors (i.e. von Kries coefficients) operating on these fundamentals, hereby employing the function $\zeta(x)$ for calculating these factors. The quantity x in this function represents the input to the gain control. According to the original von Kries hypothesis this input would be provided by the same receptor (system) that is controlled by the gain mechanism in question. It turned out, however, that matters were a little bit more complicated. The data analysis suggested that the spectral sensitivities of the gain controls were slightly different from those of the photoreceptors on which they operated. The action spectra of these mechanisms were not unfamiliar, however. That is, they might quite well be the same ones that describe the wavelength dependent (adaptation) mechanisms that Stiles derived from his two-colour threshold data, the so-called π mechanisms.

This result is not without theoretical significance, for it may shed some new light on the nature of the π mechanisms. The π spectra, which recurrently have been proposed as candidates for cone absorption spectra (Estêvez & Cavonius, 1976; Pugh & Sigel, 1977; Bowmaker & Dartnall, 1980) may now be assigned to adaptation sites rather than to the receptors themselves.

The foregoing conclusions were actually based only on data from experiments in which we avoided stimulating the short-wavelength-sensitive or "blue" cones. We did that because we did not want, as yet, to incur the complications to be expected when dealing with the blue system (cf. Mollon, 1977). However, in the next, and last study (Werner & Walraven, 1981) we employed backgrounds that varied in colour throughout the whole spectral and purple range and thus obtained data relating to the sensitivity control of all three cone types.

The results from these experiments confirmed our previous conclusions, but, as anticipated, the introduction of the blue system necessitated an extension of the model. That is, we had to assume that the gain control of the "blue" cones is not a private affair of the cones in question, but that there is also an adaptive input from the other cone types. This may seem a rather odd arrangement, but it does underscore the conclusions from other studies attesting to the complexity of the short-wave sensitivity control (e.g. Pugh & Mollon, 1979; Valeton & van Norren, 1979). Actually, our hypothesis that π spectra rather than the cone spectral sensitivities describe the action spectra of the gain mechanisms in the cone pathways, suggest that neither of the gain controls receives input from a single cone type.

This concludes this brief inventory of our recent contributions to the field of chromatic induction. We have organized it mainly along the lines of what was called the two-process interpretation of chromatic induction, but even within that already limited scope we only could touch, of course, on the main points of interest. Still, this rough sketch may serve as a unifying structure for the series of papers to be presented hereafter. As for a general evaluation of the results, in particular in relation to current problems in both the realm of fundamental and applied research, the reader is referred to the last chapter, the Epilogue.

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II. SEPARATING THE PHYSICAL AND PHYSIOLOGICAL MECHANISMS

2.1 SPATIAL CHARACTERISTICS OF CHROMATIC INDUCTION; THE SEGREGATION OF LATERAL EFFECTS FROM STRAYLIGHT ARTEFACTS

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INTRODUCTION

ONE of the many factors that may affect the perception of a visual stimulus is the presence of other stimuli in the field of view. If, for example, a small yellow spot is surrounded by a red field, this spot will at once appear to be tinged with green, the complementary colour of the surround. This is the well known effect of simultaneous colour contrast. Strictly speaking this phenomenon relates to the instantaneous effect at stimulus onset rather than to the effect resulting from prolonged viewing of the stimulus pattern. In the latter case the term (lateral) chromatic adaptation would be more appropriate, or else, the collective noun for all laterally evoked hue changes: chromatic induction.

Chromatic induction is a phenomenon apparently due to spatial interactions in the visual system. A proper understanding of the mechanism involved therefore requires knowledge concerning the effect of spatial variables. In this respect one might ask, for instance, whether lateral interactions only occur when a test and inducing field are contiguous. And also, whether it is only the border of the surround that mediates the effect, or if more distant regions are also involved. The general conclusion that can be drawn from a number of studies, often dealing only indirectly with these spatial variables, is that (a)chromatic induction may indeed occur with spatial separations of test and inducing field(s). However, the effect usually decreases rapidly with increasing separation (KIRSCHMAN, 1891; DIAMOND, 1953; LEIBOWITZ, MOTE and THURLOW, 1953; ALPERN and DAVID, 1959; JAMESON and HURVICH, 1961; MCKAVEY, BARTLEY and CASELLA, 1961; OYAMA and HSIA, 1966; WÄSSLE and HEINRICH, 1970). Increasing the diameter of an inducing field has been found to yield diminishing returns (KIRSCHMAN, 1890; DIAMOND, 1955; KINNEY, 1962; HEINRICH, 1967; WÄSSLE and HEINRICH, 1970), a result that, like the former, indicates that the interactions are mainly confined to neighbouring areas.

It is not always self-evident, however, that these results solely reflect the spatial properties of a neural lateral mechanism. An important consideration in this respect is that studies pertaining to the masking effect of glare have shown that "lateral" effects may also be caused by entoptic stray light (e.g. COBB, 1911; HOLLADAY, 1926, 1927; FRY and ALPERN, 1953a, 1953b; BOYNTON, BUSH and ENOCH, 1954a; VOS and BOUMAN, 1963; RUSHTON and GUBISCH, 1966). If a surround would be effective as a consequence of stray light only, the sloping retinal intensity profile of the latter might produce similar spatially dependent results as in the studies first mentioned.

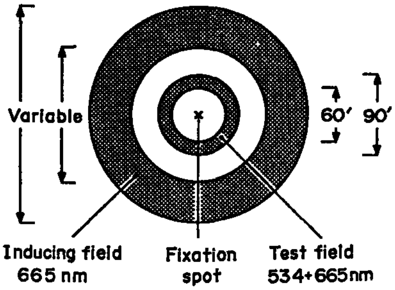

FIG. 1. Stimulus configuration.

In the present study we investigated lateral and pseudo-lateral effects (stray light) separately. Thus, we were able to determine more precisely both the spatial properties of chromatic induction and the distribution of stray light in the retinal image.

II. EXPERIMENTAL ARRANGEMENT

1. *Stimuli and apparatus*

The stimulus configuration as it appeared to the observer in the majority of the experiments is shown in Fig. 1. It consisted of a yellow test field centred in a red (665 nm) surround. Both fields were annuli, the test field having inner and outer diameters of 60' and 90' respectively, whereas the diameters of the surround could be varied between 90' and 420'. The yellow colour of the test field was obtained by mixing red (665 nm) and green light (534 nm), only the amount of red being variable.

Figure 2 shows a schematic diagram of the main light paths of the optical system. The light beam that provided the red component of the test field (R_t) originated from a 12 V, 100 W tungsten–iodine light source (S_1) run at 8A. It passed through a colour filter with dominant wavelength 665 nm (Schott RG5). Its intensity could be attenuated by two circular neutral density wedges in contra rotation. The green component of the test field (G_t) came from a tungsten ribbon filament bulb (S_3) run at 13A, resulting in a colour temperature of *ca.* 2600°K. This beam passed through a Kodak Wratten Filter No. 61 (λ_d = 534 nm). The light beam that provided the surround (R_s) had the same wavelength composition as R_t; it was derived from a similar light source (S_2) and passed through an identical filter as used for R_t. The whole pattern was presented in Maxwellian view (2 mm artificial pupil). Fixation was maintained at a central fixation point (1') of white light from an auxiliary beam not shown in the diagram. A dental bite-board in combination with a comfortable headrest ensured that the light beams always entered through the centre of the pupil.

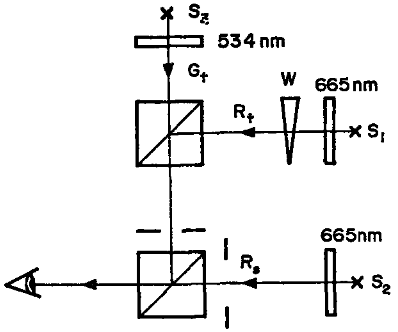

FIG. 2. Schematic diagram of the principal lightpaths in the optical apparatus. R_t and G_t, red and green light beams of the test field. R_s, red beam of the surround field. S_1, S_2 and S_3, light sources. W, neutral density wedge.

2. *Method*

A null response method was employed similar to that used by DeValois and Walraven (1963), i.e. maintaining a constant hue (pure yellow). In this case the yellow settings had to be made by varying the red content of the red–green mixture of the test field. No comparison field was present. The observer adjusted the colour until it looked neither reddish nor greenish. Since red coloured inducing fields were used the apparent colour of the test field always shifted towards green. Hence, the amount of red light (R_t) required during the test always had to be increased over its initial value (R_0) by a certain factor. This factor, R_t/R_0, was used as a measure for the contrast effect.

The test stimulus was always flashed, using a constant retinal illuminance for the green beam (G_t) of 100 td. Since about 50 td of red light were required for a yellow setting without surround (R_0), the initial retinal illuminance of the test field was 150 td.

The precision of the yellow settings was almost as good as in a direct matching procedure employing a bipartite field. This was the reason for not using the more common haploscopic comparison method with its inherent problems of binocular rivalry, difficult fixation control, and the danger of interocular interaction (DeValois and Walraven, 1967).

3. *Procedure*

After an initial 15 min of dark adaptation the test field was presented as 0·5 sec flashes with an interstimulus interval of 5 sec. The observer then started to adjust the intensity of the red beam (R_t) until the hue of the test field appeared to him as a pure yellow. After about 10 yellow settings the inducing field was added, either flashed simultaneously with the test field, or presented continuously. The observer adapted for some time (2–5 min) to this new condition and then proceeded with making another 10 settings. The mean settings of the two series of measurements were taken for computing the factor of increase of red, R_t/R_0. Each condition was presented at least three times with intervals of 1 or 2 days.

III. EXPERIMENTAL RESULTS

1. *Chromatic induction with flashing test and inducing field (simultaneous contrast)*

In this experiment we presented test and inducing field as a single 0·5 sec flash. This is an appropriate condition for measuring simultaneous contrast since indirect adaptation from eye movements back and forth between test and inducing field is virtually eliminated. Annular surrounds were used with either fixed inner diameter (90′) and expanding outer diameter (condition A), or with fixed outer diameter (420′) and contracting inner diameter (condition B). Note that in condition A the inner border of the inducing field (90′) is always contiguous with the outer border (90′) of the test field, whereas in condition B there always is a variable separation between the two.

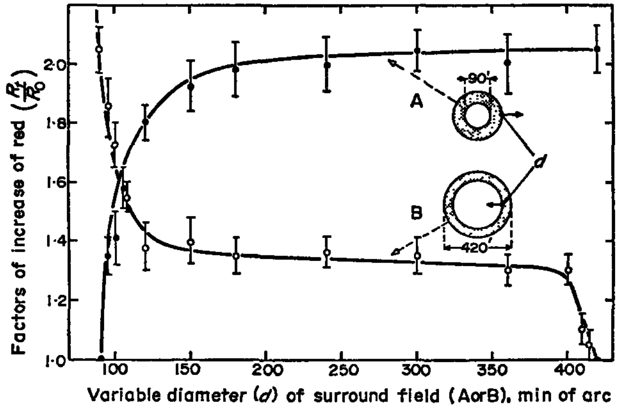

Fig. 3. Factors of increase of red required for maintaining a yellow hue of the test field in the presence of red annular surrounds with either variable o.d. (A, filled circles) or variable i.d. (B, open circles). Test and surround field are flashed simultaneously (0·5 sec flashes). Retinal illuminance of surround: 300 td. Inset shows the two types of annular inducing fields that belong to a given value of *d*. Error bars represent data *spread*.

The results for a surround retinal illuminance of 300 td are shown in Fig. 3. The abscissa of this figure represents the variable diameter, *d*, of the two types of inducing fields used. So, *d* comprises the *outer* diameter in condition A, as well as the *inner* diameter in condition B. The ordinate gives the contrast effect expressed as the factor of increase of red (R_t/R_0) that is required to maintain the yellow hue of the test field. The contrast effect apparently consists of two components. One seems to be tied to a narrow region surrounding the test field ($90' < d < 150'$), where changes in *d* result in large changes of R_t/R_0. The other component is revealed in condition B where, tracing curve B from right to left, already a sizeable effect can be observed (about 30 per cent of the maximum effect) as soon as the annulus has reached a width of about 10′ ($d = 400'$). Apparently, this effect results from the mere presence of the inducing field, since it hardly increases when *d* decreases from 400′ to 150′, despite the concomitant decrease in separation between test and inducing field and the area increase of the latter.

In this experiment the adaptive effects found ($R_t/R_0 > 1$) can be of lateral origin only, although we do not know as yet whether stray light from the surround may also have contributed to this result. In this respect it should be noted, however, that scattered (red) light from the surround flashes simultaneously with the test stimulus and therefore affects the receptors in the test field area in exactly the same way as does the red light (R_t) from the test stimulus. So, as far as the stray light falling *on* the test field is concerned, less red would be required for a yellow setting, and hence, the opposite effect of adaptation would be expected ($R_t/R_0 < 1$).

In order to determine whether similar results would be obtained in the steady state condition we also investigated the effects exerted by stationary surrounds.

2. *Chromatic induction with steady inducing field and flashing test field*

This experiment was in most respects similar to the previous one, except that now the inducing fields were not flashed but continuously present. Further, we only used annuli with an i.d. of at least 107′, thus ensuring that the test flash would remain separated from the surround by a distance of at least 8·5′. This precaution was taken in order to prevent local adaptive effects that might result from "smearing" of the retinal image because of involuntary eye movements.

In our previous experiment brightness contrast set a limit to the maximal surround intensity that could be used, as will be discussed later. In the present condition, on the contrary, chromatic induction could be pursued up to our highest attainable surround intensity (retinal illuminance 16,000 td). Much larger adaptive effects were obtained in this way, even at moderate intensities. This is not the only difference with the previous results; in Fig. 4, which shows the results for a 1500 td surround, it can be seen that the effect of increasing *d* takes a more gradual course than in Fig. 3. Furthermore, the second contrast component previously found in curve B, now seems to be completely lacking.

The dissimilarities with the findings of the previous experiment do not necessarily imply that in the present experiment we measured something else besides lateral interaction. On the other hand, we cannot, as in the condition with flashing surrounds, exclude an alternative explanation in terms of stray light. In the present condition stray light falling on the test field acts as a steady conditioning field, and may thus exert a *local* adaptive effect that overrules its colour mixing effect. Experiments designed to test this hypothesis will be discussed in the next section.

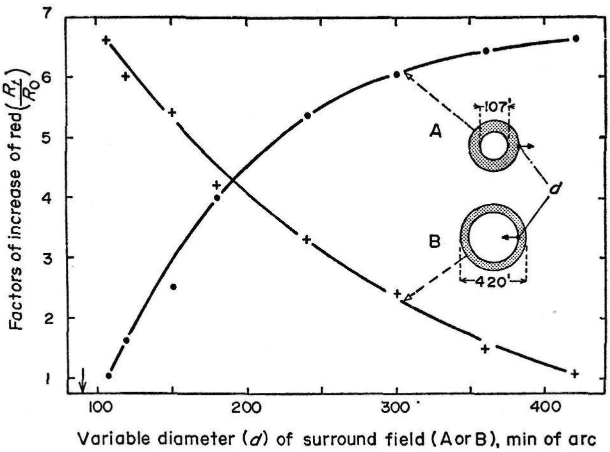

FIG. 4. Factors of increase of red for maintaining a yellow hue of the (flashing) test field in the presence of *steady* annular surrounds. Vertical arrow indicates the diameter of the test field. Retinal illuminance of surround: 1500 td.

3. *The stray light evaluation for stationary surrounds*

3.1. *The equivalent background.* The conventional psychophysical method for evaluating the effect of stray light is to present the test field superimposed on a veiling luminance, and then determine the intensity—the equivalent background—at which the result obtained with this veiling luminance matches the result found in the actual experimental condition under concern. If the scattered light is only locally effective the extent of this background is immaterial as long as it covers the test field. FRY and ALPERN (1954) showed this to be the case with respect to the apparent brightness reduction by *steady* backgrounds. We found the same with respect to colour when comparing the results of a 420′ veiling background and a 107′ background barely covering the 90′ test field. So, although the central holes of our annuli of the previous experiment varied in size, and hence, the size of the stray light patch inside, there was no need to use more than one size of veiling background for our stray light evaluation.

Figure 5 shows how the equivalent backgrounds were determined. In this figure we replotted the results of the adaptation experiment (Partition I) together with the results obtained in the condition where the test flash was superimposed on a 107′ red veiling background (Partition II). The latter served as our yardstick for measuring the effect of stray light. Note that the effect of the red background is one of attenuating red sensitivity rather than of adding red to the test stimulus; so stray light must indeed have contributed to the adaptive hue shifts measured in the previous experiment (Fig. 4). It may even have been solely responsible for the whole effect, a likely assumption when considering that relatively feeble veiling backgrounds already give rise to factors of red-increase commensurate with those obtained with surround stimulation. The specific amounts of light required for such a stray light interpretation are given by the equivalent backgrounds shown in Partition III of the diagram. The dashed lines illustrate for one point—the cross point of the curves—how the equivalent background was derived. Note that the equivalent backgrounds appear to be in the order of a few per cent of the 1500 td surround illumination (see ordinate scale

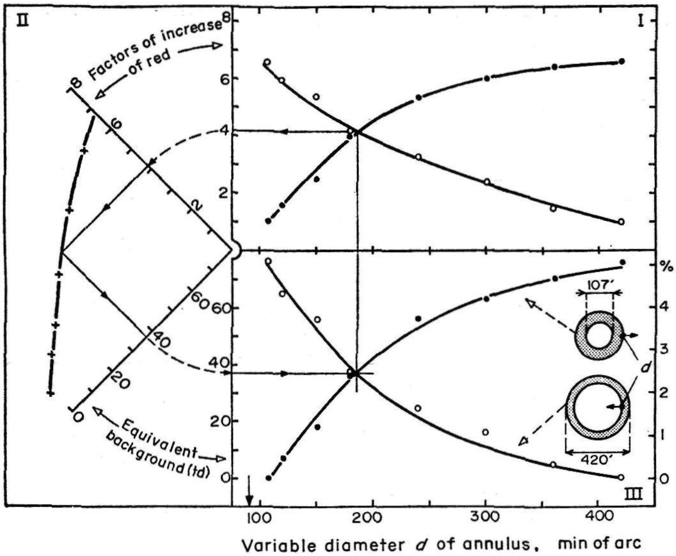

FIG. 5. Partition I: Factors of increase of red (R_t/R_0) required for maintaining a yellow hue of the test flash in the presence of *steady* red annular surrounds (1500 td) with either variable outer diameter (filled circles) or variable i.d. (open circles). Partition II: Factors of increase of red as a function of the retinal illuminance of a superimposed 107′ veiling background. Partition III: Equivalent backgrounds, i.e. the retinal illuminances of veiling backgrounds that produce the same hue shift as the surrounds given by the abscissa. Scale at the right gives the same values expressed in percentages of the surround illuminance (1500 td). Vertical arrow indicates o.d. of the test field (90′).

at the right). Since stray light must be present anyway, this finding strongly favours a stray-light interpretation of the data. Also consonant with this hypothesis is the finding that the data shown in Partition III are consistent with the additivity of stray light. This transpires from the fact that the curves drawn through the data points are mirror images of each other, and thus represent complementary amounts of veiling light. The point is that the same is true for the areas of the two annuli associated with each value of *d* (their variable diameter). Complementary amounts of (stray) light, therefore, should indeed be expected.

In order to put the stray light hypothesis to a more rigorous test we performed an experiment in which another important stray-light property was checked, i.e. the fixed ratio of stray-light to (surround) stimulus intensity. The same experiment also enabled us to test the additivity argument more critically.

3.2. *The proportionality and additivity check.* In the previous experiments the annuli were always presented at a constant retinal illumination. The following experiment shows what happens with increasing surround intensity.

Three different (stationary) surrounds were used, viz. a 90′–420′ annulus and two more fields with the same inner and outer diameter, but each consisting only of 12 sectors, constituting respectively 1/4 and 1/12 of the area of the complete annulus. In addition, yellow settings were made with the test flash superimposed on a 420′ circular veiling background.

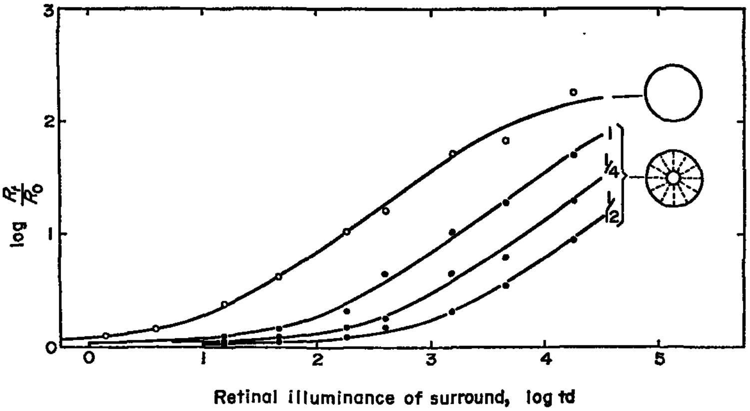

FIG. 6. Factors of increase of red required for maintaining a yellow hue of the test flash as a function of the retinal illuminance of steady red adaptation fields. Open circles: test flash superimposed on a 420′ circular field. Closed circles: test flash presented in respectively the centre of a 90′–420′ annular surround (1), and sectored fields with areas of respectively a quarter (1/4) and a twelfth (1/12) of the annular surround.

Figure 6 shows the change in yellow setting (R_t/R_0) as a function of the retinal illumination of the various fields used. First, it should be noted that the curves drawn through the data points, although differing with respect to their lateral displacement along the abscissa, all follow the same course. This finding indicates that irrespective of the intensity of the surround its adaptive effect can always be matched by an amount of veiling light corresponding to a *fixed* proportion of that particular intensity. This proportion follows directly from the distance over which the curve of a given surround is shifted with respect to that of the veiling background (leftmost curve).

A stray-light interpretation of these results is further corroborated by the fact that the curves pertaining to the sectored fields are laterally shifted, with respect to that of the annulus, over distances of respectively 0·6 log units (factor 4) and 1·1 log units (factor 12), i.e. exactly the factors by which the retinal illumination of these fields must be raised in order to yield the same amount of stray light as the annulus. This is again a finding of additivity; additivity of sectors this time, instead of the additivity of annular surrounds previously found in Fig. 5 (Partition III).

The additivity argument does not necessarily refute an explanation in terms of lateral interaction. However, one would be forced to conclude, then, that light and area are apparently indistinguishable variables for this presumed lateral mechanism. This would imply that the non-linear relationship found for R_t/R_0 as a function of the intensity of the surround should hold exactly for the spatial summation properties of this mechanism as well; a very unlikely assumption considering the different neural processing that must be involved.

3.3. *The link with glare data.* The results so far obtained with stationary surrounds have all been in support of a stray-light explanation. Therefore, the effects observed with increasing inner or outer diameter of the annular surrounds employed in the adaptation experiment (Fig. 4) may very well be ascribed to the concomitant rise and fall of the amount of light scattered on to the test field area. This implies that the results of that experiment should somehow reflect the scattering properties of the eye. The latter find their psychophysical expression in the so called glare function, an empirical formula usually presented in the form:

$$L_{eq} = K \cdot \frac{E}{\theta^n} \tag{1}$$

where L_{eq} represents the equivalent veiling luminance, E the illumination of the observer's eye by the glare source, θ the angle of the glare source from the line of sight, and K and n are constants. The values of K and n vary between authors depending somewhat on the θ range investigated. For L_{eq} expressed in cd/m², E in lx, and θ in deg, we cite:

Holladay (1926)	2·5°	$< \theta <$ 25°	$n = 2$	$K = 9{\cdot}3$
Stiles and Crawford (1937)	1°	$< \theta <$ 102°	$n = 2{\cdot}1$	$K = 11{\cdot}5$
Fry and Alpern (1953b)	0·75°	$< \theta <$ 4·5°	$n = 2{\cdot}5$	$K = 22{\cdot}4$
Vos (1963)	1°	$< \theta <$ 8°	$n = 2{\cdot}8$	$K = 29$

For small glare angles the glare formula (1) is valid only for a pointiform glare source. In our case, where the stray light is coming from an annular surround closely situated or even adjacent to the test spot, we must integrate over the distance-weighted area of the surround. Furthermore, the glare formula has to be adapted for small angles, since in its present form the function tends to infinity. Gubisch (1967) who modified the glare function for use as an optical spread function met this problem by introducing an arbitrary constant. In a slightly different way we have done the same, inserting in (1) a constant θ_0 as follows:

$$L_{eq} = K \cdot \frac{E}{(\theta + \theta_0)^n}. \tag{2}$$

The main difference with the approach of Gubisch (1967) is that his choice of the constant was based on considerations concerning the dioptrics of the eye, whereas in our case θ_0 has to be chosen so as to give the best agreement with our equivalent background data, without invalidating the particular glare formula used (at least for $\theta >$ 1–2°, the lower limit for the applicability of most formulae). It turned out that of the formulae of the authors cited above, those of Vos (1963) and Fry and Alpern (1953b) were best suited for this purpose; probably, because the experimental conditions used by these authors did not differ too much from ours (Maxwellian view, relatively small θ-range). The best description of the data was obtained by inserting $\theta_0 = 0{\cdot}13°$ in the formula of Vos:

$$L_{eq} = 29 \frac{E}{(\theta + 0{\cdot}13)^{2\cdot 8}}. \tag{3}$$

The close agreement between computed and experimental L_{eq} values is shown in Partition III, Fig. 5. The curves drawn through the data points were computed with the modified glare formula (3); they relate to an eccentricity of 37·5′ relative to the annulus centre, i.e. the location at which the (annular) test field (mean radius, 37·5′) probes the stray light profile inside the annulus.

In order to determine to what extent our results, and hence the glare function (3), pertains to entoptic light scatter only, we also measured the stray light produced by the apparatus. For that purpose an aerial image of the inducing field, formed at about 1 m behind the exit pupil of the apparatus, was scanned with a fibre optic attached to a photomultiplier.

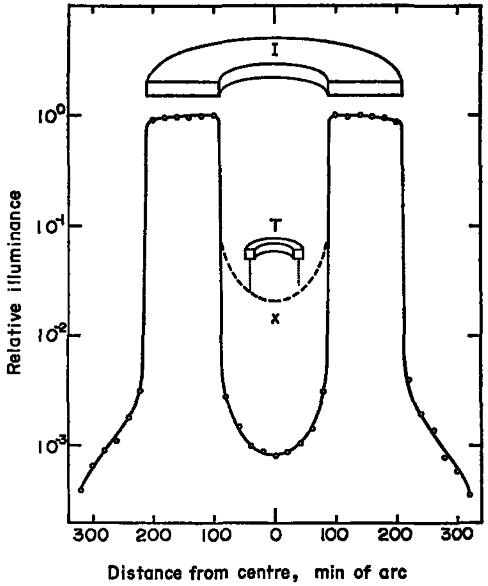

FIG. 7. Image profile of a 3°–7° annulus, measured at the exit pupil of the apparatus (ectoptic light distribution). Dashed curve represents the stray light profile in the observer's eye (entoptic light distribution) as calculated with (3). Cross denotes the fraction of entoptic stray light measured (psycho)physically by RUSHTON and GUBISCH (1964). T and I represent test and inducing field respectively.

Figure 7 shows the results thus obtained, and also the stray light profile (dashed curve) calculated for the central hole of the inducing field in question, i.e. a 3°–7° annulus. Clearly, instrumental stray light, accounting only for 4 per cent of the total amount, can hardly have affected our data.

RUSHTON and GUBISCH (1964) also used the equivalent veil technique for determining the amount of stray light in an annulus. And, since they could substantiate their findings by reflection densitometry, their data are of special interest. They measured 2 per cent stray light in the centre of a 3°–8° annulus, a value that would hardly have been different if, instead, a 3°–7° annulus had been used, like the one shown in Fig. 7. Of this 2 per cent, 0·5 per cent was due to instrumental stray light, thus leaving 1·5 per cent for entoptic light scatter, a value still in fair agreement with our estimate of 2 per cent (cf. Fig. 7).

Summarizing the results obtained so far with steady surround illumination we may conclude that these can be completely attributed to entoptic stray light, and thus represent indirect measures of stray light. The latter enabled us to derive a generalized glare formula (3) which, because of the small glare angles (i.e. the separations between test and inducing field) covered by our measurements, has a validity extending to glare angles in the order of 8′.

3.4. *The stray light evaluation for flashing surrounds.* In our simultaneous contrast experiment (cf. Fig. 3), where test and inducing field were presented as a single flash, stray light must have exerted two opposite effects. Depending on whether it fell *on*, or *around* the test field, it either mixed with the test stimulus or added to the contrast effect of the surround. The latter effect is mainly of interest in our condition with varying i.d. (condition

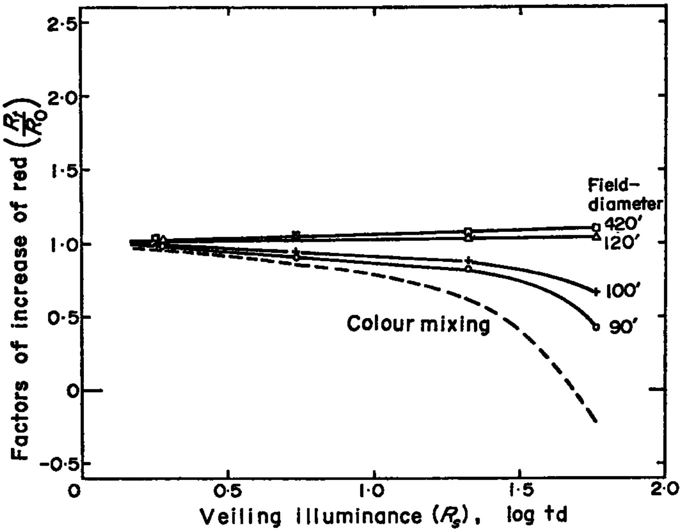

FIG. 8. Factors of increase of red for maintaining a yellow hue of the test field when *superimposed* on red veiling backgrounds of varied area and intensity. The whole pattern was flashed (0·5 sec flashes). Dashed curve represents the calculated effect of colour mixing (see text for explanation).

B) where stray light, filling the variable gap between test and inducing field, acts as a secondary surround. The inducing effect of this surround is not only determined by its (stray light) intensity but also its area. Therefore, when evaluating the effect of stray light in our contrast experiment we must make proper allowance for both the intensity and the diameter of the stray-light patch inside each annulus.

With this intent veiling backgrounds were presented with diameters of respectively 90, 100, 120 and 420′. These were flashed simultaneously with the test field at intensities ranging from 0·6 to 20 per cent of the 300 td annuli used in the contrast experiment. The results, showing the change in yellow setting (R_t/R_0) as a function of the retinal illuminance of the various veiling backgrounds used, are plotted in Fig. 8. It shows that so long as the diameter of the veil does not drop below 120′, R_t/R_0 hardly changes; thus, colour mixing and colour contrast keep each other in balance under these circumstances. For smaller diameters, however, less red is required to maintain yellow ($R_t/R_0 < 1$), indicating that colour mixing now dominates over colour contrast. If only colour mixing were involved the amount of red required for a yellow setting (R_t) would be given by R_0, the initial amount, reduced by R_s, the red light furnished by the (superimposed) veiling luminance. So we would then get

$$R_t = R_0 - R_s \tag{4}$$

and hence

$$R_t/R_0 = 1 - R_s/R_0, \tag{5}$$

which yields the dashed "pure" colour mixing curve shown in Fig. 7. Note that complete colour mixing was never found, even when the veiling background had the same diameter

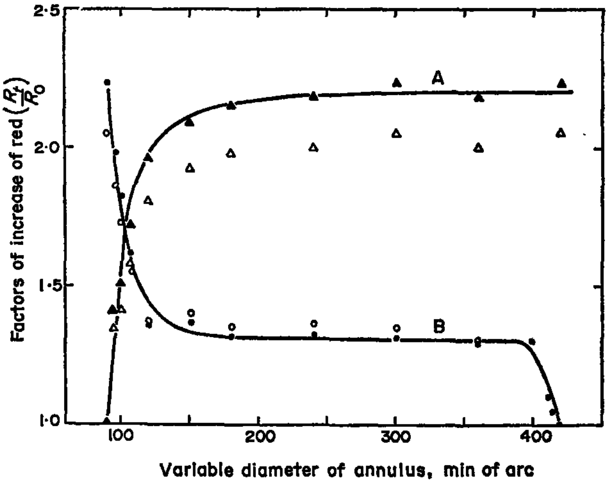

Fig. 9. Factors of increase of red required for maintaining a yellow hue of the test field in the centre of red annular surrounds. Open symbols: original data from Fig. 3. Closed symbols: same data corrected for stray light effects.

(90′) as the test field. The reason for this is that the test field, being an annulus, was never free from lateral interaction alongside its inner border.

We have now reached the point at which we can correct our contrast data for stray light artefacts. Thereto we first calculate with (3) the amount of stray light at the test field locus inside each annulus (37·5′ eccentric from the annulus centre). Then, assuming the effect of the stray light veil to be equivalent to that of a homogeneous veil of the calculated intensity and appropriate diameter (the i.d. of the annulus in question), we derive from Fig. 8 the correction to be applied. This is an approximation, of course, since the stray light veil is not homogeneous, but it seems a fair first-order estimate.

The corrected results are shown in Fig. 9 (closed symbols), together with the original data from Fig. 3 (open symbols). Clearly, only when test and inducing field are contiguous (condition A), has stray light an appreciable effect, i.e. colour mixing. The predominance of colour mixing in this case is due to the fact that the stray light is mainly confined to the test field. Conversely, in condition B, stray light also illuminates the "dark" area surrounding the test field, and thus, as Fig. 8 already showed, colour mixing is effectively cancelled by interaction from this secondary surround. In this condition, therefore, the original results hardly needed to be corrected, except with small separations between test and inducing field ($d < 120'$) where stray light constituted too small a surround for counteracting the colour mixing effect.

Now that our data are free from stray light influences we can be confident that what is left only reflects lateral interaction. Obviously, then, we may still conclude that the contrast effect consists of two components. One component, the contrast effect proper, apparently involves interactions at the test field border ($90' < d < 150'$), whereas the other, revealed in curve B ($400' < d < 420'$), seems to be independent of distance. Note that the latter component is also independent of area once it has reached its maximal value at $d = 400'$, i.e. an annular width of 10′. This could mean that this enigmatic effect is generated only by the contour(s) of the surround.

IV. DISCUSSION

The experimental results from this study fall in two categories, those that pertain to the effects of flashing surround fields, and those related to steady backgrounds. The latter show that the adaptive effect of a steady annular field is in all likelihood caused only by the stray light present in its centre. This implies that lateral adaptation is absent in this condition, or at least does not affect the 0·5 sec test flash we used.

Our finding that a yellow test flash looks green when superimposed on a steady red background demonstrates, at supra-threshold levels, what Stiles has already shown for coloured increment threshold stimuli (e.g. STILES, 1959), viz. that a coloured background selectively attenuates the response to similarly coloured light. It is noteworthy that this mechanism operates over a much larger dynamic range than simultaneous contrast. For instance, in the case of a steady 300 td superimposed background we found, taking into account that actually red light was added to the stimulus, that the quantity of red light required for a yellow setting amounted to about a hundred times that needed in the presence of a contiguous *flashing* annulus of the same intensity and diameter. The maximal contrast effect we could measure with flashing surrounds was only a three-fold increase in R_t/R_0. A further increase by using a higher intensity of the surround field was unsuccessful because of the attendant darkening of the test flash, which made colour discrimination impossible. This result seems to obey Kirschmann's third law (KIRSCHMANN, 1891), which states that colour contrast is maximal when brightness contrast is minimal. However, the maximal induction effect we found was obtained at a contrast ratio of about 2:1. So, this law did not hold for our results, any more than for others (KINNEY, 1962; BROWN and RANKEN, 1965; SHIRLEY, 1966). It is probably valid, however, if we consider only the apparent purity of the induced colour, this being affected by brightness contrast, which in turn becomes most marked as soon as the surround intensity is higher than that of the test field (HEINEMAN, 1955). In this respect it is of interest that an increase of red light in the red–green mixture of the test field can apparently compensate for the hue shift, but not necessarily so for the entailing brightness reduction. This indicates that colour and brightness are processed by different mechanisms, a finding consonant with a zone-mechanism of colour processing (WALRAVEN, 1962, 1965).

The finding that the lateral effects, revealed with flashing surrounds, show in their spatial characteristics two distinct components that build up over fairly narrow regions (30′ and 10′), suggests that these effects are mediated by coloured-coded border mechanisms. The apparent hue shift of the test field, on the other hand, is not confined to its border region. It is distributed evenly over the whole area of the test field, a familiar phenomenon that may extend over many degrees of visual angle and which in German literature is called Flächenkontrast (e.g. HEINRICH, 1967). We believe that these seemingly conflicting findings should be considered in relation to the so-called "filling-in" process postulated by WALLS (1954), and elaborated by YARBUS (1967) and GERRITS (1967) on the basis of experiments employing stabilized image techniques. The basic, and now generally accepted, assumption underlying this concept is that the visual system mainly processes the transient aspects of a stimulus. An important consequence of this mechanism is that the perception of a homogeneously illuminated field will be determined by the neural activity generated along its (moving) borders rather than by its central region, which is in fact stabilized when gross eye movements are prevented. That the central region is seen at all should be attributed, therefore, to the filling-in or spread from the neural exitation arising from the border.

Accepting such a mechanism for "normal" vision leads to the logical conclusion that it must also be incorporated in the perception of contrast colours (GERRITS and VENDRIK, 1970). There is even some evidence for this notion since the filling-in of retinal scotomas by contrast colours has been reported (TSCHERMAK, 1900). Qualitatively, simultaneous colour contrast might be understood, therefore, as resulting from the spatial extrapolation of colour decisions taken by border mechanisms that have been "biased" by lateral interference from the surround.

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Abstract—Chromatic induction as a function of the spatial relationship between test and inducing field was measured by a monocular compensation method (maintaining a constant yellow hue). Red annular surrounds were used that were either flashed simultaneously with the test field, or presented as steady backgrounds. In both conditions lateral effects were observed that clearly demonstrated the importance of spatial parameters of the inducing field. On the basis of experimental evidence and existing stray light data, however, it was shown that in the case of stationary surrounds these lateral effects can be completely attributed to entoptic light scatter. The latter finding enabled the contrast data to be corrected for stray light and also yielded a generalization of the glare formula, which extends its validity down to glare angles of *ca.* 8′.

Résumé—On mesure par compensation monoculaire (en maintenant une tonalité jaune fixe) l'induction chromatique en fonction des relations spatiales entre le test et le champ inducteur. On emploie des environnements en anneau, rouges, soit présentés en éclairs simultanés avec le test, soit comme fonds permanents. Dans les deux cas les effets latéraux observés montrent clairement l'importance des paramètres spatiaux du champ inducteur. A partir des faits expérimentaux et des données existantes sur la lumière diffusée, on montre cependant que les effets latéraux d'environnements stationnaires s'expliquent complètement par diffusion entoptique de la lumière. Cela permet de corriger les données de contraste en tenant compte de la diffusion et de généraliser les formules d'éblouissement en descendant jusqu' à environ 8 min d'arc.

Zusammenfassung—Der farbige Simultankontrast als Funktion der räumlichen Beziehung zwischen Testfeld und kontrasterregendem Feld wurde mit einer monokularem Kompensationsmethode gemessen, bei der ein konstanter gelber Farbton einzustellen war. Es wurden rote ringförmige Umfelder benutzt, die entweder simultan mit dem Testfeld zugeblitzt oder als ständiger Hintergrund dargeboten wurden. In beiden Fällen wurden laterale Effekte beobachtet, die den Einfluss räumlicher Parameter des kontrasterregenden Feldes deutlich zeigen. Aufgrund experimenteller Nachweise und bereits vorliegender Streulichtdaten wurde jedoch gezeigt, dass im Fall stationärer Umfelder diese lateralen Effekte vollständig entopischer Lichtstreuung zugeschrieben werden können. Dieses letztere Ergebnis gestattetees, die Kontrastdaten bezüglich Streulicht zu korrigieren und lieferte ausserdem eine Verallgemeinerung der Blendungsformel, die deren Gültigkeit bis herunter zu Blendwinkeln von etwa 8 Bogenminuten erweitert.

Резюме—Хроматическая индукция, как функция отношения между тестовым и индуцирующим полем, была измерена методом монокулярной компенсации (проводимом в постоянном желтом цвете). Красное кольцевое окружение было использовано так, что оно либо вспыхивало одновременно с тестовым полем, либо предъявлялось как постоянный фон. В обоих случаях наблюдались латеральные влияния, что ясно показывает важность пространственных параметров индуцирующего поля. На основании экспериментальных фактов и ланных о существующем рассеянном свете, однако, показано, что, В случае, когда имеется постоянное окружение, эти латеральные влияния

2.2 LIGHT PROFILES OF THE FOVEAL IMAGE OF A POINT SOURCE

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Abstract—Intensity profiles are given, for various pupil sizes, for the foveal image of a white point source from the very image centre to far thereoff. The profiles were constructed from fundus reflectometric data on the point spread function below 5′, from glare studies on entoptic straylight beyond 1°, and from data on straylight artifacts in colour induction in the region between. The results were also expressed in terms of the effective size of the foveal image

INTRODUCTION

The light profile of the foveal image of a point source is not known *in toto*. For small angular distances our knowledge mainly stems from fundus reflectometry, for large angles on straylight measurements from glare studies. The available data have never been brought together, however. Only Gubisch (1967), to our knowledge, came close to it, by studying small angle point spread functions and glare data as separate sections in one paper.

In this paper we will show that the present state of knowledge permits the aforementioned synthesis, so that a complete light profile can be constructed.

ANALYSIS

In 1955 Flamant published the first measurements on the light profile of foveal images for white light. Since then methods have been improved (Krauskopf, 1962; Röhler, 1962; Westheimer and Campbell, 1962), and the best available data at present seem those obtained by Campbell and Gubisch (1966). Recently, van Meeteren (1974) showed that their spread functions could well be understood from experimental data on the various aberrations in ocular imagery. Therefore, two different approaches, a direct and an indirect one, seem to converge. The Campbell and Gubisch data are accurate for visual angles up to 5′ and are available for a whole range of pupil sizes.

In 1927 Holladay published the first quantitative data on the masking effect of the visible halo around glare sources. He expressed the masking effect in terms of an equivalent veiling luminance, L_{eq}, that would produce the same masking effect. His data together with those of Stiles and Crawford (1937) established the generally used equivalent veil formula

$$L_{eq} = \frac{10E}{\theta^2} \quad (4° < \theta < 100°) \qquad (1)$$

with L_{eq} in cd/m², E in lx upon the eye, θ in degrees.

Like most results in physiological optics, equation (1) was derived for relatively young observers in the age range between 20 and 30 yr old. There are indications, however (Fisher and Christie, 1965), that the dependency on θ does not change markedly with age, nor vary between individuals. Only the proportionality factor (here 10) may vary among subjects of the same age and also show a systematic increase with age—over a factor 2–3—in the working age range.

Experiments of Fry and Alpern (1953) and of Vos and Bouman (1959) indicated that the exponent of θ tends to increase with decreasing glare angle. According to the latter authors

$$L_{eq} = \frac{29E}{\theta^{2{\cdot}8}} \quad (1° < \theta < 8°). \qquad (2)$$

Further it became increasingly clear (Vos and Boogaard, 1963; Vos, 1963; Vos and Bouman, 1964; Rushton and Gubisch, 1966) that the equivalent veil is a real light veil, produced by intra-ocular scatter.

Below 1° it is difficult to measure accurately in glare experiments because of interference of small eye movements across the large intensity jump at the border of the glare source. Recently, Walraven (1973) managed, however, to extend the equivalent veil relation to considerably smaller angular distances in his work on straylight artifacts in colour induction. Colour induction even occurs at a fairly low luminance of the inducing field, so that the mentioned interference effects play a minor role. Walraven's results can be summarized by a generalization of equation (2):

$$L_{eq} = \frac{29E}{(\theta + 0{\cdot}13)^{2{\cdot}8}} \quad (0{\cdot}15° < \theta < 8°). \qquad (3)$$

This relation was established in experiments with Maxwellian view optics, with an entrance pupil of 2 mm. One can expect that equation (3) gives an underestimation of L_{eq}, in particular for the larger pupil sizes and the smaller angular distances.

Apparently, data on the foveal image profile, coming from two sides, have now almost closed the gap of uncertainty between the "image proper" and the "straylight halo". We can now, with reasonable certainty, construct one image profile from 0° to 100°. The only thing to do is to attach an absolute value to the fundus reflectometric spread function data, so that the total amount of light under the complete two dimensional image profile adds up to

Table 1. Numerical data for the light profiles of Fig. 1. Tabulated data are fractions scattered per steradian.

angle ϑ (radians)	pupilsize ø (mm)					
	2.0	3.0	3.8	4.9	5.8	6.6
0.100E-04	0.355E+07	0.335E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.107E-04	0.355E+07	0.334E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.115E-04	0.355E+07	0.333E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.123E-04	0.355E+07	0.333E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.132E-04	0.356E+07	0.332E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.141E-04	0.356E+07	0.333E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.152E-04	0.356E+07	0.333E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.162E-04	0.356E+07	0.333E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.174E-04	0.356E+07	0.334E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.187E-04	0.355E+07	0.335E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.200E-04	0.355E+07	0.335E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.214E-04	0.355E+07	0.334E+07	0.240E+07	0.200E+07	0.150E+07	0.130E+07
0.230E-04	0.354E+07	0.332E+07	0.239E+07	0.199E+07	0.150E+07	0.129E+07
0.246E-04	0.353E+07	0.331E+07	0.239E+07	0.199E+07	0.149E+07	0.129E+07
0.264E-04	0.353E+07	0.329E+07	0.238E+07	0.198E+07	0.149E+07	0.128E+07
0.283E-04	0.352E+07	0.326E+07	0.237E+07	0.198E+07	0.148E+07	0.128E+07
0.303E-04	0.351E+07	0.324E+07	0.236E+07	0.196E+07	0.148E+07	0.127E+07
0.325E-04	0.349E+07	0.321E+07	0.235E+07	0.195E+07	0.147E+07	0.127E+07
0.348E-04	0.348E+07	0.317E+07	0.234E+07	0.194E+07	0.147E+07	0.126E+07
0.373E-04	0.347E+07	0.314E+07	0.232E+07	0.192E+07	0.146E+07	0.126E+07
0.400E-04	0.345E+07	0.310E+07	0.230E+07	0.190E+07	0.145E+07	0.125E+07
0.429E-04	0.343E+07	0.306E+07	0.228E+07	0.187E+07	0.144E+07	0.124E+07
0.459E-04	0.340E+07	0.301E+07	0.225E+07	0.185E+07	0.143E+07	0.124E+07
0.492E-04	0.338E+07	0.296E+07	0.222E+07	0.182E+07	0.142E+07	0.123E+07
0.528E-04	0.335E+07	0.291E+07	0.219E+07	0.179E+07	0.140E+07	0.122E+07
0.566E-04	0.332E+07	0.287E+07	0.216E+07	0.176E+07	0.139E+07	0.121E+07
0.606E-04	0.328E+07	0.282E+07	0.213E+07	0.173E+07	0.137E+07	0.120E+07
0.650E-04	0.325E+07	0.276E+07	0.210E+07	0.170E+07	0.136E+07	0.119E+07
0.696E-04	0.320E+07	0.271E+07	0.207E+07	0.166E+07	0.134E+07	0.118E+07
0.746E-04	0.315E+07	0.266E+07	0.204E+07	0.163E+07	0.132E+07	0.117E+07
0.800E-04	0.310E+07	0.260E+07	0.200E+07	0.160E+07	0.130E+07	0.115E+07
0.857E-04	0.305E+07	0.255E+07	0.197E+07	0.157E+07	0.128E+07	0.113E+07
0.919E-04	0.298E+07	0.249E+07	0.193E+07	0.154E+07	0.126E+07	0.111E+07
0.985E-04	0.290E+07	0.242E+07	0.189E+07	0.151E+07	0.123E+07	0.109E+07
0.106E-03	0.281E+07	0.235E+07	0.185E+07	0.147E+07	0.120E+07	0.106E+07
0.113E-03	0.270E+07	0.227E+07	0.179E+07	0.143E+07	0.117E+07	0.103E+07
0.121E-03	0.258E+07	0.217E+07	0.173E+07	0.138E+07	0.113E+07	0.100E+07
0.130E-03	0.244E+07	0.207E+07	0.166E+07	0.133E+07	0.109E+07	0.964E+06
0.139E-03	0.229E+07	0.195E+07	0.158E+07	0.128E+07	0.105E+07	0.925E+06
0.149E-03	0.212E+07	0.183E+07	0.149E+07	0.122E+07	0.100E+07	0.884E+06
0.160E-03	0.195E+07	0.170E+07	0.140E+07	0.115E+07	0.950E+06	0.840E+06
0.171E-03	0.176E+07	0.156E+07	0.130E+07	0.108E+07	0.895E+06	0.793E+06
0.184E-03	0.158E+07	0.141E+07	0.119E+07	0.100E+07	0.839E+06	0.745E+06
0.197E-03	0.140E+07	0.127E+07	0.108E+07	0.923E+06	0.782E+06	0.697E+06
0.211E-03	0.123E+07	0.113E+07	0.979E+06	0.847E+06	0.725E+06	0.649E+06
0.226E-03	0.107E+07	0.100E+07	0.878E+06	0.772E+06	0.669E+06	0.601E+06
0.242E-03	0.921E+06	0.880E+06	0.783E+06	0.700E+06	0.615E+06	0.555E+06
0.260E-03	0.789E+06	0.767E+06	0.695E+06	0.632E+06	0.563E+06	0.511E+06
0.279E-03	0.672E+06	0.664E+06	0.612E+06	0.566E+06	0.512E+06	0.468E+06
0.298E-03	0.569E+06	0.571E+06	0.537E+06	0.505E+06	0.464E+06	0.428E+06
0.320E-03	0.480E+06	0.490E+06	0.470E+06	0.450E+06	0.420E+06	0.390E+06
0.343E-03	0.405E+06	0.420E+06	0.411E+06	0.400E+06	0.379E+06	0.355E+06
0.367E-03	0.340E+06	0.358E+06	0.358E+06	0.354E+06	0.341E+06	0.322E+06
0.394E-03	0.285E+06	0.304E+06	0.311E+06	0.312E+06	0.305E+06	0.291E+06
0.422E-03	0.238E+06	0.257E+06	0.270E+06	0.274E+06	0.273E+06	0.262E+06
0.452E-03	0.198E+06	0.216E+06	0.233E+06	0.240E+06	0.242E+06	0.236E+06
0.485E-03	0.165E+06	0.182E+06	0.200E+06	0.209E+06	0.214E+06	0.211E+06
0.520E-03	0.137E+06	0.152E+06	0.171E+06	0.181E+06	0.189E+06	0.188E+06
0.557E-03	0.113E+06	0.127E+06	0.146E+06	0.157E+06	0.165E+06	0.167E+06
0.597E-03	0.935E+05	0.105E+06	0.124E+06	0.135E+06	0.144E+06	0.148E+06
0.640E-03	0.770E+05	0.870E+05	0.105E+06	0.115E+06	0.125E+06	0.130E+06
0.686E-03	0.632E+05	0.716E+05	0.883E+05	0.977E+05	0.108E+06	0.114E+06
0.735E-03	0.518E+05	0.588E+05	0.739E+05	0.826E+05	0.923E+05	0.994E+05
0.788E-03	0.424E+05	0.482E+05	0.616E+05	0.695E+05	0.786E+05	0.861E+05
0.844E-03	0.347E+05	0.395E+05	0.512E+05	0.582E+05	0.666E+05	0.742E+05
0.905E-03	0.283E+05	0.323E+05	0.424E+05	0.485E+05	0.561E+05	0.634E+05
0.970E-03	0.232E+05	0.264E+05	0.350E+05	0.403E+05	0.470E+05	0.538E+05
0.104E-02	0.190E+05	0.217E+05	0.289E+05	0.333E+05	0.391E+05	0.454E+05
0.111E-02	0.156E+05	0.177E+05	0.237E+05	0.275E+05	0.324E+05	0.380E+05
0.119E-02	0.128E+05	0.146E+05	0.195E+05	0.226E+05	0.268E+05	0.316E+05

Table 1 (*Contd*)

angle ϑ (radians)	pupilsize ø (mm)					
	2 0	3 0	3 8	4 9	5.8	6.6
0 128E-02	0 105E+05	0. 120E+05	0. 160E+05	0. 185E+05	0 220E+05	0. 260E+05
0. 137E-02	0. 867E+04	0 993E+04	0. 131E+05	0. 151E+05	0. 180E+05	0. 212E+05
0. 147E-02	0. 717E+04	0. 824E+04	0. 108E+05	0. 123E+05	0. 146E+05	0. 172E+05
0. 158E-02	0 594E+04	0 685E+04	0. 883E+04	0. 101E+05	0 119E+05	0. 139E+05
0. 169E-02	0 494E+04	0 571E+04	0. 725E+04	0. 821E+04	0. 967E+04	0. 112E+05
0 181E-02	0 411E+04	0 477E+04	0. 596E+04	0. 670E+04	0. 784E+04	0. 896E+04
0 194E-02	0 343E+04	0 400E+04	0. 491E+04	0. 547E+04	0. 636E+04	0. 718E+04
0. 208E-02	0 287E+04	0 335E+04	0 405E+04	0. 448E+04	0. 517E+04	0. 576E+04
0. 223E-02	0 241E+04	0 282E+04	0. 335E+04	0. 368E+04	0. 420E+04	0. 462E+04
0. 239E-02	0 202E+04	0 238E+04	0. 277E+04	0 303E+04	0 343E+04	0. 371E+04
0. 256E-02	0 170E+04	0 200E+04	0. 230E+04	0. 250E+04	0. 280E+04	0. 300E+04
0. 274E-02	0. 143E+04	0 168E+04	0. 192E+04	0. 208E+04	0. 230E+04	0 244E+04
0. 294E-02	0 120E+04	0 142E+04	0. 160E+04	0. 173E+04	0. 190E+04	0. 200E+04
0. 315E-02	0. 102E+04	0. 119E+04	0. 134E+04	0. 145E+04	0. 157E+04	0. 164E+04
0. 338E-02	0 861E+03	0. 101E+04	0. 112E+04	0 121E+04	0 130E+04	0. 135E+04
0. 362E-02	0. 730E+03	0 851E+03	0. 941E+03	0. 102E+04	0. 108E+04	0. 112E+04
0. 388E-02	0 620E+03	0. 719E+03	0. 791E+03	0. 855E+03	0. 902E+03	0. 930E+03
0. 416E-02	0. 528E+03	0. 609E+03	0. 666E+03	0 719E+03	0 752E+03	0. 774E+03
0. 446E-02	0. 450E+03	0 515E+03	0. 562E+03	0. 606E+03	0. 629E+03	0. 646E+03
0. 478E-02	0. 385E+03	0. 436E+03	0. 474E+03	0. 511E+03	0. 526E+03	0. 539E+03
0. 512E-02	0 330E+03	0 370E+03	0. 400E+03	0 430E+03	0. 440E+03	0. 450E+03
0. 549E-02	0. 284E+03	0. 315E+03	0. 338E+03	0. 361E+03	0. 367E+03	0. 375E+03
0. 588E-02	0. 245E+03	0 268E+03	0. 285E+03	0. 302E+03	0. 307E+03	0. 312E+03
0. 630E-02	0. 211E+03	0. 228E+03	0. 240E+03	0. 253E+03	0. 256E+03	0. 260E+03
0. 675E-02	0. 182E+03	0. 194E+03	0. 203E+03	0. 212E+03	0. 214E+03	0. 216E+03
0. 724E-02	0. 157E+03	0. 165E+03	0. 171E+03	0 178E+03	0. 178E+03	0. 180E+03
0. 776E-02	0. 135E+03	0. 140E+03	0. 144E+03	0. 149E+03	0. 149E+03	0. 150E+03
0. 832E-02	0. 116E+03	0. 119E+03	0. 122E+03	0. 124E+03	0. 125E+03	0. 125E+03
0. 891E-02	0. 997E+02	0. 101E+03	0. 103E+03	0. 104E+03	0. 104E+03	0. 104E+03
0. 955E-02	0. 855E+02	0. 861E+02	0. 866E+02	0. 871E+02	0. 871E+02	0. 872E+02
0. 102E-01	0. 730E+02	0. 730E+02	0. 730E+02	0. 730E+02	0. 730E+02	0. 730E+02
0. 110E-01	0 620E+02	0. 617E+02	0. 615E+02	0. 613E+02	0. 613E+02	0 613E+02
0. 118E-01	0. 526E+02	0. 521E+02	0. 518E+02	0. 515E+02	0. 515E+02	0. 514E+02
0. 126E-01	0. 444E+02	0. 440E+02	0. 437E+02	0. 433E+02	0. 433E+02	0. 432E+02
0. 135E-01	0. 374E+02	0. 370E+02	0. 367E+02	0. 365E+02	0. 365E+02	0. 364E+02
0. 145E-01	0. 315E+02	0. 312E+02	0. 309E+02	0 307E+02	0. 307E+02	0. 306E+02
0. 155E-01	0. 264E+02	0 262E+02	0. 260E+02	0. 258E+02	0. 258E+02	0. 258E+02
0. 166E-01	0. 222E+02	0. 220E+02	0. 219E+02	0. 218E+02	0. 218E+02	0. 217E+02
0. 178E-01	0. 186E+02	0. 185E+02	0. 184E+02	0. 183E+02	0. 183E+02	0. 183E+02
0. 191E-01	0. 155E+02	0. 155E+02	0. 155E+02	0. 154E+02	0. 154E+02	0. 154E+02
0. 205E-01	0. 130E+02	0. 130E+02	0. 130E+02	0. 130E+02	0. 130E+02	0. 130E+02
0. 219E-01	0. 109E+02	0. 109E+02	0. 109E+02	0. 109E+02	0. 109E+02	0. 109E+02
0. 235E-01	0 915E+01	0. 917E+01	0. 918E+01	0. 919E+01	0. 920E+01	0. 920E+01
0. 252E-01	0 768E+01	0. 770E+01	0. 772E+01	0. 773E+01	0. 773E+01	0. 773E+01
0. 270E-01	0. 645E+01	0. 647E+01	0. 648E+01	0. 650E+01	0. 650E+01	0. 650E+01
0. 290E-01	0. 542E+01	0. 544E+01	0. 545E+01	0. 546E+01	0. 546E+01	0. 546E+01
0. 310E-01	0. 456E+01	0. 457E+01	0. 458E+01	0. 459E+01	0. 459E+01	0. 459E+01
0. 333E-01	0. 384E+01	0. 385E+01	0. 385E+01	0 386E+01	0. 386E+01	0. 386E+01
0. 356E-01	0 323E+01	0. 324E+01	0. 324E+01	0. 325E+01	0. 325E+01	0. 325E+01
0. 382E-01	0. 273E+01	0 273E+01	0. 273E+01	0. 273E+01	0. 273E+01	0 273E+01
0. 409E-01	0 230E+01	0 230E+01	0. 230E+01	0. 230E+01	0. 230E+01	0. 230E+01
0. 439E-01	0. 194E+01	0 194E+01	0. 194E+01	0. 194E+01	0. 194E+01	0. 194E+01
0. 470E-01	0. 164E+01	0. 164E+01	0. 164E+01	0. 163E+01	0. 163E+01	0. 163E+01
0. 504E-01	0. 138E+01	0 138E+01	0. 138E+01	0. 138E+01	0. 138E+01	0. 138E+01
0. 540E-01	0. 117E+01	0. 117E+01	0. 117E+01	0. 117E+01	0 117E+01	0. 117E+01
0. 579E-01	0. 993E+00	0. 992E+00	0. 992E+00	0. 991E+00	0. 991E+00	0. 991E+00
0. 621E-01	0. 843E+00	0. 843E+00	0. 843E+00	0. 842E+00	0. 842E+00	0. 842E+00
0. 665E-01	0. 718E+00	0. 718E+00	0 718E+00	0. 718E+00	0 718E+00	0. 717E+00
0. 713E-01	0. 613E+00	0 613E+00	0 613E+00	0. 613E+00	0. 613E+00	0. 613E+00
C. 764E-01	0. 525E+00	0. 524E+00	0. 524E+00	0. 524E+00	0. 524E+00	0. 524E+00
0 819E-01	0 450E+00	0. 450E+00	0. 450E+00	0. 450E+00	0. 450E+00	0. 450E+00
0. 878E-01	0. 388E+00	0. 388E+00	0 388E+00	0. 388E+00	0. 388E+00	0. 388E+00
0. 941E-01	0 335E+00	0. 335E+00	0. 335E+00	0. 335E+00	0. 335E+00	0. 335E+00
0. 101E+00	0. 290E+00	0 290E+00	0 290E+00	0. 290E+00	0. 290E+00	0. 290E+00
0. 108E+00	0 251E+00	0 251E+00	0. 251E+00	0. 251E+00	0. 251E+00	0. 251E+00
0. 116E+00	0 218E+00	0 218E+00	0 218E+00	0. 218E+00	0 218E+00	0. 218E+00
0. 124E+00	0. 190E+00	0 190E+00	0 190E+00	0. 190E+00	0 190E+00	0. 190E+00
0. 133E+00	0. 165E+00	0 165E+00	0. 165E+00	0. 165E+00	0 165E+00	0. 165E+00
0 143E+00	0 144E+00	0. 144E+00	0 144E+00	0 144E+00	0. 144E+00	0. 144E+00
0 153E+00	0 126E+00	0. 126E+00	0 126E+00	0. 126E+00	0 126E+00	0 126E+00

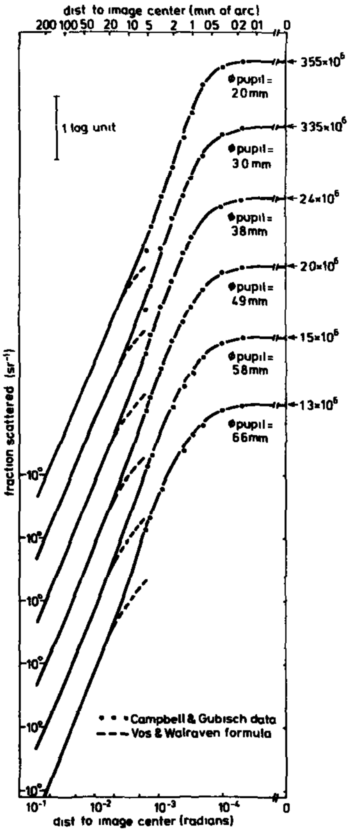

Fig. 1. Light profiles of the foveal image of a white point source for various pupil sizes. Subsequent relations are shifted downward over one log unit each time. Figures along the ordinate indicate absolute values. The drawn lines represent the best fit as tabulated in Table 1. They coincide with the experimental Vos/Walraven straylight relation for scatter angles above about 15′, but have a steeper slope where the latter can be considered indeed as an extrapolation.

100%. This was done by a few successive approximations and the results are given in Fig. 1 and Table 1 for the same pupil sizes as used by Campbell and Gubisch, and for distances θ from the image centre up to 0·153 rad (≈9°). For larger θ values, equation (1) can be used.

As a matter of fact, the deviation for 2 mm pupil size, between the drawn curve and the experimental Vos/Walraven straylight curve, is negligibly small at $\theta = 0{\cdot}15°$, the under-limit of the validity domain of equation (3). For larger pupil sizes the drawn curve increasingly exceeds the interrupted course, in accordance with the decreasing quality of the "image proper" and with the fact that the Vos/Walraven relation pertains only to a 2-mm pupil size.

From these data, cumulative light distributions were derived by numerical integration. The results, in the form of curves giving the fraction of the light content within radius θ from the image centre, are presented in Fig. 2. These graphs show, for instance, that, depending on pupil size, half of all light that reaches the retina falls further than 1′–3′ from the image centre.

The data of Figs. 1 and 2, and of Table 1 can, of course, not be considered as exact descriptions of a "normal" eye, as the accuracy of the numerical data might suggest. They can be considered, however, as a useful description of ocular imagery for a standard observer, much like the CIE tables, as used in the domain of colorimetry and photometry.

DISCUSSION

The results obtained here deviate from other data in that they rest on realistic estimates of the amount of entoptic straylight. Sliney and Freaser (1973) recently signaled the uncertainty of current spread functions in this respect. They needed these spread functions to estimate the risks of laser radiation for the retina. Obviously, smaller spread functions result in higher central intensities and thus in greater danger for retinal burn.

In the literature on this subject, data are usually expressed in terms of the effective size of the foveal image and for that reason we will translate the above obtained data in these terms.

The effective image size, d_{eff}, is defined as the diameter of a uniformly lit image with top intensity,

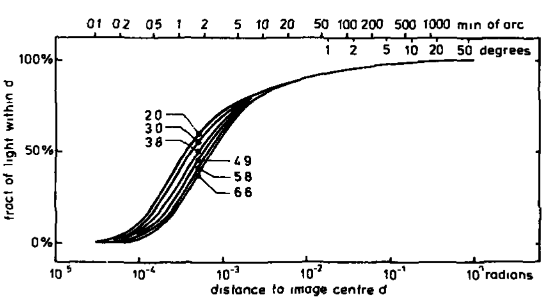

Fig. 2. Cumulative distribution of light within distance *d* to the image centre of a white point source.

I_{max}, equal to that of the real retinal image:

$$I_{max} \cdot \frac{\pi d_{eff}^2}{4} = 1, \quad \text{or}$$

$$d_{eff} = \frac{2}{\sqrt{(\pi I_{max})}} \text{ rad} = \frac{3880}{\sqrt{(I_{max})}} \text{ min of arc.} \qquad (4)$$

With equation (4) it is easy to convert the first line data of Table 1 to a d_{eff} vs pupil size relation for a white point source. This relation is shown in Fig. 3, together with three other comparison curves, i.e.

(i) a similar relation based on the Campbell and Gubisch data, that does not take into account the entoptic straylight (curve taken from Sliney and Freasier, 1973);

(ii) a relation also taken from Sliney and Freasier, calculated for the case of an ideal diffraction limited white point image;

(iii) a curve, calculated by van Meeteren (1974) for an ideally focussed monochromatic point source, on the basis of experimental data on the spherical abberrations of the human eye and taking into account the modulation transfer function of the retina according to Ohzu and Enoch (1972). As mentioned before, similar calculations for white light agree well with the Campbell and Gubisch data.

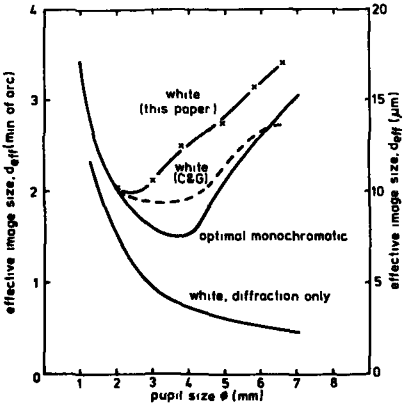

Fig. 3. The effective size of the retinal image of a point sources calculated on the basis of various assumptions. *For* details see text.

The diffraction-only curve is merely shown as a reference curve. It shows the resolution obtainable with monochromatic light, for an optically ideal eye. It is clear that this maximum resolution is never reached with natural pupil sizes. The upper curve, on the other hand, which is based on the before given considerations and calculations, can be considered as the most realistic description of the optimally focussed foveal image of a white point source.

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3.1 DISCOUNTING THE BACKGROUND—THE MISSING LINK IN THE EXPLANATION OF CHROMATIC INDUCTION

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Abstract—Using a cancellation technique (maintaining a pure yellow hue) chromatic induction was measured in the configuration of a 30′–90′ annular test field fully surrounded by a 7° red inducing field. Analysis of these data revealed the hitherto unrecognized fact that the part of the light that the test stimulus has in common with the surround does not contribute to its perceived hue. In addition to this, in essence, subtractive effect of the inducing field it was found that the latter also causes a (colour-selective) change of gain, consistent with the much disputed von Kries coefficient law. The often reported invalidity of the latter should be attributed to the fact that in the past no allowance has been made for the aforementioned differencing mechanism.

I. INTRODUCTION

Although chromatic induction (adaptation) has been a subject of prime interest throughout the history of vision research, this phenomenon is but partly understood. All that can be said is that induced hue shifts can be described in terms of selective sensitivity changes of antagonistic colour systems. The nature of the specific response reducing mechanism(s) involved, however, is still subject of speculation. Helmholtz (1866), one of the first investigators who tried to put light adaption on a quantitative basis, concluded that the effect of adaptation is the same as if the light input to the receptors is attenuated by a certain factor. This conclusion carries the important implication that the attenuation should take place at a neural stage where the nervous response is (still) linearly related to the light absorbed. In order to explain *chromatic* adaptation, von Kries (1905) simply expanded Helmholtz's (input) attenuation principle to trichromatic vision. In his so-called coefficient law he postulated separate attenuating (gain) mechanisms in each receptor system. Furthermore, the gain factor, or coefficient, of each system was supposed to be determined only by the light absorbed by that system. As for the specific relationship between the gain factor and the intensity of the adapting light, linearity has been assumed in most colourimetric studies in which a so-called von Kries transformation was applied to the data (cf. Terstiege, 1972); however, a nonlinear dependence of gain factor on adapting intensity has also been proposed (e.g. Hunt, 1958).

An important corollary of the coefficient principle is that dim and bright stimuli should be attenuated in the same proportion. For that reason the coefficient law is also known as the proportionality rule. However, it seems well established by now that this rule is quite invalid (e.g. Walters, 1942; MacAdam, 1955, 1956; Hurvich and Jameson, 1958; Heinrich, 1969; Jameson and Hurvich, 1972), the general finding being, that bright stimuli are attenuated less than dim stimuli. This is what also should be expected on the basis of another "rule", i.e. Kirschmann's third law of colour contrast (Kirschmann, 1891). This law states that colour contrast is at a maximum when luminance contrast is at a minimum. So, in the case of an inducing field surrounding two test stimuli, one much brighter than the inducing field (high contrast), the other only slightly brighter (low contrast), one observes the largest hue shift in the latter stimulus. In contradistinction, the proportionality rule would have predicted that both stimuli should exhibit the same hue shift.

The failure of the proportionality rule might be taken as indicating that the attenuating principle, as incorporated in the coefficient law, is incorrect. This view was adopted by MacAdam (1961, 1963), who was lead therefore to an alternative scheme in which adaptation is accomplished by response compression rather than attenuation. Hurvich and Jameson (1958), on the other hand, attributed the invalidity of the proportionality rule to the presence of a second process, consistent with a subtractive operation (cf. Jameson and Hurvich, 1972).

The present study proves the latter view to be correct. However, the nature of the inferred subtractive process appears to be of such a surprising simplicity, that only a slightly modified version of the von Kries coefficient law may already suffice to account for the present data.

II. METHODS

1. *General setting*

A yellow (annular) testfield was presented in the centre of a red surround (monocular viewing condition, steady fields, free fixation). Various combinations of test and surround intensities were presented, the separate intensities respectively covering ranges of *ca.* 4·5 and 4 log units.

The effect of chromatic induction was measured with the simple but sensitive cancellation method of maintaining a pure yellow hue of the testfield (for further details see later). Thus a set of data was obtained specifying the spectral composition required for a yellow hue of the testfield under a wide variety of luminance contrasts as well as absolute light levels.

2. *Apparatus*

The optical system used was essentially the same as reported before (Walraven, 1973). It consisted of a three-channel Maxwellian view system (2 mm artificial pupil); two channels feeding into a 60′–90′ annular testfield, and one into the 7° circular adaptation field. In this arrangement, with the adaptation field present at both the inside and outside of the annulus, the eye is maximally exposed to the adapting light when scanning the stimulus pattern.

The testfield was presented *superimposed* on the background, an arrangement that ensures a perfect contiguity between testfield and surround. The (incremental) annulus consisted of a mixture of green light (ΔG) and red light (ΔR), the latter being of the same wavelength composition as the surround (R_s). So, the total amount of red light in the test-stimulus is given by $R = R_s + \Delta R$ (see Fig. 1).

The two red beams that were respectively used for the test increment and the background (ΔR and R_s) originated from identical light sources (12 V, 100 W tungsten–iodine lights run at 8 A), and passed through identical filters (Schott RG5), resulting in light with a dominant wavelength $\lambda_d = 660$ nm. The green beam (ΔG) was obtained by passing light from a tungsten ribbon filament bulb (colour temp. *ca.* 2600°K) through two Kodak Wratten Filters No. 61, resulting in light with $\lambda_d = 540$ nm. Light intensity was controlled with Agfa neutral density filters and two counter-rotating circular neutral density wedges. The luminosity of the three beams was determined with the aid of a calibrated lux meter placed in the exit beam of the apparatus. The maximal retinal illuminances used for respectively testfield and surround was *ca.* 30,000 and 7000 td.

3. *Maintaining a pure yellow*

As in previous studies (DeValois and Walraven, 1967; Walraven, 1971) no reference stimulus was used for maintaining a yellow hue of the testfield. Absolute judgements were made, hereby adjusting the test stimulus until it looked neither reddish nor greenish. This method turned out to be very reliable—deviations from the mean were always less than 0·05 log unit—which is not that surprising when considering that absolute judgements of pure yellow have been found to be confined to an extremely narrow region of the spectrum (e.g. Hubbard and Dimmick, 1939; Thomson, 1954; Beare, 1963; Yager and Tailor, 1970; Siegel and Siegel, 1971). In the carefully controlled experiments of Thomson (1954), the pure yellow range turned out to be restricted to a wavelength band of less than 3 nm, with a day-to-day variability of only 0·7 nm.

We preferred this method above the conventional haploscopic matching technique not only because of its reliability, but also since we (DeValois and Walraven, 1967), and others (Gestrin and Teller, 1969) have shown that the colour of the reference field seen by the nonadapted eye can be affected by the adaptive state of the other eye.

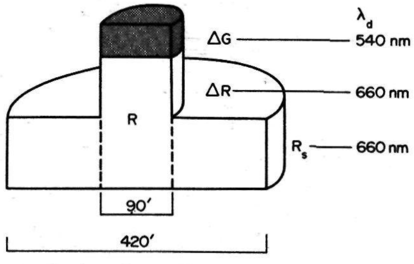

Fig. 1. The intensity profile of test and adaptation field (for simplicity the hole in the annular testfield is omitted). ΔR and ΔG represent the two incremental testfield primaries. They are superimposed on the surround R_s. The total amount of red light in the testfield ($\Delta R + R_s$) is denoted by R.

4. *Procedure*

After an initial 10 min of dark adaptation the stimulus pattern was presented. After being fully adapted to the background pure yellow settings were made by varying the intensity of the incremental red component, ΔR, of the red–green light mixture. Settings were made for nine intensities of ΔG, increasing the latter in steps of *ca.* 0·5 log unit. The intensity of the background (R_s) was kept constant during a series. In total nine background intensities, separated by *ca.* 0·5 log unit intervals, were used. In addition one series was run without background.

Test and adaptation field were presented simultaneously and *continuously*. The observer freely scanned the stimulus pattern, making at least five settings after being fully adapted to the specific stimulus condition.

5. *Rationale of the experiments*

Maintaining a yellow hue of the testfield implies, according to general belief, that the test stimulus is kept balanced with respect to the sensitivities of the antagonistic red and green systems. These systems supposedly cancel each others' activities when in equilibrium, leaving the hue response solely to the yellow–blue system. In the lateral geniculate nucleus we find this reflected in the behaviour of the opponent cells; R^+G^- and G^+R^- cells remain silent at the balancing wavelength in contradistinction to the Y^+B^- cells who then show their greatest activity (DeValois, Abramov and Jacobs, 1966).

Adaptation with red light results in a relatively stronger desensitization of the red system relative to that of the green system. This causes the equilibrium stimulus to shift to longer wavelengths (DeValois and Walraven, 1967), thus leaving a larger part of the spectrum for the green system to respond to. The latter phenomenon, which is also evident in the behaviour of the opponent cells (cf. DeValois, 1973; Fig. 2), provides a physiological explanation for the perceived hue in chromatic induction.

If this view is correct, then we are in our experiment actually trying to restore an equilibrium condition (by changing R) that has been disturbed by the action of the red surround R_s. In the context of the von Kries scheme this action of the surround should be one of (differential) attenuation at the earliest level of response processing, i.e. at a stage where the response is still linearly related to the stimulus.

III. RESULTS

1. *The (in)validity of the von Kries coefficient law, or the all-importance of transients*

Figure 2 shows the separate amounts of green and red light (including that furnished by the background) that together yield a pure yellow when presented in the centre of red surrounds of various intensities.

Note that, at any given value of ΔG, R has to be increased at subsequent higher light levels of R_s. This is the result of chromatic induction. As a measure of the strength of this effect, one may take the vertical distance from each point to the diagonal. This distance represents the log of the factor by which the initial amount of red light in the mixture has to be multiplied in order to obtain yellow, or in other words, to make it equivalent to ΔG. Clearly the induction effect is relatively less pronounced at high values of ΔG, that is, at high testfield intensities. In the latter condition R may stay fairly close to its initial value

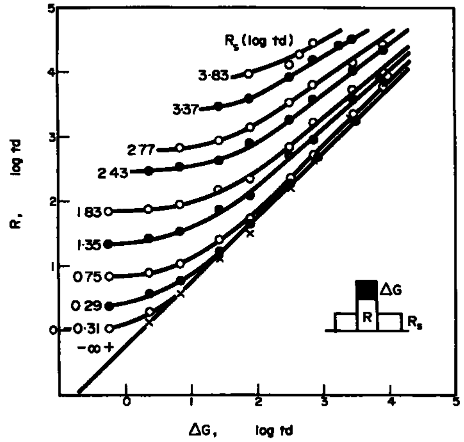

Fig. 2. Relation between the amount of red and green light (R and ΔG) required for obtaining a yellow hue of the testfield, for various intensities of the surround (R_s). At the highest background intensities the curves stop at a certain minimum value of ΔG, because at the next lower value of ΔG the testfield is below (increment) threshold.

(indicated by the crosses) that is required for neutralizing ΔG.

This result is at variance with the von Kries coefficient law since the latter would predict that the effect of the surround would be the same, irrespective of the intensity of the testfield (proportionality rule). What should have been found, then, are lines of constant R/G, i.e. straight lines with slope 1, like the one drawn through the data in the no-surround condition (crosses).[1]

In Fig. 2 we have treated the data in terms of a test field surrounded by an annulus, which is the way in which chromatic induction data have always been analysed. Quite a different picture emerges, however, when treating the data as an increment on a background. This is shown in Fig. 3 where we now plotted ΔR vs ΔG, instead of R vs ΔG.

The data, plotted in this way, speak for themselves. The fact that they all can be fitted reasonably well by straight lines with a slope of 1, implies that for any intensity of the incremental testfield, the spectral composition that is required for equilibrium yellow is fixed, and determined only by the intensity of the background ($\Delta R/\Delta G = f(R_s)$). It turns out, therefore, that the coefficient law is quite valid, provided that it is applied only to the *incremental* part of the test stimulus.

Considering that, given a fixed background, hue invariance is associated only with invariance of $\Delta R/\Delta G$, and *not* of $R/\Delta G$,[2] leads to the logical conclusion that only the incremental stimulus components contribute to colour perception. This conclusion is also consonant with the results from recent studies in brightness contrast, which show that only the incremental or decremental part of the stimulus pattern constitutes the relevant physical correlate for the perception of brightness (Whittle and Challands, 1969; Whittle and Swanston, 1974).

The finding that only the incremental stimulus component determines the colour of the testfield is of interest in connection with the results from experiments on stabilized vision. From these we know that visual perception requires the repeated on and off switching of the receptors (or more central elements), and is only triggered therefore by the discontinuities (transients) in the stimulus pattern. This does not necessarily imply, of course, that it is just the transient or difference signal which correlates with what we see. It is conceivable that, in the case of a background B, with incremental testfield ΔB, the transient information is merely a prerequisite for seeing *at all*. So, the perception of the test field, although triggered by ΔB, may in principle still be related to $\Delta B + B$. The present data suggest, however, that it is indeed only the information contained in ΔB, that enters perception; B merely seems to be effective in setting the gain of the system.

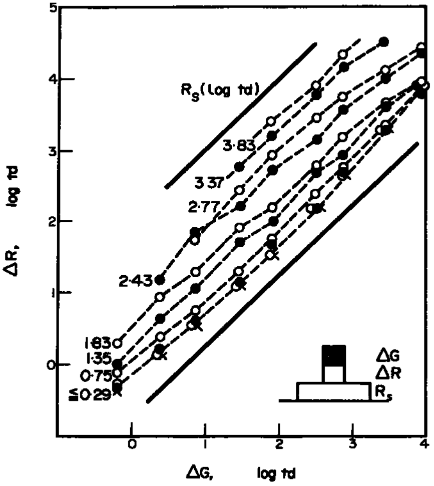

Fig. 3. Relation between the amounts of *incremental* red and green light required for obtaining a yellow hue of the testfield, for various intensities of the surround (R_s). The drawn parallel lines have slopes of 1, and thus indicate $\Delta R/\Delta G = C$.

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[1] Actually slight deviations from $R/\Delta G = C$ may be expected since the data in the *no-surround* conditions already show such tendency. What happens is that relatively more red is required for both low and high intensity yellow settings. At high intensities, in the order of 10^4 td, this effect has been observed before, i.e. in the break-down of the Raleigh match (e.g. Wright, 1936; de Vries, 1948), where it has been explained in terms of altered selfscreening properties of the bleached receptor pigments (cf. Brindley, 1953). That the effect also occurs at low intensities (near photopic threshold) might be due, perhaps, to rod intrusion or simply to noncongruent red and green stimulus–response relationships (cf. Savoie, 1973).

[2] For instance in the condition $R_s = 1{\cdot}83$ log td (Fig. 2), one easily verifies that the red/green ratio of the whole testfield, $R/\Delta G$, respectively takes values of *ca.* 100 and 2, when going from the lowest ($\Delta G = -0{\cdot}2$ log td) to the highest ($\Delta G = 3{\cdot}5$ log td) testfield intensity. In terms of wavelength this represents a shift of more than 50 nm!

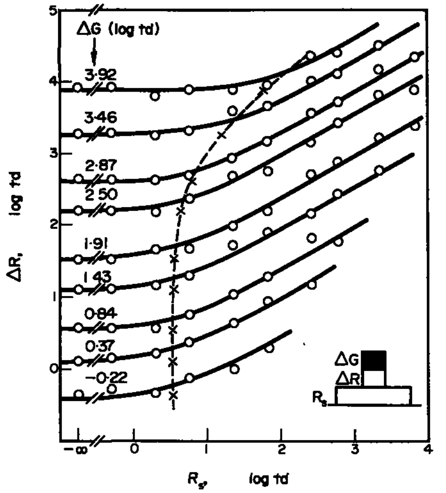

Fig. 4. Retinal illuminance of the red increment (ΔR) required to neutralize a fixed green increment (ΔG), when superimposed on a background of increasing intensity. The data are fitted by functions that are derived from a single curve, shifted only vertically and horizontally. Crosses indicate the intersections of the asymptotes of each curve.

It should be realized that ΔR and ΔG contain all the transient information in the test stimulus, since they were superimposed on R_s. If we had presented the surround as an annulus, using the same 660-nm red again, but a different red for the test stimulus, then the situation would have been quite different. In that case we should first have to express the stimulus pattern into quantum catches at the receptor level, before being able to translate annulus plus testfield into background plus increment.

2. *The role of the background*

Having established that a background exerts a fixed (differential) attenuating effect on the incremental test stimulus ($\Delta R, G$) the next step is to determine how this effect is related to the intensity of the background light. In the next figure (Fig. 4) we plotted therefore R_s as a variable, ΔG being the parameter now. In this way, taking in fact vertical cross-sections through the data of Fig. 3, we should find the function that relates the (differential) gain factor (von Kries coefficient) to the intensity of the surround. If the sole function of the background is to change the gain, independent of the (incremental) testfield intensity, then all the data should be fitted by a single function.

The data points in Fig. 4 can indeed be fitted by a single function. They were drawn along the same template, shifted only in horizontal and vertical direction. The vertical shift corresponds to R_0, the *initial* amount of red light required for neutralizing ΔG ($R_0 \approx 0{\cdot}5\,\Delta G$). The horizontal shift is due to the fact that the initial "increment", R_0, may still suffice to cancel ΔG, as long as the background is still below a certain criterion level. So, at high test field intensities (high ΔG values) it takes more light before the background starts to become effective.

It is of interest that this criterion shift of the background follows a course (see the dotted line), that can be reasonably fitted by a threshold vs intensity curve, i.e. the *threshold for* R_s to become effective, at increasing intensities of the *testfield*. The function has a "Weber fraction" of *ca.* 1%. So, R_s starts to affect R when its brightness corresponds to 1% of ΔR. This is a value of the order of magnitude to be expected for a genuine t.v.i. curve. It seems likely, therefore, that R_s indeed does not become effective until it exceeds the amount of light that is required for a just noticeable increase of R. This kind of behaviour would make sense in a mechanism that processes only the differences (transients) between adjacent stimuli. To perform such an operation the visual system must be able to recognize what the stimuli have in common. If that common part—in our case R_s—is too small to evoke a j.n.d. (at the side of the testfield), then it does not "exist", and consequently, cannot be subtracted or otherwise influence the test stimulus. The same background may be recognized as such, however, by a low intensity testfield, and manifest itself accordingly. In this context it is of interest that here again we have found a parallel with brightness contrast, since exactly the same phenomenon can be observed there, particularly in the constant-brightness curves of Whittle and Challands (1969).

The results just discussed necessitates a second, although minor, modification of the already modified coefficient law. Strictly speaking the latter only applies as long as the curves in Fig. 4 are not laterally shifted, i.e. for ΔR values up to 2–3 log td. At higher intensities it takes gradually more light before the surround gets a grip on the testfield. This is reflected in Fig. 3 by the converging tendency of the data (towards their no-surround values) in conditions where the testfield intensity is very high (indicated by a high ΔG value) compared to that of the surround. Deviations from parallelity (and hence, from the (modified) coefficient law) do not become appreciable, however, until the luminance ratio between testfield and surround is in excess of about a factor 100. So, under natural conditions where contrasts (reflectance ratios) will in general be much lower, the proportionality rule should hold quite well, provided it is applied only to the transient stimulus.

Since all curves shown in Fig. 4 pertain to conditions in which ΔG was constant, a change in ΔR (and thus in $\Delta R/\Delta G$) connotes a change in the sensitivity of the red system relative to that of the green system. The (single) function we used to fit the data might be taken as representing the intensity dependence of the gain factor (coefficient) of the red system only, were it not for the fact that we can hardly expect that the green system is completely unaffected by the red surround. We are probably dealing, therefore, with a differential gain vs intensity function of the red and green systems. It should be realized, however, that this function is not a very exact indicator of differential gain changes in the physiological substrate, since neither the red nor the green light we used did exclusively stimulate the corresponding colour systems. Consequently, the further analysis of this function becomes rather involved, and therefore, will be attended to in a future paper. Still, one conclusion can be drawn already, namely that the relationship between gain factor (coefficient) and intensity cannot be a proportional one; at least, not over the whole intensity range. If it were, an increase of the background intensity should cause the gain factors of the red and green system to increase at the same rate, and hence, no differential gain change should be expected. This argument holds true whether we apply the coefficient law to the incremental stimulus only, or to the whole stimulus. A linear form of the von Kries hypothesis is intrinsically incapable, therefore, to account for luminance dependent chromatic induction effects.

3. *Ingredients for a model*

Recent physiological studies have shown that gain changes, already take place at the receptor level (Glantz, 1971, 1972; Norman and Werblin, 1974; Baylor and Hodgkin, 1974). The receptor adaptation resulting from background illumination appears to result from a partial decay (re-set) of the initial potential evoked by the background light. The origin of this mechanism is still obscure. Possibly, it involves the removal, presumably by an autocatalytic reaction, of the light evoked substance that, by blocking the ionic channels of the receptor, is responsible for the electrical response of the latter (e.g. Baylor and Hodgkin, 1974). Whatever the mechanism involved, it hardly seems to affect the amplitude vs response function of the receptor, but only causes it to shift towards higher intensities. In other words, its action is similar to that of putting a filter in front of the receptors. So, the main postulate of the coefficient law appears to have a sound physiological basis after all.

The present data are quite compatible with such a scheme, but with the important addition that the contribution of the background signal is somehow subtracted out. Thus, in the case of a background I and increment ΔI, respectively stimulating the red and green system with backgrounds I_r and I_g, and increments ΔI_r and ΔI_g (where $(\Delta)I_{r,g}$ represent effective quantum catches) we may write for the transient responses ΔV_r and ΔV_g,

$$\Delta V_r = f\left(\frac{I_r + \Delta I_r}{k_r}\right) - f\left(\frac{I_r}{k_r}\right), \text{ and}$$

$$\Delta V_g = f\left(\frac{I_g + \Delta I_g}{k_g}\right) - f\left(\frac{I_g}{k_g}\right). \qquad (1)$$

Here $V = f(I)$ may represent the response characteristic of the receptor and k_r and k_g are the gain factors (coefficients), acting like filters in the stimulus beam. As pointed out before, the latter should be nonlinearly related to the intensity of the background $(I_{r,g})$.

On the other hand, it seems very likely that the receptor response (V) should be linearly related to the stimulus intensity at least for the intensity range investigated here. Consider in this respect our finding that the colour of the testfield is determined only by the incremental stimulus, $\Delta I_{r,g}$. This implies that the visual system must be capable of separating the incremental input from the total input. Such a differencing operation seems possible only as long as the response is (still) proportional to the stimulus. Assuming at least approximate linearity, which, as will be discussed henceforth, actually does not seem to be such a tall assumption, our former expression for the colour signal $\Delta V_{r,g}$ reduces to

$$\Delta V_r = c_r/k_r . \Delta I_r, \text{ and } \Delta V_g = c_g/k_g . \Delta I_g \text{[3]} \qquad (2)$$

in which $c_{r,g}$ is just a constant of proportionality.

The surprising simplicity of the model put forward so far, derives mainly from our assumption that there must be a good deal of linear processing going on in the visual system. The fact that the intensity of the incremental stimulus may be increased over more than 3 decades without appreciable changes in the required red/green equilibrium ratio ($\Delta R/\Delta G$) suggests that linear processing extends over at least a similar intensity range. This conclusion is corroborated by the results obtained by Alpern, Rushton and Torii (1969, 1970), who showed, on the basis of psychophysical evidence and ERG measurements, that the receptor output may be linearly related to light intensity over at least 3 log units.

Linearity is no longer observed, of course, when the receptor starts to saturate. The response functions recorded from physiological preparations usually take the form

$$V/V_{\text{max}} = I^n/(I^n + \sigma^n) \qquad (3)$$

in which σ corresponds to the half-saturating intensity. It follows that linearity requires in the first place the exponent n to be close to unity. This has indeed been found in various studies (e.g. Baylor and Fuortes, 1970; Penn and Hagins, 1972; Dowling and Ripps, 1972; Norman and Werblin, 1974), although n may vary depending on the stimulus condition used, and response parameter studied (e.g. Normann and Werblin, 1974; Baylor, Hodgkin and Lamb, 1974).

A second prerequisite is that the constant σ should not be too small, since the response starts saturating as soon as I becomes larger than σ. The σ values found in most studies dealing with receptor responses, typically ensure proportionality to hold over 2–3 decades. This range may be larger, however, i.e. extended to lower stimulus intensities, depending on what intensity is taken as representing threshold. In this respect one also should consider that the range over which proportionality holds, is determined by the specific response parameter used. For instance, this range may be considerably extended when taking as response criterion the *rate* of rise rather than the peak amplitude (Fuortes and Hodgkin, 1964; Glantz, 1968, 1971; Penn and Hagins, 1972; Baylor *et al.*, 1974). In sum, it appears that the linear processing as inferred from the present data is not inconsistent with what is known about receptor physiology.

IV. DISCUSSION

The main conclusion to be drawn from this study is that a steady chromatic background affects a test stimulus in two ways. Firstly, the part it has in common with the test stimulus is linearly subtracted from

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[3] Since we used a null-response method, our data do not allow any inference as to the specific (antagonistic) fashion in which ΔV_r and ΔV_g may finally determine the hue response.

the latter, thus leaving only the transient component of the stimulus as effective signal for further processing. Secondly, a change of gain takes place consistent with the von Kries coefficient law, the coefficients (gain factors) probably being nonlinearly related to the (background) stimulation of the specific colour systems involved.

The fact that the visual system seems to be capable of performing the aforementioned differencing operation strongly suggests that there exists an approximate linear range in the relationship between stimulus and (receptor) response. Moreover, since this principle is observed over an intensity range of more than three decades, linearity should extend over a similar range. As has already been discussed, this conclusion is not incompatible with recent physiological and psychophysical evidence. On the other hand, the present theoretical framework does not exclude, of course, that nonlinear processing takes place *after* the formation of the $\Delta V_{r,g}$ signal. In fact, such an assumption would already be required for explaining the Bezold–Brücke hue shift (cf. P. L. Walraven, 1961).

The present results may resolve a long standing controversion concerning the validity of the von Kries coefficient law. The dispute finds its origin in the fact that application of this principle *alone*, that is, without making allowance for the differencing process, easily may lead to quite sizeable discrepancies. Ironically, because of this misapplication the coefficient law actually has been discredited most by its own users. Still, the general consensus has always been—and still is, particularly among colourimetrists—that the (wrongly applied) coefficient principle yields a fair first order approximation for predicting induced hue shifts (Terstiege, 1972). This may indeed be true, more or less, in the field of colourimetrics. Most of the research in this field has been prompted by the need for determining the colour rendering qualities of "white" light sources, and therefore, the adapting illuminants employed are usually fairly neutral (e.g. MacAdam, 1955; Burnham, 1959). Under such circumstances only moderate induction effects are obtained, that do not provide a critical test for the validity of the von Kries transformation.

Hurvich and Jameson (1958), already concluded that the failure of the coefficient law should be attributed to the fact that chromatic adaptation involves more than only multiplicative sensitivity changes. They proposed that in addition to the attenuating effect of a background, also a separate "incremental" process has to be considered. The latter, which is attributed to mutual (lateral) interactions between testfield and surround (Hurvich and Jameson, 1964), is supposed to bias the antagonistic colour response mechanisms by increasing the *output* of one opponent response component at the expense of the other (Jameson and Hurvich, 1973). On the other hand, the multiplicative attenuation effect of the surround is thought to differentially affect the *inputs* to the opponent colour mediating channels.

The present data do not necessitate such a distinction, but this is just a side issue anyway. More important is that our results suggest an altogether different approach to a field still infested with disputes going back to Helmholtz and Hering. What should be recognized is that what the experimenter may consider to be a testfield surrounded by an annulus, is treated by the visual system as an increment on a background.

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3.2 COLOUR SIGNALS FROM INCREMENTAL AND DECREMENTAL LIGHT STIMULI

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Abstract—A red stimulus (ΔR) was presented in the centre of a red background (R), either as an increment (ΔR > 0), a decrement (ΔR < 0), or a pseudo-increment (ΔR = 0, but surrounded by a narrow decremental border of varying depth. A green cancellation stimulus (ΔG), coincident with ΔR, was adjusted until the test field looked neither reddish nor greenish, and thus yielded a measure for the strength of the red colour signal at the test field locus. The results are consistent with the hypothesis that chromatic vision is subserved by (colour specific) *difference* signals, which arise from *incremental* discontinuities in the retinal image profile. Decremental inputs seem to feed only into the achromatic system, generating a blackness signal.

Key Words—colour contrast; decrement; colour processing; achromatic signals.

INTRODUCTION

In a previous communication we reported that the perceived (yellow) hue of a test field that is superimposed on a red background, is determined by the spectral composition of the incremental stimulus rather than by that of the increment *plus* background (Walraven, 1976). So, although the background adds physically to the test stimulus, its colour mixing effect is discounted somehow. This finding suggests that the eye performs a differencing operation by which only the colour information contained in the stimulus transient is abstracted. The background seems to be effective only in setting the gain of the various colour systems.

So far our conclusions were based only on *incremental* test stimuli, i.e. red–green mixtures in which the red component, ΔR (which is cancelled by ΔG, the green component), is incremental with respect to the red background (R). We do not know what happens in the case of a test stimulus (ΔR, ΔG) in which ΔR represents a *decrement*, or in other words, takes negative values. All that can be derived from the previous experiments is that reduction of ΔR to zero, or more accurately, to a value below the Weber-fraction, also reduces the red (antagonistic) signal to zero.

The fact that in the case of ΔR > 0 a green test stimulus can be neutralized implies that in this condition red and green signals can interact in an antagonistic fashion. But what happens when ΔR < 0? Do we have to consider the possibility that now *decremental* red signals are processed, which, being of negative sign have an opposite effect on the red/green balance, and thus facilitate the green response? Or may we assume that decremental signals, as opposed to incremental signals, are no longer colour-coded? There is room for many more speculations in this respect but it is clear that the answers can only come from doing the experiment, which is what we set out to do in the first part of this study.

In the second part we studied a slightly more complicated spatial condition. That is, we created a "pseudo-increment" by surrounding the test field locus with a narrow decremental border of variable depth. Such an encircled centre of the background is neither an increment nor decrement when compared to the rest of the background, but may be considered as an increment relative to the decremental border surrounding it. One may assume that in this configuration the adaptive state of the test field locus will hardly differ from that found in the absence of a border. So, on that account, one should not expect the results to be different from those obtained in the condition in which ΔR = 0. That is, the red signal always should be too weak for cancelling the superimposed ΔG probe, even if the latter is brought to threshold. On the other hand, if the pseudo-increment behaves like a "real" increment, we may expect an increasing red signal with increasing depth of the decremental border, and hence a commensurate increase in the amount of cancellation green.

As will be discussed henceforth, the results of the experiments discussed above, allow some interesting inferences with respect to the mechanisms subserving human colour perception.

METHODS

The apparatus (a three-channel Maxwellian view optical system), and technique (maintaining a pure yellow hue) have already been described (Walraven, 1973, 1976), and so a brief summary of the essentials may suffice. A yellow 30′–90′ annular test field, composed of a red component ΔR ($\lambda_d = 660$ nm) and a green component ΔG ($\lambda_d = 540$ nm), was superimposed on a 7° circular red background, R ($\lambda_d = 660$ nm). The observer's task was to maintain a pure yellow hue of the test field (by varying ΔG), or if not possible (see later), to find a grey that looked neither reddish nor greenish. Test field and background were presented simultaneously and continuously, allowing the observer to freely scan the stimulus pattern[1]. No com-

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[1] We found that this presentation mode yields data that are very similar to those obtained with a flashing test field on a steady background. Here, eye movements do the flashing by moving the fovea back and forth over respectively background, and background *plus* test stimulus.

parison field was used, so absolute judgements were made. This method, which is very reliable—deviations from the mean are typically less than 0.05 log unit—was chosen for reasons already discussed before (cf. Walraven, 1976, p. 290). The author served as subject but spot-checks of the data were also made by one naive observer.

In the present study we investigated the cancellation intensity of the red component (ΔR) of the test field when respectively presented as an increment ($\Delta R > 0$), a decrement ($\Delta R < 0$), and a pseudo-increment ($\Delta R = 0$; with the test field surrounded by a 10′ wide decremental border). Hereby, ΔR is specified as the amount of red light in the stimulus that is either above or below the background level.

The various stimulus configurations were obtained by combining the lights in the way shown in Fig. 1. Only the amount of red light below the dashed line was provided by the background light. So, in the case of decrements and pseudo-increments the total background intensity resulted from combining the lights from test and background beam (ΔR and R).

The decremental step size was varied by equating the two red beams for intensity, and inserting calibrated neutral density filters that were complementary in their transmittances. For instance, a 30% transmitting filter in the ΔR beam, combined with a 70% transmitting filter put in the R beam, yields a decremental step of 30% with the intensity of the background (i.e. the sum of the intensities of the two red beams, ΔR and R) held at 30 + 70% = 100%.

The retinal illuminance for each beam was determined by putting a calibrated lux-meter at a known distance (*d*) from the place where the observer's pupil normally would be located; care was taken that the light receiving surface of the meter was completely filled with light. Conversion to trolands was achieved by multiplying the lux-meter reading by a factor $10^6 \cdot d^2$, *d* being expressed in m.

RESULTS

Increments and decrements

Figure 2 summarizes the results obtained with incremental and decremental stimuli. From left to right there is a gradual change from incremental to decremental stimuli (expressed as a percentage of the background level). The amount of green light (ΔG) required for cancelling ΔR, for three background intensities, is plotted along the ordinate. Each data point represents the mean of at least ten ΔG settings, spreading over a range of *ca.* 0.1 log units.

Before discussing the quantitative aspects of these data we first want to draw attention to a rather unexpected finding. It turned out that it was not possible to make the test field appear yellow when it was presented in the decremental mode. The perceived hue was either reddish (when ΔG was too weak) or greenish, with a fairly narrow achromatic transition zone in between. The latter might be called a "pure" grey (as found for object colours) that turned into black at increasing decremental steps. It should be stressed that, under these circumstances, it was definitely impossible to make the test field appear brown, the hue one might have expected, perhaps, in case of a yellowish decrement. Brown was perceived, however, when the red surround was replaced by a white surround.

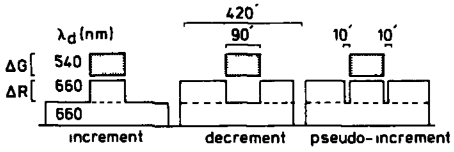

Fig. 1. Intensity profiles of the three stimulus conditions used. The dashed lines show how the (pseudo)-increments and decrements were made by superimposing two fields provided by the (red) test and background beam respectively. The green test stimulus (hatched area) is shown separately for clarity only (all pattern components were presented simultaneously and continuously).

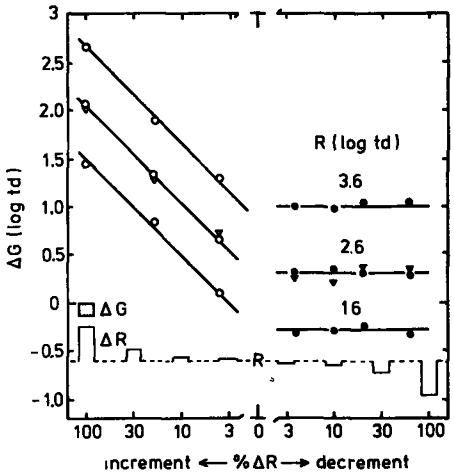

Fig. 2. The amount of green light (ΔG) required for obtaining an equilibrium hue (yellow or grey) when added to red increments and decrements (ΔR) as indicated along the abscissa. The data relate to three different intensity levels of the background (R). Circles refer to data obtained by the author, triangles represent a data sample from a naive subject (NB). Filled symbols refer to grey settings.

As for the condition $\Delta R = 0$, the uniform background, we encountered the problem that when ΔG was decreased in intensity (bringing it close to threshold), the test field not only became less green, but also started to fade away. Under these circumstances, with the test field losing its contour and merging into the background, we were unable to determine a transition point from green to red (if there was any); hence the lack of data points at $\Delta R = 0$.

When we now turn to the data again, and first have a look at the left-hand part of the data, we may conclude that the amount of ΔG required for obtaining equilibrium yellow, has to be proportional to the *incremental* amount of red light (ΔR) at the test field locus (the lines drawn through the data points have a slope of -1, and abscissa and ordinate have logarithmic scales with equal unit size). This result was to be expected on the basis of the findings already obtained in our earlier, more extensive, experiments with incremental test fields (We therefore determined ΔG at only three incremental values of ΔR.) What could not be predicted, however, is that the amount of cancellation light reaches a stationary value when changing over from the incremental to the decremental stimulus mode. This result implies that variation of the amount of red light incident at the test field locus does not result in a *varying* red signal, neither antagonistically nor synergistically; otherwise, this should have been reflected in the amount of required cancellation green.[2]

It is of interest that although the perceived redness of a red decrement may be strongly reduced or completely absent, small decremental steps ($<20\%$) may still look quite reddish. Since the red appearance decreases with increasing decremental step-size one might be tempted to attribute this to a declining input to the red channel. However, since this is not reflected in our ΔG measurements, we would rather attribute this to an increasing blackness signal. Thus the reduction of perceived redness may be imputed to a yielding of redness to blackness, supposedly at a neural level central to the stage of antagonistic colour interactions. (Otherwise, the red/green balance would have been affected, and so would ΔG.) We thus make a distinction between variations in perceived redness that result from a varying input signal (red-excitatory, green-inhibitory), and those resulting from a *constant* input signal, but varying output, due to interaction with blackness signals.

The assumption of an actively generated blackness signal, as already proposed by Hering (1874) squares with the large body of psychophysical evidence that calls for such a concept (Evans, 1964; Jameson and Hurvich, 1964; Heggelund, 1974a, b). Moreover, we also find this reflected in the physiological substrate, i.e. in the on- and off-centre units at the retinal level (e.g. Barlow, FitzHugh and Kuffler, 1957; Krüger and Fisher, 1975), in the Black$^+$ White$^-$ and White$^+$ Black$^-$ cells at the geniculate level (e.g. DeValois, 1972; Krüger and Fisher, 1975), and in the B- and D-neurons at the cortical level (cf. Jung, 1973).

Now that we have assumed that the variation in *perceived* redness in a red decrement is due to intrusion of a blackness signal, we are left with the problem to explain where the red response came from in the first place. We think that the answer can be found in Walls' filling-in principle (Walls, 1954), as demonstrated and analysed in experiments with stabilized vision (Krauskopf, 1963; Yarbus, 1967; Gerrits and Vendrik, 1970). That is, the redness seen in the centre of the background may be attributed to the filling-in or spread of the neural excitation generated at its *outer* border. We know already that this *must* be true for uniform backgrounds ($\Delta R = 0$), the argument being that the central part of the field is actually stabilized (barring gross eye movements). We propose that in the case of a decrement the situation is essentially the same, i.e. no chromatic signals forthcoming from the *inner* border of the background, except for the small residual signal already mentioned before. In addition, however, there are now achromatic (blackness) signals, which neutralize or overrule the filling-in of redness at the test field locus, and the more so, the stronger the decremental stimulation. The same mechanism also may be involved in preventing the *outward* spreading of neural activity [i.e. outside the (outer) border of the background]. We thus think along the same lines as Gerrits (1968), who postulated that neural spreading of border-generated activity is halted by the next border that signals a difference in intensity or colour of the light stimulus.

Pseudo-increments

From the results obtained so far we may conclude that only incremental intensity changes give rise to chromatic signals. So, in the case of a uniform red background ($\Delta R = 0$) and a green increment ΔG, there will be no signals that convey the red colour of the background. Is there a way, other than incrementing the background ($\Delta R > 0$), by which we can put red and green signals on a more equal footing? The obvious answer is that we must provide the red system with a contour of its own. We therefore introduced a decremental border (10′ wide) in the stimulus pattern, separating the test field locus from the surround, and thus obtained what we have called earlier a pseudo-increment.[3]

Figure 3 shows the results obtained with such pseudo-increments ($\Delta'R$), the step size varying along the

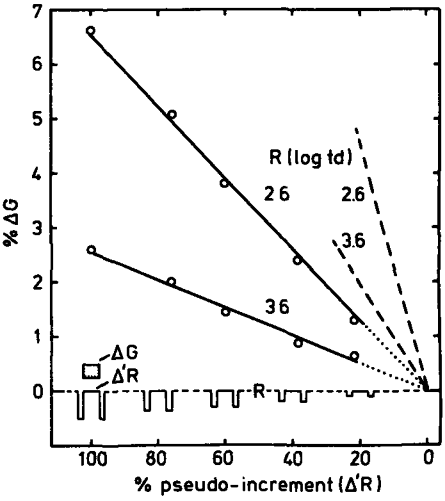

Fig. 3. The amount of green light (ΔG) required for obtaining a pure yellow when added to a red pseudo-increment ($\Delta'R$). Percentages are relative to the background intensity used (R). Dashed lines would fit the data of the previous experiment, for *real* increments, if plotted in this figure.

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[2] Apparently, there must be some (constant) residual signal present, since we find that ΔG *can* be neutralized. It turned out, moreover, that the amount of cancellation green does not correspond to the (increment) threshold intensity—as would be expected if there were no red signal at all—but is about 0.3 log unit more than that. That cancellation with ΔG yields gray rather than yellow suggests that this residual signal is too weak to activate the yellow-blue geniculate cells.

[3] Considerations that have led to this particular choice of border width are, that a narrower border would tend to reduce its effect (partly due to filling up by straylight, and partly because of less stimulation of neural off-centre units), whereas a wider border might affect the adaptive state at the test field locus, and thus introduce an effect we wanted to keep constant for a given background.

abscissa, and the cancellation intensity (ΔG) along the ordinate. Two background intensities were used, the highest (2.6 log td) and second highest (1.6 log td) level from the previous experiment. Both the green incremental step and the red (relative) incremental step are expressed as a percentage of the background intensity employed.

As in the previous experiment we found that ΔG was proportional to the amount of (pseudo-)*incremental* light, and furthermore, that the combination of the two test field components yielded a yellow *equilibrium hue*. So, pseudo-increments behave like real increments. (We now used a linear plot, to better illustrate that ΔG indeed extrapolates to zero—indicating a total absence of an antagonistic colour signal—in the case of a uniform background.)

Another similarity with the results from the previous experiment can be found in the role played by the background. Again, the sole effect of the latter is to differentially attenuate the red and green colour signals. We find this reflected in the slopes of the two lines drawn through the data points. The lower the slope, the stronger the attenuation of the red signal relative to the green signal (a smaller percentage of ΔG may now suffice to cancel Δ'R). The change in (differential) attenuation when going from one background intensity to the other (*ca.* a factor 2.5) corresponds closely to that found in the previous experiment. Due to the different ways of plotting, however, this is not immediately apparent from comparing Figs. 2 and 3. Therefore, we have drawn two more (dashed) lines in Fig. 3, that indicate the slopes of the lines along which the (real) increment data from Fig. 2 would have fallen.

Although real and pseudo-increments behave similarly with respect to the aspects discussed above, there are also two notable differences. First, relative increments are *less effective than real increments* in cancelling ΔG. Under comparable conditions, i.e. same background and same step-size of the (pseudo-)increment, the former are about a factor 4 less effective than the latter (compare with the dashed lines in Fig. 3). Second, increasing the step-size of a pseudo-increment is not attended by a change in its apparent brightness. So, pseudo-increments, as opposed to real increments, do not look different from the rest of the background, as one may readily verify by drawing a black circle (a decremental border) on a piece of coloured paper.

Starting with the latter observation, we may conclude that the brightness of *the pseudo-increment*, as opposed to its cancellation intensity ΔG, is not affected by the presence of the decremental border. In other words, it seems that the on-signals arising at the decremental border, are processed only by the chromatic channels. Maybe the achromatic system only utilizes the signals from the off-centre neurons (in order to code the intensity of the decremental border), and derives the brightness of the pseudo-increment either locally, or by assigning the value obtained by on-centre cells activated by the outer border of the background. This might be achieved by filling-in of this border-generated activity, which is then locally "written over" by the blackness signals from the off-centre neurons stimulated by the decremental border. We must admit, however, that this "explanation" is taylored to fit the present data only, and may have to be changed or abandoned upon further understanding of the mechanisms involved.

Turning now to the second dissimilarity between the real and pseudo-increments, i.e. their difference in cancellation intensity, we suggest that this may be attributed mainly to an incomplete decay of the steady state response during the temporarily switching off of the receptor on-activity by the *(moving)* decremental border. This would cause the "neural image" to be less steeply modulated than one should expect on the basis of the retinal light profile. Consequently, the incremental on-signal, generated at the transition from decremental border to pseudo-increment, should not reflect the actual intensity step, but rather correspond to that obtained by a lower contrast border.

Another factor to be considered in this respect is the contrast lowering effect of straylight, particularly since we are dealing with a narrow decrement (10'). However, a straylight estimate based on the point-spread function derived by Vos, Walraven and Van Meeteren (1970) yields a value of *ca.* 12%[4], which can only account, therefore, for *ca.* 15% of the observed discrepancy in the cancellation intensities of the two types of increments.

DISCUSSION

The results of this study stress the importance of discontinuities in the retinal image as determinants of perceived colour. Perhaps this is a point that hardly needs emphasizing, considering the well known "Mondrian" demonstrations of Land and coworkers (e.g. Land, 1964; McCann, McKee and Taylor, 1976). Traditionally, however, colour vision theories have focused (and most still do) on the rather unnatural condition of a light patch seen in isolation (or juxtaposed to another of the same luminosity), and thus tend to treat the surround dependence of colour as an interesting side-effect (called simultaneous contrast) rather than a consequence of a basic principle of the processing involved.

The dependence of colour processing on spatial luminance transients is best demonstrated in the case of a uniform background (ΔR = 0). We have shown that in this condition the intensity of ΔG, our measure for the red signal forthcoming from the test-field locus, approaches zero (cf. Fig. 3). This may explain a curious aspect of heterochromatic increment thresholds. Stiles (1959) has shown that a green test stimulus, brought to threshold on a red background, is detected only (or almost so) by the π_4 colour system (which we might call the green system, although Stiles has never committed himself to linking his π-systems to colour sensations). This is brought about by the fact that π_5, the red system, is rendered (relatively) insensitive by this background and thus requires more energy than the green system in order to respond to the test stimulus. All this makes sense, but the background itself, being quite above the π_5 threshold,

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[4] We are indebted to Dr. A. M. van Meeteren for his computational efforts in this respect.

should produce a strong red signal *at the test field locus*, that, when combined with the weak π_4 signal from the test stimulus, should produce a reddish rather than a greenish colour. That we find the opposite is now understandable, because we have shown that the test field locus can only produce a red signal when there is a (red) contour to generate it.

The present results suggest that chromatic colour vision is subserved only by *incremental* discontinuities in the intensity profile of the light stimulus; decremental inputs seem to feed only into the achromatic system, generating a blackness signal. The latter, probably encoded in the responses of off-centre neurons, may enable the visual system to respond much quicker (and stronger) to decremental intensity steps than otherwise would be the case if it were to depend only on the relatively slow extinction of preceding ongoing activity. So, rather than having to keep track of the response decay of on-centre cells, the eye can employ the principle of "overwriting" with positive (blackness) signals. This may explain why the reduction in chromaticity that is observed when decrementing a coloured stimulus does not resemble the colour that would result from reducing the intensity of that stimulus seen in isolation. Rather, it appears that the chromaticity of the stimulus is masked, and finally wiped out, by blackness. We thus may also explain, as pointed out before, why a varying appearance of the decremental test field was not attended by a varying cancellation intensity.

If we are correct in assuming that no chromatic signals are forthcoming from a decremental border, we must conclude that the traces of colour still perceived in weak decrements find their origin in the activity generated at the *outer* border of the surround (i.e. the same filling-in process that underlies the perception of the colour seen in the centre of a uniform background). One also should recall in this respect the well known illusionary luminance differences resulting from edge information carried over subthreshold luminance gradients (O'Brien, 1958; Krauskopf, 1963, 1967; Craik, 1966; Cornsweet, 1970). It is of interest that the extrapolated intensity information from such artificial contours is differential rather than absolute (Arend, Buehler and Lockhead, 1971; Arend, 1973). Thus, a contour specifies only the *difference* in the light intensity of two adjoining areas, and not their actual local intensities. Clearly, this is exactly what our results also suggest. This is most conclusively shown in the case of relative increments, since here we varied only the intensity of the decrement surrounding the test field, instead of the intensity of the (pseudo)-increment itself. Thus, eliminating the possible effect of the total quantum catch at the test field locus, we abstracted the effect of the transient only, and found this to determine the cancellation intensity of the increment.

Variations in the cancellation effect of a pseudo-increment are not reflected in its perceived colour or brightness. This is the opposite paradox therefore, as observed with decrements, where we found no variation in cancellation intensity despite large changes in perceived redness and lightness of the decrement. These observations show that a varying percept does not necessarily imply the presence of a varying (potential) colour signal, and vice versa. There are more examples, of course, showing a discrepancy between the appearance of a stimulus and its interactive effect on other stimuli. Best known in this respect is the finding that the increment threshold is unaffected by the apparent (induced) brightness or colour of the background (Cornsweet and Teller, 1965; Burkhardt, 1966; Sternheim, 1970). There is a principal difference, however, between these findings and those discussed here. The former show that the increment threshold is determined by the physical reality at the test field locus rather than by the "aberrant" perception of the background. In the present case, however, there is no conflict between physical reality and the perception. The test field locus becomes less red (with increasing decrement), or does not change at all (with relative increments), all of which is in accordance with the local stimulus situation. After adding ΔG, however, the situation changes, because now colour interactions come into play, interactions that take place only between signals that are generated by incremental intensity transients.

The differencing process we proposed in order to account for the data might be attributed to a temporal scanning mechanism rather than a purely spatial process. The results of stabilized vision experiments, showing the necessity of temporal luminance changes for maintaining perception, have been interpreted as supporting this view (Arend, 1973). However, in an earlier experiment, employing simultaneously flashing test field and background, and thus eliminating temporal interactions, we obtained results that show the same differencing principle operating. That is, we found that although the simultaneously flashed background lowered the apparent brightness of the test field (due to the reduction of contrast) it hardly affected its yellow hue (Walraven, 1973; cf. Fig. 8). This is exactly what should be expected if only the (absolute) spatial transient (which is not affected by a superimposed background) determines the hue of the test field[5]. At the time we did not interpret the data in those terms, but merely stated that colour mixing and colour contrast kept each other in balance. Actually this was true only when the background overlapped the test field by at least 15′, which strongly suggests that the differencing mechanism is subserved by neural units with diameters in the same order of magnitude. Thus, there is every reason to believe that spatial contrast can be abstracted in the spatial domain only, i.e. without a temporal stimulus intercomparison. Very strong evidence for this view is also provided by the fact that the colours seen in Land's two-colour projections (which can be explained only on the basis of spatial interactions) can be seen in flashes as short as 6 μsec (Land and Daw, 1962). We believe therefore, following others (e.g. Gilbert and Fender, 1969; Keesey and Jones, 1967), that temporal luminance changes mainly serve to (re)activate neural units that abstract intensity differences by comparing signals in space rather than in time.

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[5] Fairly weak backgrounds (up to 40% of the test field intensity) and long flashes (500 msec) were used. We do not know whether the complete discounting of the background as found under these circumstances also occurs under conditions that are much different in this respect.

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LETTER TO THE EDITORS

3.3 NO ADDITIVE EFFECT OF BACKGROUNDS IN CHROMATIC INDUCTION

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In an attempt to study chromatic induction with a less complicated stimulus arrangement than is usually the case, Walraven (1976) performed an experiment in which the classical configuration of a test stimulus centred in an annular inducing field was obtained by simply presenting a (yellow) test stimulus as an increment on a (red) background. The main merit of this stimulus arrangement was that it invited (and enabled) a new type of data analysis, in which the test stimulus is no longer treated as a field in the centre of an annular *surround*, but rather as an increment on a *background*, conform the way it was presented. Thus, it could be shown that the visual system processes test and background stimulus separately, hereby subtracting out the additive contribution of the background at the test field locus.

Recently, Shevell (1978) virtually replicated Walraven's experiment, but obtained results that led him to reject Walraven's "discounting of the background" hypothesis. He felt that his study "... clearly demonstrated that for color contrast this view (i.e. Walraven's) is incorrect... (p. 1655)", and arrived instead at a "two-process" explanation, reminiscent of that proposed by Jameson and Hurvich (1972). Walraven's result was dismissed as being "... a special case of the two-process interpretation... (p. 1650)". This calls for some comment of course, hence this reply.

Before discussing the data reported by Shevell, a few words about the experiments. As in Walraven's experiment chromatic adaptation was measured by maintaining a constant (yellow) hue of a 60′-90′ annular test field consisting of a mixture of red (660 nm) light, ΔR, and green (540 nm) light, ΔG, which was presented superimposed on a red (660 nm) background, R. The subject's task was to adjust ΔG, so as to obtain a pure yellow hue of the test field for various values of ΔR and R. Shevell employed three different viewing conditions, called by him the "temporal and transient" case (flashing test stimulus, steady background), the "spatial transient" case (steady test stimulus, steady background, *steady fixation*), and the "temporal transient" case (flashing test stimulus, *spatially coincident* with 2° steady background). Clearly, the two last conditions, in which either temporal or spatial transients are avoided are not representative for normal viewing, and one can hardly expect therefore, that the results obtained in these conditions will reflect the way in which the visual system normally operates. Specifically, the separate processing of the (incremental) test field, as implied in Walraven's hypothesis, might be difficult to realize due to the less distinct spatio-temporal separation between test and background stimulus. This would apply, in particular, at low contrast (small transients), that is, when the (fixed) intensities of the increment ΔR are relatively low compared to the intensity of the background.

As expected, the results obtained with limited transient information (see Shevell's Figs 3 and 5) show deviations from Walraven's proposition (non-additivity), be it only at the two highest of the 6 background intensities that were employed. Here it was found that ΔG did not increase with ΔR, until the latter was fairly large, thus indicating that here the "transient" ΔR is but partly effective as such. Shevell considered the result of these experiments as an unresolved difference between his and Walraven's results, whereas this actually is due to his comparing of different experiments. Exactly the same "unresolvable" differences can be found when comparing some of these results with those from his "spatial and temporal" condition.

As for Shevell's "spatial and temporal" case, this is the condition that actually comes closest to the free-viewing condition employed in Walraven's experiment. In the latter, background and test stimulus were continuously present, but eye movements provided for the necessary transient stimulation, both spatially and temporally[1]. It follows then, that only the data from the "temporal and spatial" condition should be compared to Walraven's results. The data in question are reproduced in Fig. 1, which shows a replot of Shevell's Fig. 7 and Walraven's Fig. 3. (The dotted lines shown in Fig. 1b indicate the intensity region covered in Shevell's experiment.)

In as far as Shevell's data can be fitted with lines of unity slope (45°), they are consistent with Walraven's hypothesis, since the latter predicts

$$\Delta G = \Delta R g(R) \qquad (1)$$

where $g(R)$, the adaptation factor, only depends on the intensity (R) of the background. According to Shevell, however, we should write

$$\Delta G = [\Delta R + f(R)]g(R) \qquad (2)$$

where $f(R)$ represents the additive effect of the background (the second process of the two-process explanation). Note that equation (2) reduces to the same expression as equation (1) for $f(R) \ll \Delta R$.

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[1] In the free-viewing condition, with the fovea fixating respectively background, and test plus background, the eye essentially receives the same stimulation as in the condition with flashing test field and steady background.

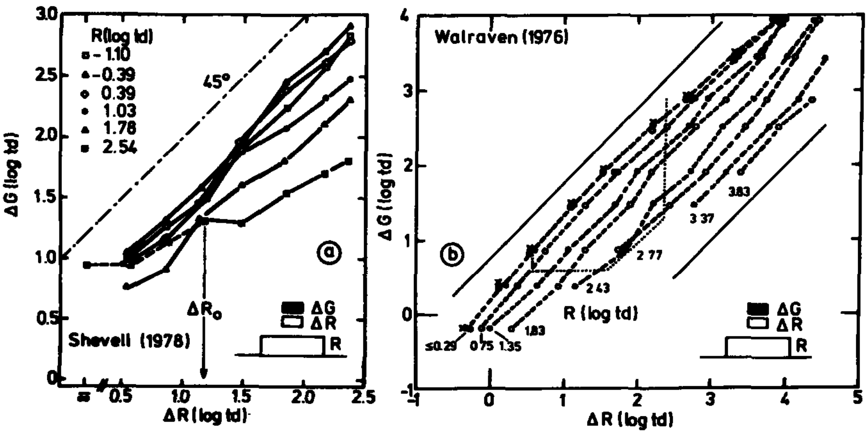

Fig. 1. Relation between the amounts of incremental green (ΔG) and red (ΔR) light required for maintaining a yellow hue of the test field, for various intensities of the steady background (R). (a) Results of Shevell (1978) obtained with flashing test field ("spatial and temporal transient" condition). The dashed curve connects data for which ΔR is below or at increment threshold (indicated by the arrow). (b) Results of Walraven (1976), obtained under free-viewing conditions (implying temporal and spatial transients). The dotted lines indicate the intensity region covered in Shevell's experiment.

Shevell's data (Fig. 1a) are quite similar to Walraven's results, except for some obtained at the highest background intensity ($R = 2.53$ log td), i.e. the filled squares. Here, the line passing through the data for $\Delta R \geqslant 1.5$ log td does not fit the data obtained with lower values of ΔR, i.e. those connected by the dashed curve. Now it is of interest that the latter relate to values of ΔR that are at or even below increment threshold (see the vertical arrow in Fig. 1). This clearly is a rather special situation, and will be discussed separately therefore. As for the remaining data (*ca.* 90% of the total), these do not seem to suggest an explanation in terms of the two-process hypothesis. This can be easily demonstrated by fitting the data points with lines of 45° slope, which enables estimates of $g(R)$ for each of the backgrounds used. Thus, applying equation (1), one can calculate ΔG, for each of the various (fixed) values of ΔR, and compare the calculated and experimental ΔG intensities. This is done in Fig. 2, which shows that there is a fair agreement between experimental and calculated data. There is no need therefore, to invoke a two-process mechanism for explaining these results.

As for the 4 data points not shown in Fig. 2, those for which ΔR was at or below increment threshold (ΔR_0), it should be recognized that in that condition the whole test field is close to threshold as well. Under such conditions it is extremely difficult to judge the colour of the test field (subjects typically may be at a loss to report what they see). There are indications of a vague, hueless impression (an achromatic interval?) at the transition from seeing green (when ΔG is above threshold) to seeing red (when the test field is below threshold). The perception is very unstable, however, and in no way resembles the distinct yellow transition zone that is observed when the stimulus has a clearly visible contour. Training may induce a certain criterion of course, but it is questionable whether that reflects a valid hue judgement or just the response to seeing anything at all. In this respect it should be noted that the results of the two observers in Shevell's study (SS and MB) are quite disparate when $\Delta R \leqslant \Delta R_0$. This is shown in Fig. 3, where the data in question are shown (those of Shevell can be obtained by interpolation from his Fig. 8, which plots ΔG vs R with ΔR as parameter). Also plotted are the data for the zero background condition (filled circles), which shows that SS and MB are quite similar with respect to their yellow settings. So are their settings when ΔR is distinctly visible. But, this is no longer the case when $\Delta R \leqslant \Delta R_0$. Observer SS needs more green, then, in his yellow setting, thus showing a much stronger additive effect.

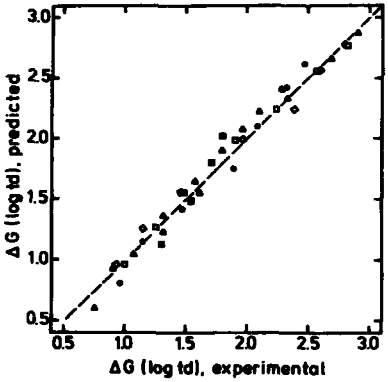

Fig. 2. Comparison of experimental values of ΔG (from Fig. 1b) with those calculated from equation (1) upon substitution of appropriate values of $g(R)$. The calculated ΔG intensities, when plotted in Fig. 1b, would lie on straight lines with slopes of 45°. The 4 values for which ΔR was below or at threshold (ΔR_0), were omitted.

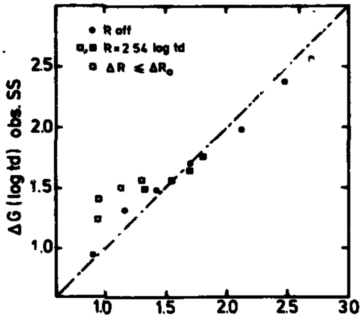

Fig. 3. Comparison of ΔG values collected by observers SS and MB respectively, at $R = 0$ and $R = 2.54$ log td. Open symbols, representing values for which the test field is close to threshold ($\Delta R \leqslant \Delta R_0$), show that in this condition there is less agreement between the two observers.

Shevell's two-process explanation would predict a ΔG vs ΔR relationship similar to the Weber–Fechner relation. That is, at low values of ΔR, where ΔR is small relative to $f(R)$, ΔG should approach a horizontal asymptote at

$$\Delta G = f(R).g(R) = c \tag{3}$$

as can be seen upon substituting $\Delta R = 0$ into equation (2). Shevell remarked that "Since Walraven used ΔG intensity steps of about 0.5 log units, he simply may have skipped over the horizontal and curved portions of the curves (p. 1665)". If that were true, one might expect, then, that in Shevell's "spatial and temporal" condition, where ΔG *was* variable, these missing portions would be clearly manifest. Fig. 1a speaks for itself in this respect; the only evidence for horizontal and curved portions comes from a few (threshold) data, i.e. the dashed portion of the curve for $R = 2.54$ log td. Note that the measurement at $\Delta R = 0$ does not turn up at any of the other background intensities. This is a consequence of the fact (not mentioned by Shevell) that in these instances the mixture of ΔG and R always looked greenish as long as ΔG was not below threshold. This confirms Walraven's proposition that the background only can cancel the green stimulus transient when there is a red stimulus *transient* (i.e. a contour) at the test field locus, to convey the redness of the background. This has been explicitly shown in an experiment (Walraven, 1977) in which the test field locus was surrounded by a decremental border (10′ wide). In that condition the encircled portion of the background (which was called a pseudo-increment, $\Delta' R$), *did* neutralize ΔG, its efficacy being proportional with the depth of the border.

The absence of data in the condition where ΔG is presented alone on the background ($\Delta R = 0$) is casually mentioned in Shevell's description of his experimental procedure ("... often the subject found the $\Delta R = 0$ case to be impossible... (p. 1651)"), but is further not discussed. This is an important point, however. The two-process hypothesis predicts, as is shown by equation (3), that there always should exist a value of ΔG that provides for a yellow hue of the test field, even if $\Delta R = 0$. Actually, this is the only condition in which the two-process explanation might lead to an outcome that is substantially different from that predicted by equation (1) (when $\Delta R \gg f(R)$, equations (1) and (2) yield similar results). Hence, the failure of showing an additive effect (measurable by ΔG) in the condition where it should be most pronounced (when $\Delta R = 0$), provides strong evidence against Shevell's two-process explanation.

In sum, the visual system's ability to process stimulus *transients* only, is reflected in the non-additivity of test and background light, as is also evident in Shevell's study. However, when spatial or temporal transients are more or less avoided in the stimulus pattern, the eye may be less successful in separating transient and continuous information, particularly when contrast is low. This expectation is borne out in the results of Shevell's "temporal transient" and "spatial transient" experiments, where indeed deviations from non-additivity may be observed. Under the less constrained viewing condition of Shevell's "spatial and temporal transient" experiment, however, non-additivity is the rule again, thus confirming Walraven's earlier, more extensive results.

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IV. THE NATURE OF THE FIRST PROCESS

4.1

The Derivation of Nerve Signals from Contrast Flash Data

A Re-analysis

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Abstract. This paper presents a new analysis of the contrast flash data of Alpern et al. (1970a–d). It was prompted by the criticism of Wandell (1976) who pointed out that Alpern et al.,main conclusion, i.e. that the *inhibitory* signal $N^*(\phi)$ elicited by the contrast flash (ϕ) takes the form $N^*(\phi)=\frac{\phi}{\phi+\sigma}$, would imply an unrealistic *excitatory* photo response. The present analysis shows the data to be consistent with an inhibitory signal of the form $N^*(\phi)=\left(\frac{\phi}{\phi+\sigma}\right)^n$.

Introduction

Psychophysical experiments on visual adaptation seldom provide data that can be directly related to the neural transducer function involved. A notable exception in this respect might be found in the work of Alpern et al. (1970a–d). Employing the contrast flash technique, as introduced by Alpern (1965), these authors (to be referred to as A.R.T., following their convention) derived a stimulus response function that takes the same form as that recorded from photoreceptors. The response in question or, as A.R.T. called it, the nerve signal N, is an *inhibitory* response. It is measured in terms of the intensity of an annular contrast flash (ϕ) that is required to bring a (preceding) test flash to threshold. It may be described, according to A.R.T., by

$$N(\phi)=\frac{\phi}{\phi+\sigma}, \tag{1}$$

where σ represents the semi-saturation constant, i.e. the intensity that yields $N=0.5$. Note that for $\phi \ll \sigma$, N is approximately proportional with ϕ.

Equation (1) applies to the dark adapted condition. As for the light adapted state, A.R.T. (1970b) concluded that the effect of a steady conditioning field (θ) is to attenuate N down to the fraction $\theta_D/(\theta_D+\theta)$. Thus the adapted signal would be described by

$$N(\phi,\theta)=\frac{\phi}{\phi+\sigma}\,\frac{\theta_D}{\theta_D+\theta}, \tag{2}$$

where θ_D is a constant, the "dark light" *(eigengrau)* of the eye.

Although A.R.T. presented a large body of data that seemed to support Eqs. (1) and (2), there are nevertheless reasons for concern with respect to the validity of their conclusions. Wandell (1976) has shown that Eq. (1) cannot both describe the excitatory "straight-through" signal N *and* the laterally travelling inhibitory signal (which he called N^*) that actually was measured with A.R.T.'s contrast flash technique. Since A.R.T.'s data analysis is based on the implicit assumption that $N=N^*$, the conclusions derived from their analysis have to be reconsidered. This is the purpose of the present paper. It provides an explanatory framework that distinguishes between an excitatory and an inhibitory signal, the latter being a non-linear transformation of the former. It will be shown that two more assumptions, i.e. a gain control qualitatively similar to that proposed by A.R.T., and a "discounting" of the background (high-pass filtering) as demonstrated by Walraven (1976, 1977), enable accurate numerical descriptions of A.R.T.'s major results.

The main reason for reanalysing A.R.T.'s data is that there is a growing interest in explaining psychophysical measurements of visual adaptation in terms of the properties of the transducer function described by Eq. (1) (e.g. Hood, 1978; Hood et al., 1978; Fulton and Rushton, 1978; Dawis, 1978; Geisler, 1979). In fact, A.R.T. were the first to do so. It is important to know, however, what can, and what cannot be inferred from these data. The criticism of Wandell (1976), although correct, is not very helpful in this respect; it signals the problem, but leaves the data unexplained.

Analysis

The Inhibitory Signal $N^*(\phi)$

In its simplest form, the contrast flash paradigm (for rods) involves the presentation of a brief test flash λ (10 ms) followed after 90 ms by the contrast flash ϕ (100 ms) surrounding (and contiguous with) the test field (see Fig. 1a). The experiment can be performed in two ways; either λ, or ϕ is varied in order to have the test flash just cancelled by the contrast flash.

The derivation of Eq. (1), as given in A.R.T. (1970a) is based on the results of an experiment in which a sectored template, the so-called windmill-stop, is placed in the ϕ beam. This stop served to radially reduce the area of the (annular) ϕ flash by 1/8. The interesting result of that experiment was that over a range of ca. 3 log units the reduction in area could be compensated for by a commensurate increase of ϕ. In other words, area could be traded for intensity. This implies that adding receptor outputs (increasing area) has the same effect as adding intensity. This result can be easily understood if the photo response is proportional with light intensity (over the range for which the area vs. intensity trade-off was found to hold). It is also possible, in principle, to obtain this result with a non-linear transducer function, i.e. a power function (cf. Wandell, 1976). However, one has to assume, then, that the (non-linear) receptor outputs always combine in such a way that the (integrated) signal increases with area in conformity to the same power function that describes the photo response as a function of light intensity. This seems very unlikely, considering the entirely different mechanisms that must be involved. It also seems unlikely in view of the existing physiological evidence showing an (initially) linear, rather than a non-linear photo response.

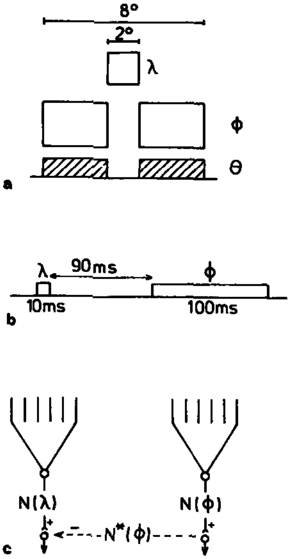

Fig. 1a–c. Spatial intensity profile **a** and temporal arrangement **b** of the stimuli used in the contrast flash paradigm. The contrast flash (ϕ) is presented after the test flash (λ), with a delay of 90 ms. The annular contrast flash may be presented superimposed on a steady background (θ), spatially coincident with ϕ but avoiding the test area. The scheme **c** of neural interaction shows the (pooled) *excitatory* signals $N(\lambda)$ and $N(\phi)$ of test and contrast flash respectively, and the laterally travelling *inhibitory* signal $N^*(\phi)$ that interacts with $N(\lambda)$

It should be recognized however, that although the results of the windmill-stop experiment suggest a photo response quite compatible with Eq. (1) – $N(\phi)$ is linear for $\phi \ll \sigma$ – this does not exclude that the laterally travelling *inhibitory* signal actually measured by A.R.T., is subjected to a non-linear transformation before interacting with the test signal. This is the situation portrayed in Fig. 1c. It deviates from the scheme proposed by A.R.T. in that it incorporates a non-linear stage, in the inhibitory pathway, in which the (integrated) photo response $N(\phi)$, or the "excitatory" signal, as Wandell (1976) called it, is transformed into the inhibitory signal $N^*(\phi)$.

In A.R.T.'s so-called "staircase" analysis it is assumed that reducing the ϕ-area by a certain factor causes a commensurate reduction of the inhibitory signal. This is formally equivalent to the statement that $N(\phi) \sim N^*(\phi)$, which would mean that both $N(\phi)$ and $N^*(\phi)$ are to be described by Eq. (1). However, Wandell (1976) has pointed out that if $N^*(\phi)$ indeed were to be described by Eq. (1), this[1] would imply, given the experimental results, that $N(\phi)$ would be proportional to ϕ^2 rather than ϕ^1. Such a transducer function seems utterly incompatible with the existing physiological evidence.

Now that the possibility of an inhibitory signal conform Eq. (1) has to be rejected, and hence, A.R.T.'s "staircase" analysis, we must look for other ways to analyse the data. As mentioned above the area vs. trade-off as found by A.R.T. strongly suggests a linear (excitatory) transducer function over the range where this principle was found to hold. So, when relatively weak test flash intensities (λ) are employed, as is true for all A.R.T.'s experiments, we may assume the

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[1] This asymmetry would also occur when assuming $N(\phi)$ to be described by a power function

receptor's response to the test flash to be described by

$$F(\lambda)=c\lambda\,. \tag{3}$$

In the condition where the perception of the test flash is just prevented by the action of ϕ, we assume, following A.R.T. (1970b), that the test signal is just cancelled by the ϕ signal, to that

$$N^{*}(\phi)=F(\lambda)\,. \tag{4}$$

From Eqs. (3) and (4) follows

$$N^{*}(\phi)\sim\lambda(\phi)\,. \tag{5}$$

In words, the function that describes λ as a function of ϕ, also describes (apart from a constant) N^{*} as a function of ϕ. Data showing λ (and hence, N^{*}) as a function of ϕ are presented in Fig. 2. They were taken from A.R.T.'s 1970a paper (their Fig. 5).

The curve drawn through the data points has the form

$$N^{*}(\phi)=\left(\frac{\phi}{\phi+\sigma}\right)^{n} \tag{6}$$

with $\sigma=3.7$ log scotopic *td* and $n=0.5$. Thus we conclude that the inhibitory signal $N^{*}(\phi)$ is not described by the transducer function of Eq. (1), as A.R.T. claimed, but rather by a *compressed form of the latter.*

It is tempting to assume that Eq. (6) reflects the properties of two separate processes, an excitatory transducer function in conformity to Eq. (1) followed by a power transformation in the inhibitory channel. Considering the abundant physiological evidence for Eq. (1) (e.g. Penn and Hagins, 1972; Dowling and Ripps, 1972; Normann and Werblin, 1974; Baylor and Hodgkin, 1974; Fain, 1976; Normann and Perlman, 1979) this would seem the most plausible way to account for the data.

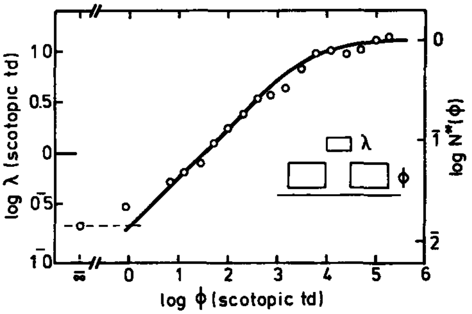

Fig. 2. Test flash threshold (λ) as a function of contrast flash intensity (ϕ). Data reproduced from A.R.T. (1970, Fig. 5). The ordinate on the *right indicates (within the context of the present analysis) the size of* the inhibitory signal $N^{*}(\phi)$. The curve drawn through the data points is conform Eq. (6) with $n=0.5$ and $\sigma=3.7$ log scotopic td. The dashed line indicates the test flash threshold in the absence of ϕ

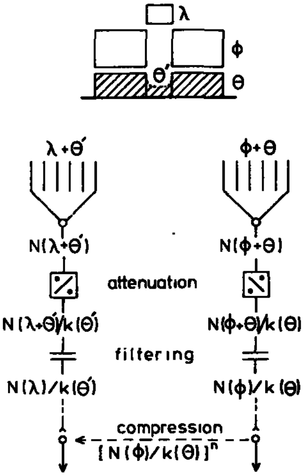

Fig. 3. Scheme showing the inferred neural processing involved in the contrast flash effect

Adaptation by Steady Backgrounds

So far, only the situation has been considered where ϕ is presented in the dark. Matters become more complicated when ϕ is presented superimposed on a steady background (θ), spatially coincident with ϕ, but avoiding the test field locus. The background affects the visibility of both λ and ϕ. The raise in λ threshold caused by θ, or rather, by the straylight (θ') produced by it (A.R.T., 1970b), was called λ_0 by A.R.T. The changes of λ threshold relative to this initial threshold, i.e. λ/λ_0, was taken as a measure for the inhibitory effect exerted by the ϕ flash alone.

Two aspects have to be considered when dealing with the data obtained with ϕ superimposed on θ. First, there is the *adaptive* effect of θ (change in gain) resulting in a reduced efficacy of ϕ. Second, there is the *excitatory* effect of θ, that is, its contribution to the total quantum catch in the surround ($\phi+\theta$), and hence, to the total (excitatory) surround signal $N(\phi+\theta)$. However, it has been shown (Walraven, 1976, 1977) that the visual system is able to "discount" a *steady* background, as far as its excitatory contribution to a (transient) test light is concerned. So, although θ and ϕ are physically added at the receptor level, and hence, transduced together as $N(\phi+\theta)$, we assume that only the transient component, $N(\phi)$, is transmitted.

The most parsimonious scheme for implementing the various processing stages of both ϕ and λ is shown in the diagram of Fig. 3. The first stage comprises the transducer process (N) which applies to the test light plus the stray light added to it ($\lambda+\theta'$), but also to the ϕ flash plus background ($\phi+\theta$). The (excitatory) signal then passes a volume control, with attenuation factor k, set by the steady background θ (for the surround signal), or by the stray light θ' (for the test signal). The next step assumes a high-pass filter which separates the transient signal (due to ϕ or λ, respectively) from the total signal. Finally, there is a compression of the lateral inhibitory signal, consistent with the exponent n of Eq. (6). Thus, the transient inhibitory signal ΔN^* that finally interacts with the test signal is given by

$$\Delta N^*(\phi,\theta)=[N(\phi)/k(\theta)]^n \tag{7}$$

whereas the test signal itself becomes

$$\Delta N(\lambda,\theta')=N(\lambda)/k(\theta'). \tag{8}$$

The relationship between the attenuation factor (k) and background intensity (θ) was found to be best described – when trying to fit theoretical curves to the data (see later) – by

$$k(\theta)=N(\theta+\theta_D)/N(\theta_D), \tag{9}$$

where the constant θ_D represents the "dark light" or "eigen grau". Equation (9) implies a volume control that aims at a fixed (minimal) steady-state output, i.e. $N(\theta_D)$. To appreciate this, consider that $N(\theta+\theta_D)$ corresponds to the initial response to the background (plus the ever present θ_D), whereas $N(\theta_D)$ is the response after attenuation down to the "eigen grau" level.

A.R.T. measured the test threshold (λ) relative to its initial threshold, i.e. in the absence of ϕ but in the presence of θ' (the stray light scattered onto the test locus). At λ_0, the test signal should correspond to $N(\lambda_0)/k(\theta')$, which, if the threshold criterion is constant, requires a constant inhibitory signal N_c^* for its cancellation. Thus, the balance of signals at the lower limit of the signal range is given by

$$N(\lambda_0)/k(\theta')=N_c^*. \tag{10}$$

For the supra-threshold range, where $\lambda>\lambda_0$, the cancelling signals are described by Eqs. (7) and (8), that is,

$$N(\lambda)/k(\theta')=[N(\phi)/k(\theta)]^n. \tag{11}$$

Combining Eqs. (10) and (11) yields

$$N(\lambda)/N(\lambda_0)=[N(\phi)/k(\theta)]^n/N_c^* \tag{12}$$

or, assuming $N(\lambda)\sim\lambda$ (for $\lambda\ll\sigma$)

$$\lambda/\lambda_0=[N(\phi)/k(\theta)]^n/N_c^*. \tag{13}$$

Equation (13) with $N(\phi)$ specified as in Eq. (1), and $k(\theta)$ as in Eq. (9) provides the quantitative basis for describing A.R.T.'s contrast flash results.

Results

Rod Data

Although A.R.T. performed a variety of experiments it is sufficient to restrict the analysis to only one of them, since they are all related to each other in their manipulation of the three parameters: ϕ, θ, and λ/λ_0.

The experiment to be discussed is essentially an increment-threshold experiment (of ϕ on θ) in which the threshold criterion can be manipulated by varying the intensity of the test flash (λ) that has to be cancelled by ϕ. The theoretical ϕ vs. θ function (with λ/λ_0 as parameter) can be derived from Eq. (13) hereby solving for ϕ. The derivation of this function is given in the Appendix, and takes the form.

$$\phi=\frac{c(\theta+\theta_D)\sigma}{(1-c)(\theta+\theta_D)+\sigma} \tag{14}$$

with the constant c determined by

$$c=\frac{\sigma}{\theta_D}\left(\frac{\lambda}{\lambda_0}N_c^*\right)^{1/n}. \tag{15}$$

The data to be described by the above expressions are shown in Fig. 4. They are reproduced from A.R.T. (1970b, Fig. 8). The curves were calculated with $n=0.65$, $\sigma=3.25\log$ scotopic td, $\theta_D=-1.6\log$ scotopic td and $N_c^*=0.004$. Note that Eq. (14) not only

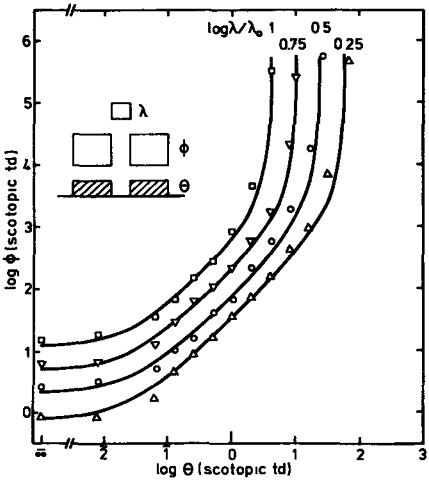

Fig. 4. Contrast flash intensity (ϕ), required for cancelling test flashes of fixed criterion (λ/λ_0), as a function of background intensity (θ). The data, re-drawn from A.R.T. (1970b, Fig. 8), are fitted by curves calculated with Eq. (14) with $\sigma=3.25\log$ scotopic td, $n=0.65$, $\theta_D=-1.6\log$ scotopic td

describes the shapes of the curves but also their vertical displacement. There have been other attempts to describe the results of Fig. 4 (Williams and Gale, 1978; Shevell, 1979), but these cannot account for the vertical positioning of the curves. (A.R.T. themselves did not give an expression relating ϕ to θ.)

Cone Data

A.R.T. (1970c) also applied the contrast flash technique for studying the response properties of cones. Figure 5 shows data reproduced from their Fig. 2, i.e. a λ/λ_0 vs. ϕ function obtained with green test flashes that, as Alpern and Rushton showed (1965), are detected only by the "green" cone system. The data are fitted by the function generated by Eq. (13) with $\sigma = 5$ log td, $n = 0.2$, $N_c^* = 0.11$, and $k(\theta) = 1$ (i.e. the zero background condition). Results relating to "red" cones (obtained with red test flashes) require a lower value of σ for their description ($\sigma = 4$ log td), but this may reflect a variable σ (see later) rather than a real difference between the red and green cone mechanisms.

The λ/λ_0 range over which ϕ is effective is about one order of magnitude smaller than that found for rods, a consequence of the much stronger compression of the N^* signal ($n = 0.2$).

A.R.T. also performed experiments with ϕ superimposed on θ, although for one λ/λ_0 criterium only. The results as obtained with green test flashes are shown in Fig. 6 which is a replot of A.R.T.'s (1970c, Fig. 4). Here the same saturation phenomenon as found for rods is also observed with cones. This result may seem curious in view of the different adaptive properties of rods and cones. Cones, in contrast to rods, are supposed to be protected from saturation (by *steady* backgrounds) due to their ability to shift their operating characteristic along the log intensity axis, that is, increase σ with increasing adaptation level (e.g. Normann and Werblin, 1974; Normann and Perlman, 1979). However, the *dynamic* response range that thus may be maintained, remains restricted. It may always be quite adequate for small incremental responses, but it can not accommodate, of course, the high intensity contrast flashes (up to 10^6 td) used in A.R.T.'s experiments. Such intensities can be handled only when the cones are fully adapted to a light level of the same order of magnitude. The adaptation levels used by A.R.T. however, were about 300 td at the most.

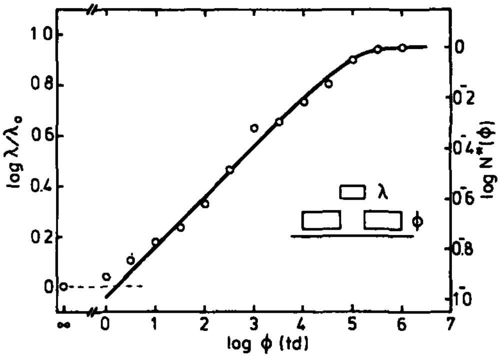

Fig. 5. Relative increase in test flash threshold (λ/λ_0) as a function of contrast flash intensity (ϕ). These data, pertaining to cone vision, were taken from A.R.T.'s (1970d) paper (Fig. 2). The curve drawn through the data points is generated by Eq. (13) with $n = 0.2$, $\sigma = 5$ log td, $k(\theta) = 1$, and $N_c = 0.11$

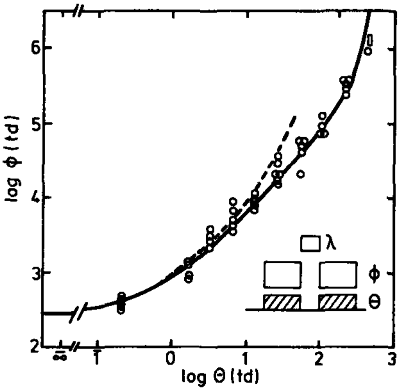

Fig. 6. Contrast flash intensity (ϕ) as a function of background intensity (θ) obtained with test flash criterion $\log\lambda/\lambda_0 = 0.47$. These (cone) data are reproduced from A.R.T. (1970d, Fig. 4). The solid curve is generated by Eq. (14) with $n = 0.2$, $\sigma = 5.5$ log td and $c = 630$. The dashed curve results when taking $\sigma = 4.5$ log td. It is shown to illustrate that the solid curve can also be described with a sequence of σ values, increasing with background intensity

The curve drawn through the data points in Fig. 6 is generated by Eq. (14) upon substituting $\theta_D = 0.45$ td, $\sigma = 5.5$ log td, $\log\lambda/\lambda_0 = 0.47$ (as given by A.R.T.), and $c = 630$. This calculated curve provides a reasonable fit to the data, and one might be tempted to agree with A.R.T. therefore, that the same theory that led to satisfactory descriptions of the rod data, also applies to cone vision. This implies, among other things, a fixed σ level. However, the evidence provided by Fig. 6 is not conclusive. This point would not have been brought up were it not for the fact that, apart from the evidence from the animal experiments mentioned before, there are also psychophysical data which indicate that cones can adjust their operating range to the prevailing light level. This multi-range meter principle, as first shown by Craik (1940), has also been demonstrated in the work of Thijssen and Vendrik (1971), Walraven (1976), Hood et al. (1978), and Geissler (1978a, b).

Turning now to the data at hand, it should be recognized that the background intensity at which saturation occurs (θ_s) is determined by the value of σ as found *at that particular background level.*

However, this is not necessarily the same value of σ that applies to dark adapted cones. Suppose, for example, that the dark adapted value of σ would be 4.5 log td. That would yield a ϕ vs. θ function as indicated by the dashed curve in Fig. 6. That curve fits all the data up to a background level of ca. 10 td. At background intensities $\theta > 10$ td the curve saturates, but only because σ is assumed to remain fixed at 4.5 log td. If, on the other hand, σ is allowed to increase the curve would flatten out and fall along the straight 45° portion of the ϕ vs. θ function calculated for $\sigma = 5.5$ log td. Thus, the function calculated for $\sigma = 5.5$ log td may actually represent the limen of a family of curves with σ increasing from its dark adapted value up to 5.5 log td.

Discussion

The present analysis of A.R.T.'s contrast flash data was initiated in order to comply with Wandell's (1976) criticism that A.R.T.'s "stair-case" analysis leads to a positively accelerating *excitatory* transducer function. It now turns out that a more realistic stimulus response relationship, i.e. the well known (rectangular) hyperbolic function of Eq. (1), is not inconsistent with A.R.T.'s data. However, one then has to introduce a compression stage, in the inhibitory pathway, causing $N(\phi)$ to change into $[N(\phi)]^n$.

As fas as *rods* are concerned this analysis confirms A.R.T.'s conclusion that light adaptation does not increase the semi-saturation level (cf. also Rushton, 1972). This implies that, in principle, the sensitivity of the rods themselves, or rod pools (Lennie et al., 1976) is unaffected by the presence of a steady background. Maintenance of a high input sensitivity is advantageous, of course, for a system that has to operate at extremely low light levels. However, the price to be paid for such an arrangement is that the rods are not protected from saturation. (The gain control only prevents signal overload in the structures proximal to the rods.) In fact, the gain mechanism invites saturation by raising the threshold requirement for the incoming rod signals. On the other hand, this may be a desirable property for a duplex retina since it renders the rods ineffective at photopic light levels where they might otherwise interfere with cone mediated vision.

Alpern (1974) already pointed out that A.R.T.'s estimates of the value of σ (which are not much different from those suggested by the present analysis) are much larger than those obtained by microelectrode recordings of the rod photoresponse. Physiologically measured values of σ (of rods) range from 30–50 quanta absorbed rod^{-1} (100 ms) flash^{-1}, assuming that a scotopic td corresponds to ca. 4 quanta absorbed rod^{-1} s^{-1} (Denton and Pirenne, 1954; Rushton, 1965).

The estimates of the σ values of cones also seem much too high. The discrepancy is even larger here, considering that the σ value indicated by turtle and mudpuppy data are in the order of 150–300 quanta absorbed cone^{-1} flash^{-1} which should be compared to the $10^{5.5}$ quanta absorbed cone^{-1} (100 ms) flash^{-1} that can be derived from the ϕ vs. θ function shown in Fig. 5. (One may estimate a photopic td to correspond to ca. 10 quanta absorbed cone^{-1} s^{-1}.) Such a huge discrepancy can be understood only if we assume that the value in question represents some light adapted rather than the dark adapted level of the (variable) σ of cones. The estimate of σ for "red" cones, i.e. ca. $10^{3.7}$ absorbed quanta cone^{-1} flash^{-1}, seems closer to reality, but probably is still too high. It is of interest in this respect, that (local) ERG recordings from monkey cones by Valeton and van Norren (in preparation), confirming earlier results of Boynton and Whitten (1970), yield a σ level of ca. $10^{3.3}$ absorbed quanta cone^{-1} flash^{-1}, and furthermore, a compressed transducer function, with $n = 0.5$ [when fitting the data with Eq. (6)]. It is conceivable therefore, that the substrate that mediates the contrast-flash effect (horizontal cells, Müller cells?) is the same as that probed by the ERG electrode.

In conclusion, this analysis shows the contrast-flash data to be described by Eq. (6) rather than Eq. (1). Thus, these data, like all psychophysical data, can only indirectly be related to photoreceptor (?) activity.

Appendix

In order to derive Eq. (16) we substitute Eqs. (1) and (9) into Eq. (15), which gives

$$\lambda/\lambda_0 = \left[\frac{\phi}{\phi+\sigma}\bigg/\frac{N(\theta_D+\theta)}{N(\theta_D)}\right]^n \Big/ N_c^* .$$

After re-arranging, and writing $N(\theta_D+\theta)$ and $N(\theta_D)$ conform Eq. (1), this becomes

$$\frac{\phi}{\phi+\sigma} = (\lambda/\lambda_0 N_c^*)^{1/n} \frac{\theta_D+\sigma}{\theta_D} \frac{\theta+\theta_D}{\theta+\theta_D+\sigma}$$

or, since $\theta_D \ll \sigma$

$$\frac{\phi}{\phi+\sigma} = (\lambda/\lambda_0 N_c^*)^{1/n} \frac{\sigma}{\theta_D} \frac{\theta+\theta_D}{\theta+\sigma} .$$

Taking constants together, that is,

$$c=(\lambda/\lambda_0 N_c^*)^{1/n}\frac{\sigma}{\theta_D}$$

we may write

$$\frac{\phi}{\phi+\sigma}=c\frac{\theta+\theta_D}{\theta+\sigma}$$

which, after solving for ϕ, yields

$$\phi=\frac{c(\theta+\theta_D)\sigma}{(1-c)(\theta+\theta_D)+\sigma}.$$

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4.2 PERCEIVED COLOUR UNDER CONDITIONS OF CHROMATIC ADAPTATION: EVIDENCE FOR GAIN CONTROL BY π MECHANISMS

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Abstract—Chromatic adaptation was studied with the method of maintaining a constant hue (unique yellow) of the test flash. The test field was presented super-imposed on backgrounds varying in wavelength (540–660 nm) and retinal illuminance (0.5–5 log td). The results can be described by assuming non-addivity of test and adapting light, cone spectral sensitivities as estimated by Vos and Walraven (1970), and receptor-specific gain controls that have the same action spectra and gain characteristics as Stiles' π mechanisms.

INTRODUCTION

Chromatic adaptation is generally believed to result from selective gain adjustments in the colour mediating channels of the visual system. The action of such multiplicative response-modifying mechanisms can be described in terms of changes in the relative heights of the cone action spectra. This is the principle underlying the so-called Coefficient Law (Von Kries, 1905), the "coefficient" being the factor by which the receptor's sensitivity is reduced. Intracellular recordings from vertebrate cones showing the receptor's ability to adjust its operating range to the prevailing light level (e.g. Normann and Werblin, 1974; Baylor and Hodgkin, 1974; Fain, 1976; Normann and Perlman, 1979) provide physiological support for such a scheme. However, it has been known for quite some time that the coefficient principle *alone* cannot account for the induced shifts in hue as observed in the classical stimulus configuration of a test field surrounded by a chromatic conditioning field (Walters, 1942; MacAdam, 1956; Hunt, 1958; Hurvich and Jameson, 1958). There are good reasons for assuming that a second process must be involved (cf. Jameson and Hurvich, 1972), one that is consistent with a subtractive rather than a multiplicative response reduction.

The nature of the "second process" in chromatic adaptation has been demonstrated in experiments in which the test stimulus was presented *super-imposed* on a background rather than in the centre of an annular surround (Walraven, 1976). It thus could be shown that the visual system processes test and background stimulus separately, hereby discounting the additive contribution of the background light at the test field locus. This implies that the light that the test field has in common with the light surrounding it, is somehow subtracted out. This same principle has also been demonstrated for brightness perception (Whittle and Challands, 1969; Whittle, 1973). These and other results (Walraven, 1977) suggest that only the spatio-temporal *transients* in the stimulus pattern are processed by the visual system.

It is only after making allowance for the discounting principle, that one may evaluate the properties of gain mechanisms in chromatic adaptation. It can be shown, then, that the Coefficient Law is quite valid after all (Walraven, 1976). However, we still do not know how the gain factors (coefficients) that operate on the cones depend on the intensity and the colour of the background. The answer to this question, which stands central to the whole problem of chromatic adaptation, might be found in the work of Stiles (cf. Stiles, 1978). That is, the function we are looking for might be the same gain function that was found to describe the threshold elevation of isolated colour systems (π mechanisms), i.e. the function $\zeta(x)$, as tabulated by Wyszecki and Stiles (1967).

The purpose of this study is to test whether it is indeed possible to employ the concepts derived from two-colour increment thresholds, for predicting changes in perceived hue under conditions of chromatic adaptation. As has already been concluded by Stiles (1961) the findings from previous work on chromatic adaptation would seem to discourage such an attempt. In these older studies, however, the results were analysed exclusively in terms of the coefficient principle, and hence, the different effects of gain changes (multiplication) and discounting (subtraction) were confounded.

METHODS

Apparatus

A conventional three-channel Maxwellian view optical system was used. Two channels, respectively providing red (640 nm) and green light (555 nm) were used to produce a 1° circular test field, variable in colour in the spectral region covered by those two primaries. The test stimulus was flashed (500 msec) and presented superimposed on a circular 8° background field provided by the third channel. The light from this adaptation field (I_{λ_A}) was varied over the spectral range of 540–660 nm. It was rendered monochromatic by an Oriel grating monochromator (10 nm ½ peak bandwidth), and so was the red test primary; the green primary was provided by an interference filter (Balzer). The light sources used were 100 W tungsten-iodide bulbs, slightly under-run at 8 A.

The retinal illuminances of the test primaries, called ΔI_{640} and ΔI_{555}, were controlled by calibrated neutral density wedges (Agfa). The latter were under computer control so as to maintain a constant luminance of the test light when varying the relative contributions of the red and green primaries. Test and background lights were varied in unison (thus maintaining a constant contrast) by having (step) filters placed in their common pathway. The test-to-background intensity ratio (contrast) was kept at unity, except at the highest background level (5 log td), where, due to apparatus limitations, the test intensity was about one third of that of the background. The test flash was presented at 10 sec intervals, so as to ensure that the test light would not affect the adaptive state induced by the background.

Calibrations

The luminosity of the 555 m light was determined with a calibrated mlux meter (laboratory designed), put at a known distance (*d*) from the Maxwellian image. Conversion to trolands was done by multiplying the meter reading (in lux) by a factor $10^6 d^2$, with *d* expressed in metres. Heterochromatic photometry (flicker rate 15–20 Hz) was used to determine the retinal illuminances of the other lights used.

Procedure

The observer's task was to maintain a pure yellow hue of the test field by adjusting the ratio $\Delta I_{660}/\Delta I_{555}$ of the red and green primaries. No reference field was needed, nor wanted (cf. Walraven, 1976, p. 290); deviations from the mean (of 5 settings) were typically less than 0.05 log unit, corresponding to less than 2 nm in terms of equivalent wavelength.

Each session started with 10 min of dark adaptation followed by a presentation of the test light at a retinal illuminance of ca. 100 td. The average of 10 settings made in this condition defined the reference for measuring the size of the compensatory hue shift required for maintaining yellow in the presence of the backgrounds presented thereafter. The reference settings showed only slight day to day variability, the extremes (of log $\Delta I_{630}/\Delta I_{555}$) being less than 0.1 log unit apart.

The data to be presented are from only one observer, the author. However, a complete set of data from a naive subject, obtained in a follow-up study (Werner and Walraven, in preparation) attests to the general validity of the results.

RESULTS

Analytical framework

When a yellow test field is presented on a chromatic background its hue will shift in a direction opposite to that of the background, a consequence of the relatively stronger adaptation of the photoreceptors (and/or more central neural stations) that are most sensitive to the background light in question. Thus, in order to maintain the yellow hue of the test field a compensatory hue shift is required, which in the present experiments is achieved by changing the ratio of the red and green primaries ($\Delta I_{640}/\Delta I_{555}$) constituting the test stimulus. Since the eye is virtually dichromatic for wavelengths >550 nm we may assume that the test light only stimulates the long-wavelength-sensitive and middle-wavelength-sensitive cones (to be called *L* and *M* cones from now on). Hence, the analysis will be confined to these two cone types only.

Figure 1 shows a sample of the results; that is, as obtained with the test field presented on respectively red (640 nm) and green (555 nm) back-grounds of increasing intensity. The data show that the red-green

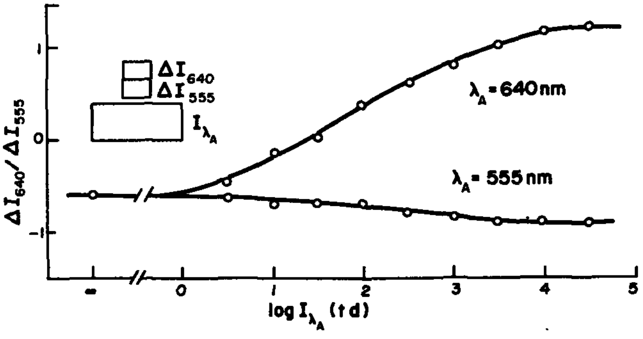

Fig. 1. Red-green ratio ($\Delta I_{640}/\Delta I_{555}$) of the test flash as is required for maintaining (unique) yellow in the presence of red ($\lambda_A = 640$ nm) or green ($\lambda_A = 555$ nm) backgrounds of varying intensity (I_{λ_A}).

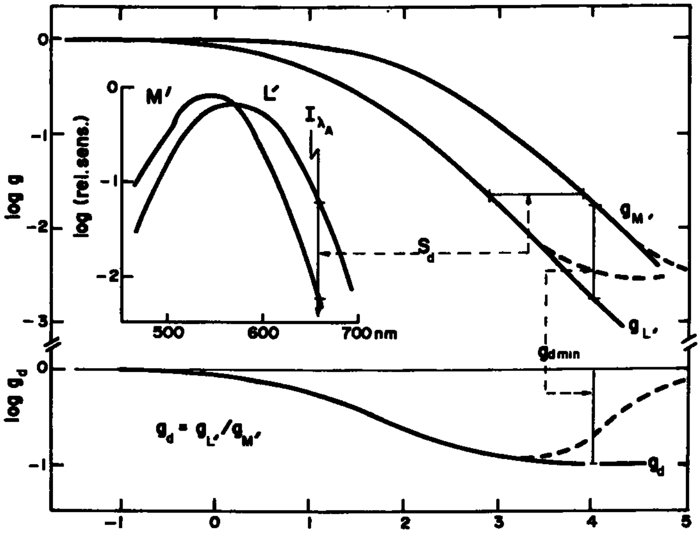

Fig. 2. Example, illustrating how separate gain factors $g_{L'}$ and $g_{M'}$, in conformity with Stiles' $\zeta(x)$ function, define a differential gain g_d. The lateral separation between the individual gain characteristics corresponds to the gain mechanisms' differential sensitivity (s_d) at the adapting wavelength λ_A. The insert shows arbitrary (field) spectral sensitivities L' and M' of the gain mechanisms (which do not necessarily match those of the cones). Note that g_d reaches a minimum ($g_{d_{min}}$), which is equal to s_d^{-1} once $g_{M'}$ and $g_{L'}$ increase at equal rates (in proportion with I_{λ_A}).

The dashed portions of the curves show, qualitatively, how bleaching causes the individual gain factors to come to a standstill, hereby reducing the differential gain.

ratio has to be changed in the direction of more red, when presented on red backgrounds, whereas the opposite is true for the (less chromatically selective) green backgrounds. This is the expected result. Note, however, that the compensatory hue shift approaches a maximum. This implies that the differential adaptive effect caused by the background no longer increases after a certain intensity has been reached. Such a result suggests the presence of two separate gain mechanisms, operating on the outputs of the L and M cones respectively, that first decrease their gain at different rates (one having a start) but finally decreases at the same rate. This explanatory principle, adopted from Stiles' analysis of the two-colour increment threshold, is exemplified in Fig. 2. It shows two gain functions, g_L, and g_M, which are just inverted threshold vs intensity functions; that is, they are drawn in conformity with Stiles' standard $\zeta(x)$ function (Wyszecki and Stiles, 1967).

The action spectra of the gain mechanisms (represented by the curves shown in the insert) are not necessarily identical to the cone spectral sensitivities L and M (it is conceivable that the gain control receives inputs from more than one class of cones). In fact, anticipating the results, we shall conclude that they are slightly different and therefore, refer to them as L' and M' respectively.

In the example shown in Fig. 2 it is assumed that, at the adapting wavelength λ_A, the differential sensitivity (s_d) of the gain mechanisms, i.e. $(L'/M')_{\lambda_A}$, is exactly equal to 10. As a consequence, the gain function g_M, is laterally shifted, by one log unit, relative to $g_{L'}$. Note that the log of the *differential* gain function, g_d, is given by the vertical separation of the two individual gain functions. This function is plotted in the lower panel of Fig. 2, which shows g_d to gradually approach a fixed lower level, once the individual gain factors both decrease in proportion with intensity, in accordance with Weber's law. It is this result, but in the opposite direction (since we have to compensate for it), that we believe to be reflected in the maxima exhibited by the data shown in Fig. 1.

So far, we have not considered the effect of bleaching of the photopigments. From what is known of the kinetics of bleaching we may expect that at very high light levels the photoreceptors will become equally sensitive to the adaptation light, any initial difference in sensitivity being cancelled by a commensurate loss in pigment. Furthermore, bleaching will become near-proportional with intensity, so the signals from the cones and hence, the input to the (neural) gain mechanism, will virtually come to a standstill. These effects of bleaching are indicated, qualitatively, by the dashed portions of the (differential) gain functions shown in Fig. 2. Of course, such effects only can be seen reflected in the data, if the latter are no longer expressed as red-green light ratios, but rather as ratios of *absorbed* quanta in the L and M cones. This is what we have done, hereby employing some reasonable assumptions to be detailed in the next two sections.

If the present data indeed can be explained in terms of the simple hypothesis outlined above, then the requirement for maintaining yellow, when adapted to a light I_{λ_A}, can be stated as

$$\left(\frac{\Delta Q_L}{\Delta Q_M}\right)_{\lambda_1,\lambda_2} \equiv c\left(\frac{g_{M'}}{g_{L'}}\right)_{I_{\lambda_A}} \tag{1}$$

where ΔQ_L and ΔQ_M are the effective quantum catches of the L and M cones, as provided by the red and green test primaries (ΔI_{λ_1}, ΔI_{λ_2}) and $(g_{M'}/g_{L'})_{I_{\lambda_A}}$ is the differential gain at I_{λ_A}. The constant c represents the quantum-catch ratio that is required for seeing yellow in the absence of the background (which implies $g_{L'} = g_{M'} = 1$). Note that only the quantum-catch from the (incremental) test light, rather than that from test plus background light, is assumed to determine the hue of the test field. This is how the principle of discounting of the background enters the analysis.

In the sequel we shall test whether equation (1) may indeed describe the data. Thereto the data will first be expressed in quantum-catch ratios, i.e. the left-hand side of equation (1). To do so one has to make some assumptions with respect to the L and M spectral distributions, bleaching kinetics and (maximum) pigment densities, which will be detailed in the next two sections. After that we shall deal with the (theoretical) right-hand side of equation (1), i.e. the differential gain, hereby applying Stiles' function $\zeta(x)$, and appropriate gain spectral sensitivities L' and M' to be discussed later.

Effective quantum-catches

In order to convert light ratios ($\Delta I_{640}/\Delta I_{555}$) to quantum-catch ratios ($\Delta Q_L/\Delta Q_M$), we started from the assumption that equal troland values represent equal quantum-catches, whatever the wavelength of the lights under consideration. We further assumed, that the captured quanta are distributed over the L and M cones in proportion with their relative spectral sensitivities (l_λ, m_λ) at the wavelength of the light under consideration*. Neglecting for the moment the effect of bleaching of the pigments the dark-adapted quantum-catch ratio thus can be expressed as

$$\left(\frac{\Delta Q_L}{\Delta Q_M}\right)_{\lambda_1,\lambda_2} = \frac{l_{\lambda_1}\Delta I_{\lambda_1} + l_{\lambda_2}\Delta I_{\lambda_2}}{m_{\lambda_1}\Delta I_{\lambda_1} + m_{\lambda_2}\Delta I_{\lambda_2}} \tag{2}$$

where l and m represent the relative spectral sensitivities (summing to unity) of the L and M cones at the wavelengths indicated by the subscripts λ_1 and λ_2 (here 555 and 640 nm).

Bleaching

At high background intensities, where bleaching becomes appreciable, equation (2) has to be modified, so as to make allowance for the change in concentration of the photo pigments.

To account for the effect of pigment bleaching we started from the expression given by Rushton and Henry (1968), i.e.

$$p = \frac{I_0}{I + I_0} \tag{3}$$

where p is the fraction of unbleached pigment and I_0, the retinal illuminance (i.e. 4.3 log td) that bleaches 50% of the pigment. Rushton and Henry (1968) reported that the white light they used bleached the L and M cones at equal rates. Hence, the quantum catch provided by the (white) bleaching light was distributed equally over the L and M cones. When these were bleached half-way therefore, each system received the quantal equivalent of 4 log td. This implies that if a light could be found that exclusively stimulates a single cone type, then 4 log td of that light would produce a 50% bleach. Such a light does not exist, of course, although one may expect that in the case of a deep red light, the half-bleaching constant for the L cones will indeed be close to 4 log td. In general, when dealing with a monochromatic adaptation light (I_{λ_A}), rather than with a white light, the half-bleaching constants for the M and L cones may respectively be defined as

$$\begin{aligned} I_0(M, \lambda_A) &= 10^4 m_{\lambda_A}^{-1} \\ I_0(L, \lambda_A) &= 10^4 l_{\lambda_A}^{-1} \end{aligned} \tag{4}$$

Bleaching affects both the height and the shape of the cone spectral absorption functions. The change in shape is due to selfscreening of the photo pigments and thus depends on the optical density of the pigment. The latter may be appreciable, as is indicated by various psychophysical studies (e.g. Brindley, 1953; Walraven and Bouman, 1960; Terstiege, 1967; Wyszecki and Stiles, 1980), and recent densitometry studies (King-Smith, 1973a, b). We assumed a maximal optical density (D_{max}) of 0.7, which is about intermediate between the extremes of the psychophysical estimates.

The factor β by which bleaching (due to I_{λ_A}) reduces light absorption, for any given light (test as well as background light), depends on the wavelength λ of that light, and is given by

$$\beta(\lambda) = A'(\lambda)/A(\lambda) \tag{5}$$

where $A'(\lambda)$ and $A(\lambda)$ relate to the absorption (at λ) in the light-adapted and dark-adapted state, respectively. The value of $A'(\lambda)$, for a given cone pigment, depends

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* The assumptions made here carry the important implication that the receptor outputs are linearly related to light intensity, and moreover, that these outputs combine in a linear fashion in the mechanism that underlies the luminous efficiency curve (V_λ) of the eye. The additivity of heterochromatic luminosity and a variety of other visual phenomena (cf. MacLeod, 1978, p. 617) are quite consistent with that notion. The linearity assumption only holds over a restricted intensity range, of course. So, when equating lights for equal (flicker) luminance, one should do so at low light levels.

on the fraction p of pigment left unbleached (by I_{λ_A}) and the relative optical density d_λ (i.e. relative to D_{max} of the pigment in question), in accordance with

$$A'(\lambda) = 1 - 10^{-d_\lambda p D_{max}}. \tag{6}$$

The value of d_λ follows from the density spectrum of the pigment in question, whereas p (which depends on I_{λ_A}) can be calculated with equation (3) upon substitution of the appropriate value of I_0, as specified in equation (4). The dark-adapted absorption factor $A(\lambda)$ is given by the same expression (one then has $p = 1$), so $\beta_L(\lambda)$ and $\beta_M(\lambda)$, the factors specifying the reduced absorption of the L and M cone pigments, can now be calculated with equation (5).

In order to correct the test quantum-catch ratio for the effect of bleaching, we multiplied the individual L and M quantum-catches (as provided by the test primaries ΔI_{λ_1}, ΔI_{λ_2}) with the appropriate reduction factors, using equations (3–6). When we introduce these factors, i.e. $\beta_L(\lambda_1)$, $\beta_L(\lambda_2)$, $\beta_M(\lambda_1)$ and $\beta_M(\lambda_2)$, into equation (2), the quantum-catch ratio, corrected for bleaching, becomes

$$\left(\frac{\Delta Q_L}{\Delta Q_M}\right)_{\lambda_1,\lambda_2} = \frac{\beta_L(\lambda_1) l_{\lambda_1} \Delta I_{\lambda_1} + \beta_L(\lambda_2) l_{\lambda_2} \Delta I_{\lambda_2}}{\beta_M(\lambda_1) m_{\lambda_1} \Delta I_{\lambda_1} + \beta_M(\lambda_2) m_{\lambda_2} \Delta I_{\lambda_2}} \tag{7}$$

The values we used for the relative spectral sensitivities l_λ and m_λ are based on the set of cone spectral sensitivities derived by Vos and Walraven (1970) as tabulated by Vos (1978). That is, at 640 nm we used

$$l_{640} = 0.875, m_{640} = 0.125$$

and at 555 nm,

$$l_{555} = 0.452, m_{555} = 0.548$$

Now that the results can be expressed in terms of effective quantum-catches the next step is to define the characteristics of the gain mechanisms that should account for them.

Gain functions

As mentioned before, the gain function to be employed for describing the data is assumed to have the same characteristics as Stiles' standard function $\zeta(x)$. The quantity x is proportional to the effective quantum-catch of the gain mechanism involved. In line with the assumptions made before we assume the quanta delivered by the adaptation light I_{λ_A} to be distributed over the L and M cones in proportion with their relative spectral sensitivities. These quantum-catches, corrected for bleaching, somehow provide the input to the gain systems. If the latter connect with only one of each of the cone types, the input to, say, the L' system would simply be equal to the quantum-catch Q_L of the L cones, which (at I_{λ_A}) is $l_{\lambda_A} I_{\lambda_A} \beta_L(\lambda_A)$, where $\beta_L(\lambda_A)$ is the factor that corrects for bleaching [see equation (5)]. If however, interactions do occur, the input $x_{L'}$—to the gain function $\zeta(x)$—will no longer be equal to Q_L. It may be described, then, as $\mu_{\lambda_A} Q_L$, where μ_{λ_A} may vary with both the colour and the intensity of the background. Note that μ_{λ_A} defines to what extent the action spectrum of the gain control deviates from the pigment absorption function (where the latter is already corrected for the loss of pigment). Rather than using μ_{λ_A} in defining $x_{L'}$, which would yield $\mu_{\lambda_A} [l_{\lambda_A} I_{\lambda_A} \beta_L(\lambda_A)]$, we shall replace $\mu_{\lambda_A} l_{\lambda_A}$ by l'_{λ_A}, which might be considered as a first order approximation of the relative spectral sensitivity of the L' system at λ_A (which will be stable as long as μ_{λ_A} does not vary). Thus, the inputs (x) of the L' and M' systems at I_{λ_A} can be described as

$$x_{L'} = l'_{\lambda_A} I_{\lambda_A} \beta_L(\lambda_A)$$
$$x_{M'} = m'_{\lambda_A} I_{\lambda_A} \beta_M(\lambda_A) \tag{8}$$

where l'_{λ_A} and m'_{λ_A} are relative sensitivities (summing to unity) of action spectra. It is possible, of course, that the action spectra are hardly different from the pigment absorption functions (implying $\mu_{\lambda_A} = 1$), but this remains to be tested.

With equation (8) specifying the inputs to the gain function $g = \zeta(x)$, the separate gain factors $g_{L'}$ and $g_{M'}$, become

$$g_{L'} = \zeta(x_{L'})$$
$$g_{M'} = \zeta(x_{M'}) \tag{9}$$

with x expressed in trolands. For calculating purposes we used the following approximation for the $\zeta(x)$ function:

$$\zeta(x) = \left[1 + \left(\frac{x}{x_0}\right)^n\right]^{-1/n} \tag{10}$$

where $n = 0.7$ and the constant x_0, the "dark" light, is equal to 25 td. This value implies a Weber-fraction of ca. 2%, as is consistent with Stiles' findings (Stiles, 1953). Figure 3 shows that values generated by equation (10), i.e. the crosses in Fig. 3, are in close agreement with the tabulated function. The shape and positioning of this function are quite critical for the theoretical description of the data.

Now that the characteristics of the gain mechanisms have been defined, there only remains the question what (gain) spectral sensitivities (L', M') should be used. There are various possibilities worth considering in this respect. However, we decided to first test whether the model would work at all, hereby allowing the differential spectral sensitivity s_d (i.e. l'/m') of the L' and M' systems to be used as a free parameter.

Testing the theory

Some of the results, those obtained with 640 and 555 nm backgrounds, have already been shown in Fig. 1, but these were still expressed in terms of the red–green ratio of the test field. The same data, together with those obtained in other background conditions, are shown in Fig. 4, but now plotted in terms of quantum-catch ratios, $(\Delta_L/\Delta Q_M)$, normalized

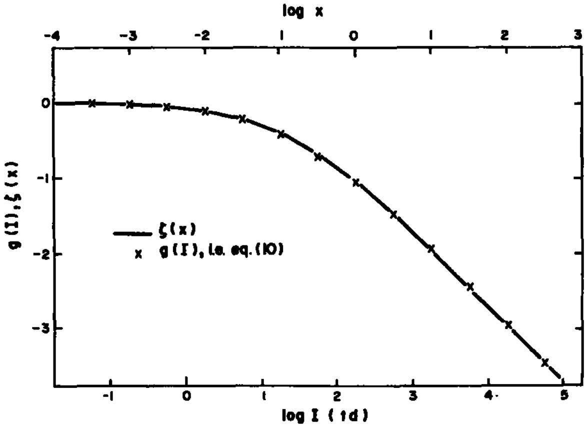

Fig. 3. The function $\zeta(x)$, reproduced from the table given by Stiles and Wyszecki (1967, p. 578), and its approximation (crosses) calculated with equation (10) upon substitution of $I_D = 25$ td. Equation (10) defines the gain function $g(I)$ that is used for describing the data; $1/g(I)$ describes the increment–threshold function for homochromatic test and conditioning field.

with respect to the quantum-catch ratio that yields yellow in the absence of a background [the constant c in equation (1)].

Figure 4 shows that the compensatory quantum-catch ratios we measured exhibit the kind of optimum that we should expect on the basis of the model exemplified in Fig. 2. That there is more than just a qualitative agreement between data and theory is shown by the drawn curves. The latter represent the differential gain functions $(g_L/g_M)I_{\lambda_A}$—which should describe the data [see equation (1)]—as calculated with equations (8–10) upon substitution of the appropriate values of the (differential) gain spectral sensitivities $s_d(\lambda_A)$. The values in question are shown with each curve.

At the highest background intensity used (5 log td), the data deviate from the theoretical predictions. It should be recognized, however, that these are quite bright backgrounds, capable of bleaching more than 80% of the photo pigment. It is to be expected that in these conditions the action spectra do not retain their original shape. Also, other mechanisms, not incorporated in the model, may come into play. It is of interest in this respect, that at these high light levels the hue of the reddish backgrounds may exhibit the kind of colour reversals as described by Cornsweet *et al.* (1958), that is, change from red through yellow to a saturated green. It seems likely that the model proposed by Cornsweet (1962) to account for this phenomenon (which is based on bleaching kinetics) may have to be called upon to describe the data at these very high light levels.

The values of $s_d(\lambda_A)$ shown in Fig. 4 are not much different from those that would result when using the action spectra of Stiles' π_4 and π_5 mechanisms. Full agreement with the latter would require $s_d(555) = 0.82$, $s_d(580) = 1.27$, $s_d(600) = 1.88$, $s_d(620) = 2.85$, $s_d(640) = 3.80$, values that are rather close to those shown in Fig. 4. There is a complication, however, when making this comparison. That is, at relatively high background levels one should rather consider

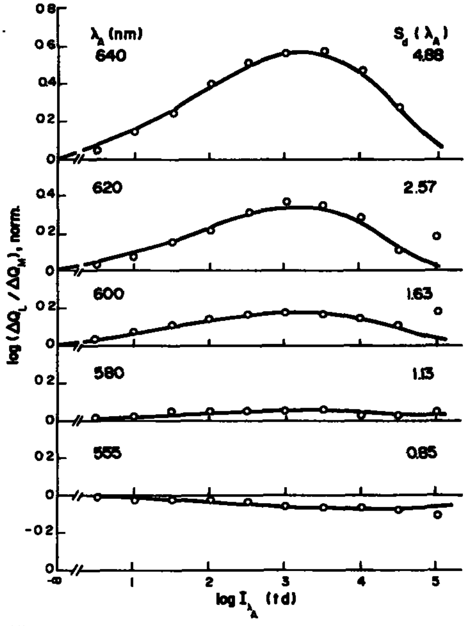

Fig. 4. Effective quantum-catch ratios $(\Delta Q_L/\Delta Q_M)$, normalized relative to the dark-adapted value, as required for maintaining unique yellow in the presence of coloured backgrounds of increasing intensity (I_{λ_A}). The data are fitted by theoretical functions, generated by equations (8–10) upon substitution of differential spectral sensitivities s_d (of gain systems) as shown.

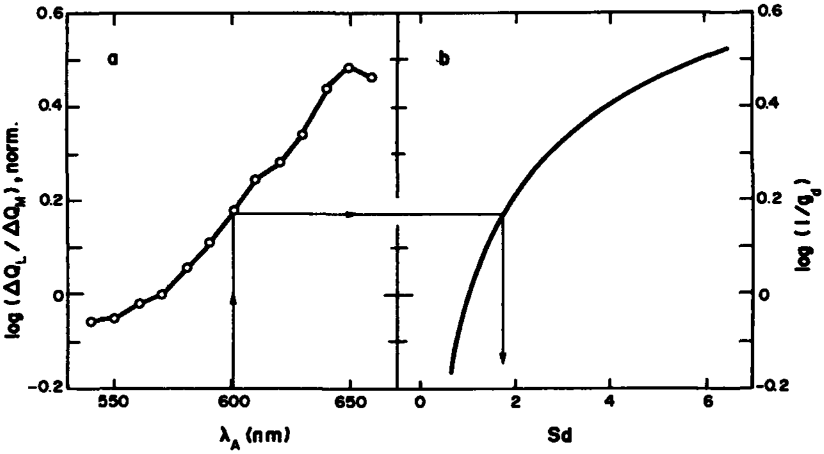

Fig. 5. Derivation of differential (field) sensitivity s_d (of gain mechanisms) for wavelengths (λ_A) in the 540–660 nm spectral region. a. Effective quantum-catch ratios (normalized) required for maintaining unique yellow when varying the wavelength (λ_A) of a background of constant retinal illuminance (180 td). b. Relationship between $1/g_d$ (which should match $\Delta Q_L/\Delta Q_M$) and s_d, as calculated from equations (8–10).

the modified (high-intensity) π mechanisms, i.e. π'_4 and π'_5 (Stiles, 1959). By the same token, we might have tried to fit our data with intensity dependent (gain) spectral sensitivities and in fact, the corrections for bleaching that we applied are a first step in that direction. By doing so, however, a comparison with the π' spectral sensitivities becomes problematic since the latter were derived without such bleach corrections. Therefore, it would be better to confine the comparison to the "normal" π mechanism and moreover, only do so for data obtained in conditions where bleaching is negligible. Such data were obtained in a separate experiment.

Comparison with π action spectra

In order to obtain a more detailed picture of the spectral properties of the L' and M' systems (at low levels of stimulation), the test flash was presented on backgrounds that were varied in wavelength steps of 10 nm (between 540 and 660 nm), hereby keeping the retinal illuminance of the background fixed at 180 td. At this level bleaching is insignificant (less than 1%) and we are probably still within the range where the π rather than the π' mechanisms are in evidence. By measuring the compensatory quantum-catch ratio at each wavelength (λ_A) we obtain a measure of the differential gain (g_d) at that wavelength, this being our basic assumption as stated in equation (1). The (normalized) quantum-catch ratios (and hence, g_d) as measured as a function of λ_A, are shown in the left panel of Fig. 5.

Since we are interested in the differential sensitivity s_d (at λ_A) rather than g_d (i.e. $g_{L'}/g_{M'}$), we expressed g_d as a function of s_d, hereby using equations (8–10). The function thus obtained is the curve shown at the right in Fig. 5. With the aid of that function we can now determine s_d (knowing g_d) for each of the wavelengths λ_A used, as is shown by the arrows in Fig. 5.

The l'/m' ratios that were inferred from Fig. 5 were compared with the π_4 and π_5 action spectra (Wyszecki and Stiles, 1967) by plotting log $(l'/m')_{\lambda_A}$ relative to log π_5. That is, we pinned l'_{λ_A} to the π_5 function and plotted the corresponding value of m'_{λ_A} relative to that point. As is shown in Fig. 6, which shows Stiles' average observer's π_4 and π_5, the values of m'_λ thus inferred from the data are quite well fitted by π_4. It seems quite likely therefore, that the L' and M' gain mechanisms that we postulated are actually the π mechanisms that Stiles derived from his two-colour threshold data.

Disparate spectral sensitivities for cone and gain systems?

The fact that we arrived at π action spectra, at the level of the gain mechanisms, while assuming the Vos and Walraven (1970) fundamentals to apply at the pigment level, is not without theoretical significance, of course. However, this might just be an accidental result. One should like to know, first of all, whether it was really necessary to call upon both, (slightly) different, sets of spectral sensitivities, rather than employing just one of them. The answer to that question is affirmative (within the context of the present theory) as may be appreciated from the following argument.

First, let us return to Fig. 2. There it can be seen that, if we ignore for the moment the effect of bleaching (we shall come to that later), the differential gain g_d reaches its minimum when the separate gain functions decrease in proportion with the quantum catch (Weber's law). When that happens g_d equals s_d^{-1}, i.e.

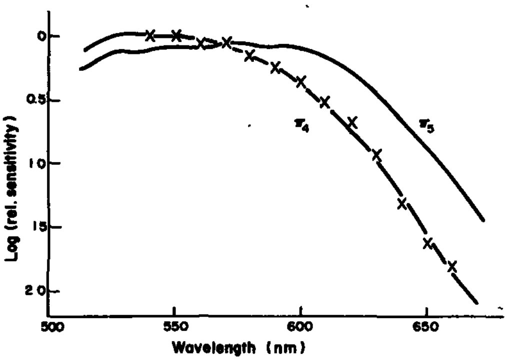

Fig. 6. Differential sensitivities $(l'/m')_{\lambda_A}$, as obtained from Fig. 5, plotted relative to Stiles' π_5 action spectrum. The points thus obtained (crosses) fall close to π_4 which implies $(l'/m')_{\lambda_A} = (\pi_5/\pi_4)_{\lambda_A}$.

m'/l' and we may write therefore,

$$g_{d_{min}} = (m'/l')_{\lambda_A} \tag{11}$$

with λ_A representing again the wavelength of the background.

The maximum red–green (quantum) ratio that can be mustered for compensating the differential gain is that provided by the red primary test primary alone, i.e. l/m_{640}. In terms of the red–green *light* ratio this would imply that $\Delta I_{640}/\Delta I_{555}$ approaches infinity, ΔI_{555} being zero or at least insignificant relative to ΔI_{640}. This is actually what should be predicted if we were to assume a single set of spectral sensitivities, since in that case equation (11) shows $g_{d_{min}}$ to become equal to m/l_{640}. This prediction is illustrated in Fig. 7, which shows the theoretical functions for $\Delta I_{640}/\Delta I_{555}$ when assuming a single set of gain and cone spectral sensitivities, either those of Vos and Walraven (curve I), or those consistent with Stiles' π mechanisms (curve II). Also shown is the function that results if we use two sets, rather than one set of spectral sensitivities (curve III) and the data in question.

Figure 7 clearly shows that the results cannot be described with the same set of spectral sensitivities for cone and gain systems. The theoretical functions that thus result are positively accelerating (curves I and II), while the data require a function with diminishing returns.

DISCUSSION

The main result of this study is that it shows that the conceptions derived from two-colour increment thresholds can be applied for the prediction of perceived hue under conditions of chromatic adaptation. As far as the present data are concerned this conclusion only applies to the red–green domain of colour vision ($\lambda > 550$ nm). However, the data of a follow-up study (Werner and Walraven, in preparation), in which a *white* test field was used to probe the adaptive effect of coloured backgrounds (throughout the whole spectral and purple range), are in full agreement with the present findings.

An interesting parallel of this study, extending its conclusions to brightness perception, can be found in the work of Whittle (1973). He measured the bright-

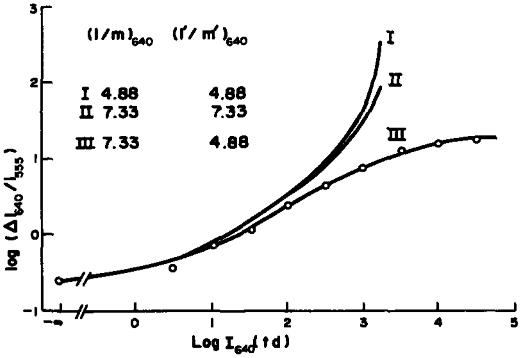

Fig. 7. Same data as shown in Fig. 1 (for $\lambda_A = 640$ nm) and three predictions that result when either applying a single set of spectral sensitivities (curve I and II), for both cone and gain systems, or two sets (Curve III).

ness of coloured flashes on coloured backgrounds and showed, like we did, the π mechanisms in evidence at superthreshold levels. He also pointed out that the (steady) backgrounds did not add to the perceived brightness of the test flashes (see also Whittle and Challands, 1969), which confirms our assumption of the non-addivity of background and test flash*.

If one accepts the present analysis one has to conclude that the cone and gain systems have disparate spectral sensitivities (see Fig. 7). The validity of that conclusion hinges on the validity of our assumption that the differential gain measured by the yellow test flash can be attributed to (two) gain functions with the same characteristics as Stiles' standard function $\zeta(x)$. The main argument supporting this proposition is that this function, the reciprocal of the classical Weber–Fechner relation, is well documented and seems to be the most relevant in the context of our experimental paradigm. Another important consideration is that, when applying this function for deriving the (differential) spectral sensitivities of the L' and M' gain systems (Fig. 6), we arrived at the π_4 and π_5 action spectra. So, whatever is measured with two-colour thresholds, and this includes $\zeta(x)$, is probably also at the root of our experimental findings.

The hypothesis of disparate cone and gain (i.e. π) spectral sensitivities runs counter to the notion that the π spectral distributions represent cone absorption spectra. Supporting evidence for the latter proposition may be found in the fact that π_5, π_4 and (truncated) π_3 spectra can be fitted with linear combinations of Stiles and Burch's (1958) colour-matching functions (Estevez and Cavonius, 1977; Pugh and Sigel, 1978). However, these results only show the feasibility of that idea. There is other evidence arguing against it, in particular with regard to π_1 and π_3 (e.g. Pugh, 1976; Pugh and Mollon, 1979), but also with respect to π_5 (Boynton *et al.*, 1966) and π_4 (Williams and McLeod, 1979). And then there is the problem, of course, of the enigmatic π' mechanisms (Stiles, 1959). It is a pity that despite the impressive advances in microspectrophotometry, the recordings of primate cone pigments (e.g. Bowmaker and Dartnall, 1980; Bowmaker *et al.*, 1980) still lack the precision (and density range) that is required for (in) validating the current psychophysical candidates for cone absorption spectra.

Sigel and Pugh (1980) re-examined the disputed (cone) status of π_5 and concluded that one cannot disprove (but neither prove) the hypothesis that the first log unit of π_5 adaptation is determined exclusively by the quantum-catch of the L cones. However, this leaves still another 4 log units of change in gain that probably are controlled by more than one cone type. It should be mentioned in this respect that Cicerone *et al.* (1975) already concluded (from the invariance of unique hues) that at least one receptor type has its gain changed by other receptor types.

Ingling and Tsou (1977) have shown that π_5 can be described as a vector sum of weighted responses from achromatic and chromatic channels, where the latter are linear combinations of Smith and Pokorny's (1975) cone fundamentals (which are very similar to those of Vos and Walraven). So, it is possible, in principle, to describe the π mechanisms as resulting from interactions between different classes of cones.

Physiological data have often yielded spectral sensitivities that seemed to reflect the action of a single pigment, but that, on the evidence of microspectrophotometric data, probably should be considered as being the result of interactions among different classes of cones (Abramov, 1972). Sirovich and Abramov (1977) have proposed a model for such "pseudo-pigments" that might also account, perhaps, for the relative stability of the π spectra.

Although the model presented here enables an accurate quantitative account of the data this does not mean, of course, that there are no alternative hypotheses to be considered. It is conceivable, for example, that if we assume a gain function other than $\zeta(x)$ we might also arrive at acceptable data fits. One even might speculate that, by applying a gain function with a slope <1, only a single set of spectral sensitivities might suffice to describe the data. However, one would thus deny Weber's law and forfeit the link with Stiles' π mechanisms. For the present, therefore, we would rather pursue the present line of investigation, and try next to gain more insight in the nature of the "interface" between cone and π spectra.

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* Violations of non-additivity have been observed in conditions where the (transient) test signal is less well separated from the (steady) back-ground signal, either spatially, or temporally (Shevell, 1978). Otherwise, deviations from non-additivity are within experimental error (Walraven, 1979), although there is still some dispute going on as to what happens with test flashes that are virtually at threshold (Shevell, 1980). However, the present data were collected with test fields of the same retinal illuminance as the backgrounds on which they were superimposed. Under such conditions one may safely disregard any effect of background additivity.

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4.3 EFFECT OF CHROMATIC ADAPTATION ON THE SUBJECTIVE NEUTRAL POINT: THE ROLE OF CONTRAST, LUMINANCE, AND BACKGROUND COLOR

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Abstract - Two superimposed test lights of complementary spectral composition were presented as 60'-90' incremental test flashes on 480' steady background fields. Two observers adjusted the ratio of the two test lights to maintain an achromatic appearance under various conditions of adaptation that varied with respect to background luminance, chromaticity and stimulus contrast. The adaptive hue shifts thus measured confirm and extend a model of chromatic adaptation that has the following properties: (1) Non-additivity of (flashing) test and (steady) conditioning field, in the sense that the background, although adding physically to the testflash, only affects its hue by way of altering the gain cone pathways. (2) Vos-Walraven (1971) cone spectral sensitivities (3). Adaptation sites that have the same action spectra as Stiles' π_5, π_4 and (modified) π_1 mechanisms, and that generate receptor-specific attenuation factors (Von Kries coefficients) according to Stiles' generalized threshold vs. intensity function $\zeta(x)$.

INTRODUCTION

Perceived color depends on many variables, one of which is the state of chromatic adaptation, or color tuning of the eye. There have been many attempts to elucidate the mechanisms subserving chromatic adaptation, but a firm theoretical base is, as yet, still lacking. The point of departure for most theoretical models of chromatic adaptation phenomena has been the von Kries (1878, 1905) coefficient rule, which states that chromatic adaptation results can be described in terms of receptor-specific attenuation factors (coefficients). An important implication of the coefficient rule is the *proportionally theorem* (von Kries, 1905), according to which adaptation of the eye has the same effect as reducing all stimuli acting on the eye to certain fractions of their values. That is, dim and bright test flashes (low and high luminance contrasts) should be affected in the same way. However, numerous tests of the coefficient rule and its corollary, the *proportionally theorem*, have indicated that it often does not provide an adequate account of the changes in color appearance under chromatic adaptation (e.g., Walters, 1942; Wright, 1947; MacAdam, 1956; Hurvich & Jameson, 1958). Yet, the failure of the von Kries scheme as a complete account of chromatic adaptation does not render the coefficient rule irrelevant. Rather, most recent models of chromatic adaptation have incorporated a von Kries-type (multiplicative) transformation in conjunction with a second "incremental" (additive or subtractive) process (e.g., Hurvich & Jameson, 1958; Jameson & Hurvich, 1972; Walraven, 1976; Shevell, 1978). However, although the necessity of a two-process model of chromatic adaptation is generally acknowledged, there is less agreement about the nature of the second process.

Walraven (1976) performed experiments in which the stimulus configuration of a focal stimulus with an annular surround was obtained by superimposing incremental test flashes on top of a steady uniform background. This stimulus arrangement had a technical advantage over classical methods of producing the stimulus (there was perfect contiguity between the test field and surround), but more importantly, it invited an analysis that revealed an interesting principle of visual processing. That is, it turned out that the (steady) background, although physically adding to the test field did not seem to mix with it. The effect, called "discounting the background", can be described as a subtractive process (the afore-mentioned second process), but we prefer to treat it in terms of contour or transient processing (high-pass filtering), as discussed by Walraven (1977). It has been shown (Walraven, 1976) that, when acknowledging the discounting process, the proportionality theorem does indeed obtain.

Recently it has further been shown (Walraven, 1981) that the gain mechanisms responsible for the chromatic adaptation effect may actually be the same mechanisms that are revealed by the heterochromatic threshold technique, i.e. the well-known π mechanisms (e.g., Stiles, 1953, 1978). This conclusion was based on data covering a wide range of background illuminances (0.5 - 5 log td), but the wavelengths employed were restricted to the red-green range of the color domain, thus stimulating only the middle- and long-wavelength-sensitive cones.

In the present investigation which focusses on the chromaticity rather than the intensity aspect, a white test field was used and a broader range of background colors, thus allowing sensitivity changes to be measured in all three cone types. Moreover, we also varied the luminance ratio of test and background, a crucial variable for testing the applicability of the von Kries coefficient scheme.

METHODS

Apparatus and stimuli

Fig. 1 shows a schematic representation of the apparatus, a four-channel

Maxwellian-view optical system. The source (S) for each channel was a 100 Watt tungsten-iodine lamp (run at 8 amps). The test field consisted of two beams (originating at S_3 and S_4) that were combined by a beam splitter, collimated and passed through a 60'-90' annular field stop (FS_t). The annulus was presented as a flashed increment (3 s on, 3 s off) and was superimposed on a 480' circular background field. A luminance profile of the stimulus is shown in the inset of Fig. 1. The two test beams, ΔI_λ and $\Delta I_\lambda'$, were chosen to be of complementary spectral composition for the individual observers. The spectral composition of the background, ΔI_λ, was identical to that of, one of the test beams. This background originated with S_1 or S_2, depending upon whether a narrow-band (M_1) or broad-band (F_1) light was required.

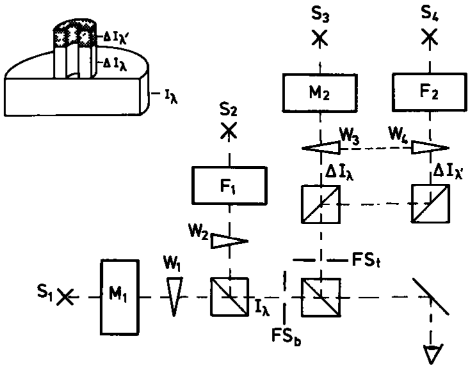

Fig. 1. Maxwellian-view optical system. Abbreviations: S = source, F = broad-band filters, M = monochromator, W = neutral density wedge, ΔI_λ and $\Delta I_\lambda'$ = incremental test lights, I_λ = background field, and FS = field stop.

The intensity of the beams was controlled by calibrated neutral density filters (Agfa) and counter-rotating neutral density wedges in the test-field beams. The latter were under computer control so that the observer could vary the luminance ratio ($\Delta I_\lambda/\Delta I_\lambda'$) of the two beams without changing the retinal illuminance of the increment in question ($\Delta I_\lambda + \Delta I_\lambda' = c$).

The entrance and exit slits of the grating monochromators were set at 1.5 mm to yield a 10 nm bandpass at half power. Several types of filters were used to shape the spectral distribution of S_2 and S_4. The half-bandwidth of the Schott double interference filters (DAL) was 10-20 nm. These filters, and a Schott glass filter (RG5), were specified by their equivalent wavelength, as determined by matching to a monochromatic beam when the broad-band and monochromatic beam were presented in bipartite fields. The chromaticity coordinates of the (purple) Kodak Wratten filters were determined *in situ* by a photoelectric tristimulus colorimeter (Hoelen, Verkaik & Walraven, 1970). We obtained the following values: W32, x = 0.555, y = 0.230; W36, x = 0.336, y = 0.105; and, for a combination of W32 and W34A, x = 0.457, y = 0.158. The accuracy of these calibrations was verified by a common intersection at the (subjective) white point when the broad-band lights were mixed with the empirically determined monochromatic complementaries.

Retinal illuminance was determined by converting the output of a calibrated lux meter to trolands. This measurement was made only for a 568 nm reference light; all other beams were equated to this reference (for each subject) by heterochromatic flicker photometry or by direct homochromatic brightness matching.

Observers

Two adults, both with normal trichromatic vision served as observers. Observer J.W., one of the authors, has had extensive training as a psychophysical observer, whereas observer N.B. had only limited experience and was naive as to the purpose of the experiment.

Psychophysical task

The observer's task was to maintain an achromatic appearance of the test field by adjusting the ratio of the two complementary lights comprising the test stimulus. As was to be expected already from earlier studies, in which a yellow test field was used (cf. Walraven, 1976), we found that observers can make reliable white point settings without a reference field. This confirms earlier reports by Helson and Michels (1948), and Bergström, Derefeldt & Holmgren (1978).

The effect of chromatic adaptation on the white point locus was measured for 11 different chromatic backgrounds. Three retinal illuminance levels were used for each of the backgrounds: 5, 25, and 250 td. At each level of each of the chromatic backgrounds there were three levels of luminance contrast: 0.2, 1.0 and 5.0. Contrast was defined as the ratio of the incremental test field luminance to the background luminance, i.e., $(\Delta I_\lambda + \Delta I_\lambda')/I_{\lambda_A}$. For N.B. a contrast of 0.5 was used instead of 0.2 because her settings at the latter contrast level were extremely variable. Thus, the matrix of chromatic background x background illuminances x contrast levels yielded 99 conditions, although in a few conditions, all involving the yellow background used, no measurements could be made due to the relatively low short-wave output of the optical system.

Determination of complementaries and subjective white point

The complementaries that were used for the (subjective) white point settings, i.e. lights that were complementary to the lights used for the backgrounds, were determined empirically. Thereto the observer was presented with a mixture of a fixed light (of the same colour as a background) and a light that could be varied with respect to both its wavelength and intensity (while keeping the retinal illuminance of the mixture constant). The latter was varied until the (complementary) wavelength was found that yielded the observer's subjective white point. This procedure, which is similar to Guild's (1925-1926) method of vector colorimetry, was repeated for all background wavelengths. The intersection of lines connecting the various complementary pairs provided a rough, graphical, fix of the white point locus. A more precise determination was obtained from averaging over the chromaticity coordinates of the various white point determinations.

The chromaticity coordinates of the white point locus were $x = 0.30$, $y = 0.32$ for J.W., and $x = 0.38$, $y = 0.37$ for N.B. The white point locus was found to be invariant for both observers over a range of 3-4 log units. Therefore, the results were not likely to be complicated by the non-linearity of the yellow-blue opponent chromatic channel (Larimer, Krantz & Cicerone, 1974; Werner & Wooten, 1979).

Procedure

Each session started with at least 7 minutes of dark adaptation followed by the presentation of the complementary primaries of the test flash. The observer then adjusted the light ratio of the complementaries so as to obtain the dark-adapted white point setting. These settings were made for at least 3 intensity levels, corresponding to the test field intensities used for the 3 contrast levels of the 25 td background. A minimum of 5 settings was made at each intensity level. The mean white point settings for a given session occasionally showed a slight deviation from the original determinations in its exact chromaticity coordinates. A transformation was accordingly applied to all data (neutrally and chromatically adapted conditions) for that session such that all adaptive hue shifts could be evaluated relative to a fixed reference (the average white point).

In each daily session only one chromatic background was tested. For each background all 3 intensity levels were evaluated in order of increasing background illuminance. For a given background intensity the observer began by viewing the background in the absence of the test field for at least

4 minutes. Following this adaptation period, the test flashes were presented against the steady adapting field for the medium contrast level, followed by high, low, and again medium contrast. At least 5 settings were made for each contrast and illuminance level.

In all conditions the observers were allowed as many stimulus presentations as they felt were necessary for confident settings. It is important to note that the observer never felt the need for changing the predetermined complementaries. Thus satisfactory settings could be obtained by just varying the ratio of these lights.

RESULTS

The chromaticity of lights that appear achromatic

When a focal stimulus is viewed against a chromatic adaptation field a hue is induced in the test stimulus that is complementary, or at least approximately complementary, to that of the adapting light. To restore the test flash to its appearance in the neutral state of adaptation it is necessary, therefore, to add light to the test flash that is of the same chromaticity as the background (e.g., Helson & Michels, 1948; MacAdam, 1950; Jameson & Hurvich, 1961). This fundamental fact of chromatic induction is illustrated in Fig. 2, which presents the data of the various conditions of chromatic adaptation in terms of CIE chromaticity coordinates. The three panels at the top and bottom show the data of J.W. and N.B. respectively. What is plotted here are the chromaticities of the total test stimuli (i.e. the mixture of test plus background light). So, no allowance has been made, as yet, for the assumed non-additivity of test and background (discounting principle). For each observer, the different illuminance levels of the background (I_{λ_A}) are presented in separate panels. Different symbols within the panels are used to denote the three contrast levels. The data points thus represent the chromaticity of lights that appear achromatic under various conditions of chromatic adaptation. The stimulus that is perceived as white in the dark adapted state is indicated by the central cross in each diagram. The lines radiating from this center to the circumference of the CIE diagram connect with the chromaticities of the adapting backgrounds used, which are all located on this circumference except for the somewhat desaturated extra-spectral (purple) background. Since the complementary lights under neutral adaptation remained complementaries under chromatic adaptation, the data points necessarily fall on the lines radiating from the center to the circumference.

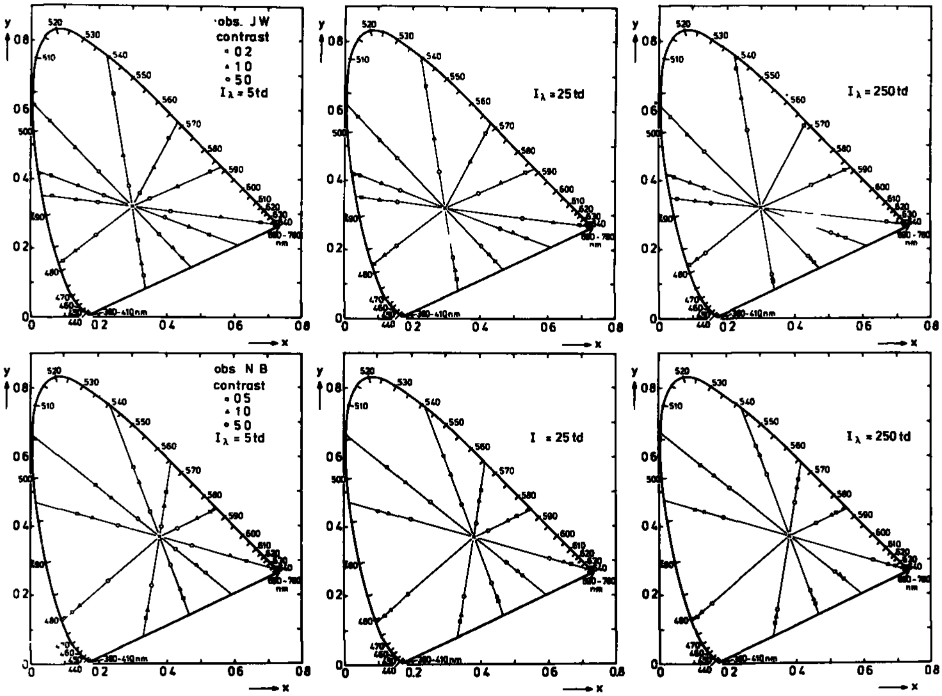

Fig. 2. Chromaticity coordinates of lights that were adjusted to appear achromatic under different conditions of chromatic adaptation. Coordinates were calculated on the basis of the total stimulus configuration ($\Delta I_\lambda + \Delta I_\lambda' + I_\lambda$). Each row of 3 panels presents the data of a single observer. Results for each of the 3 retinal illuminances of the background, I_λ, are presented in separate panels while the different contrasts are denoted by different symbols. Lines connect the white point under neutral adaptation (the central cross) with the chromaticity coordinates of the adapting backgrounds.

The retinal illuminance of the background increases across the panels of Figure 2 from left to right from 5 to 250 trolands, and correlated with this increase is, as expected, an increasing adaptive hue shift of the achromatic point. Furthermore, the shift for any given luminance increases with decreasing contrast, a phenomenon that would not be expected on the basis of a simple von Kries transformation (the latter would yield the same hue shift for all contrasts).

The importance of the luminance relationship between test and adaptation field is further illustrated in Fig. 3, which shows the same data as before (for observer J.W.) but now with the contrast fixed within a panel; different symbols now denote different retinal illuminances of the background. These data can be regarded as the aperture-mode analogue to a color

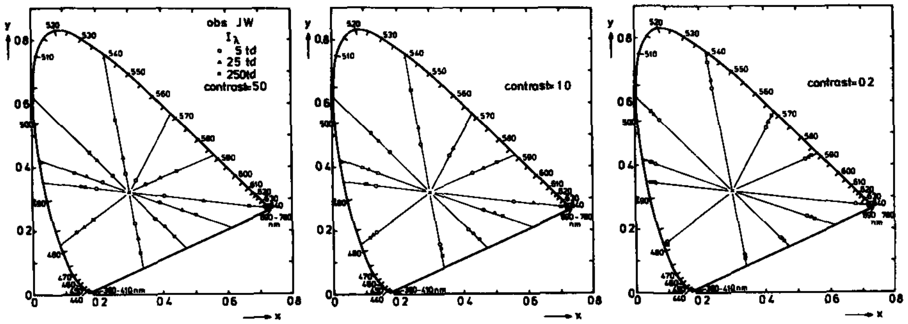

Fig. 3. The same data as shown in Fig. 2, but now plotted with contrast as parameter.

constancy experiment. A change in background illuminance now implies a change in overall light level. Quite clearly, an increase in light level causes a hue shift (although this may be very small for low contrasts), so exact color constancy does not obtain under these laboratory conditions.

The role of luminance contrast on induced color has always been notoriously difficult to capture in straightforward formulations (e.g., Valberg, 1974; Bergström et al., 1978). This is the main reason for the often reported problems with the application of the von Kries coefficient law. We propose, following Jameson & Hurvich (1972), that this is due to the confounding effect of a second process, a process which, in the present experimental paradigm, we believe to be accounted for by the afore-mentioned discounting effect.

Discounting the background

According to our hypothesis the background and the test flash are processed separately. Therefore, a more appropriate way to illustrate the adaptive hue shifts is to present the chromaticities computed not on the whole physical stimulus, but on the basis of the incremental portions of the stimulus ($\Delta I_\lambda + \Delta I_\lambda'$), that is, with the background contribution deleted. The data are presented in this way in Fig. 4. In this figure the magnitude of the adaptive hue shift appears to be independent of luminance contrast, thus confirming the validity of von Kries' proportionality theorem. It also confirms our proposition that the effect of luminance contrast observed in Fig. 3 is simply a consequence of not acknowledging the discounting phenomenon.

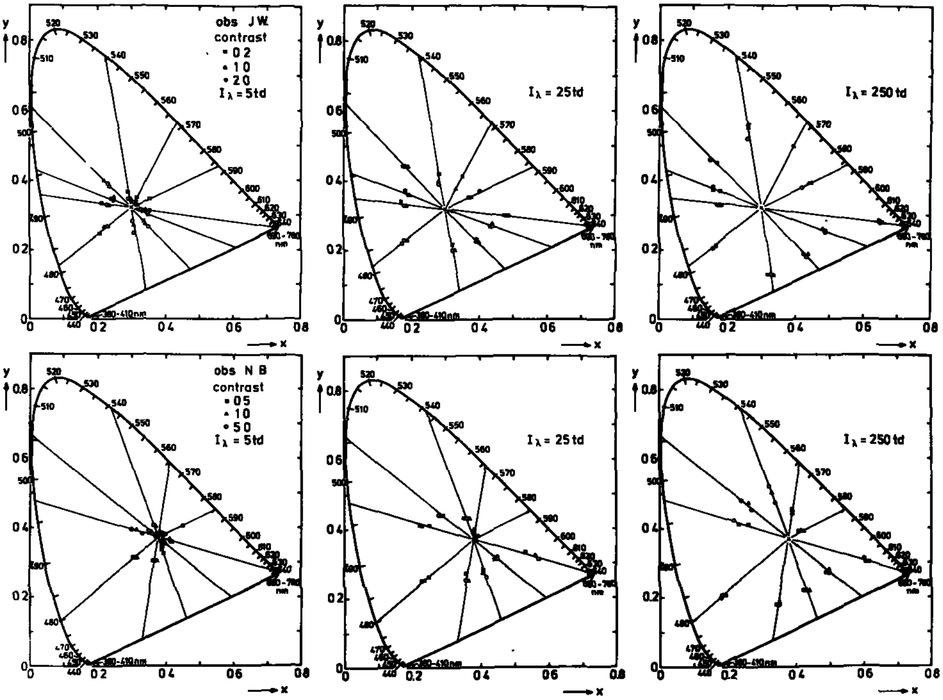

Fig. 4. The same data as shown in Fig. 2, but now with the chromaticity coordinates of the test field calculated on the basis of the (flashed) incremental portion ($\Delta I_\lambda + \Delta I_\lambda'$).

Another way of showing that the proportionality theorem applies is by plotting ΔI_λ as a function of $\Delta I_\lambda'$. For each background level the ratio $\Delta I_\lambda/\Delta I_\lambda'$ should be constant for a given background condition; so, ΔI_λ *vs* $\Delta I_\lambda'$ should fit a straight line with slope of unity (on a double log plot). For each background chromaticity one can thus plot three sets of ΔI_λ *vs* $\Delta I_\lambda'$ (one for each background level), with each set consisting of three points (one for each contrast). Fig. 5 shows the data thus obtained for each background chromaticity, condensed by vertical translation (thus generalizing over background level) to a straight line with slope of unity. Any deviation from this 45° line is a violation of the proportionality theorem and/or the discounting principle. The data were fitted to the function by eye, but slope calculations for each set of 3 data points (for the different contrasts of a fixed background level) confirm the subjective impression that the fit was indeed acceptable. The mean slope was 0.99 for J.W. (range: 0.91-1.06) and 1.01 for N.B. (range: 0.81-1.15). These results show that

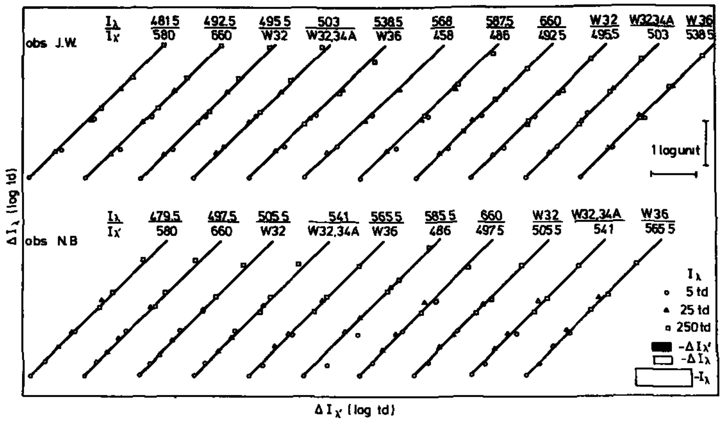

Fig. 5. Log ΔI_λ plotted as a function of log $\Delta I_\lambda'$ for each condition. The placement of the origin for each set of data is arbitrary. The sets of data points for each background level (which are indicated by the symbols in the inset) are vertically translated to facilitate comparison with the solid line having a slope of unity. The chromaticity of the increments for each condition is indicated by I_λ (ordinates) / I_λ' (abscissae). The background chromaticity is identical to that of the increment that is plotted on the ordinate.

the deviations of non-additivity and/or proportionality are quite small, too small anyway to warrant a more complex type of analysis.

Determination of the von Kries coefficients

Since the data apparently lend themselves to a description in terms of the von Kries coefficient rule, we set out to determine the coefficients in question. Denoting the spectral sensitivities of long-wave-sensitive, middle-wave-sensitive and short-wave-sensitive cones, by L, M and S respectively, the associated coefficients may be defined as,

$$k_L = L/L_A \quad (1a)$$
$$k_M = M/M_A \quad (1b)$$
$$k_S = S/S_A \quad (1c)$$

where L_A, M_A and S_A are the cone spectral sensitivities after chromatic adaptation.

According to theory the observed changes in the white point settings should define the von Kries coefficients, that is,

$$k_L = \Delta Q_L/\Delta Q_{LA} \quad (2a)$$
$$k_M = \Delta Q_M/\Delta Q_{MA} \quad (2b)$$
$$k_S = \Delta Q_S/\Delta Q_{SA} \quad (2c)$$

where ΔQ is a quantity that is proportional with the effective (incremental) quantum catches of cones with action spectra L, M and S (before adaptation), and L_A, M_A, S_A (after adaptation). We hereby assume (cf. Walraven, 1981) that the quantum catch of, say, the L cones, may be represented by $\Delta Q_L = K \int \Delta I_\lambda l_\lambda d_\lambda$, where l_λ is a *relative* spectral sensitivity and ΔI_λ is measured in trolands.

The quantum-catch ratios in eq. (2), and hence, the von Kries coefficients, can be computed from the x and y chromaticity coordinates of the white point before (W) and after (W_A) adaptation. The procedure is to determine first the CIE tristimulus values (X, Y and Z), and then make the conversion from CIE to L, M, S color space. We use the cone spectral sensitivities as derived by Vos & Walraven (1970) - tabulated by Vos (1978) - for which the conversion formulae in question are given by Vos (1978). Actually the latter are in terms of the x'_λ, y'_λ coordinates of Judd (1951), but this poses no problem since the conversion from the CIE (1931) x_λ, y_λ chromaticity coordinates to those of Judd is also given by Vos (1978). We thus arrived at the following expressions for the computation of the von Kries coefficients

$$k_L = \frac{0.1552\ X'_W + 0.5431\ Y'_W - 0.0372\ Z'_W}{0.1552\ X'_{W_A} + 0.5431\ Y'_{W_A} + 0.0372\ Z'_{W_A}} \qquad (3a)$$

$$k_M = \frac{-0.1552\ X'_W + 0.5431\ Y'_W - 0.0372\ Z'_W}{-0.1552\ X'_{W_A} + 0.5431\ Y'_{W_A} - 0.0372\ Z'_{W_A}} \qquad (3b)$$

$$k_S = 0.0073 \frac{Z'_W}{Z'_{W_A}} \qquad (3c)$$

where X' and Z' can be computed by applying the colorimetric relations

$$X' = \frac{x'}{y'} Y', \quad Z' = \frac{z'}{y'} Y' \qquad (3d)$$

The quantity Y' is the luminance of the stimulus in accordance with a revised CIE luminosity function (cf. Vos, 1978). Actually this was irrelevant for the present calculations since the luminance of our test stimulus was the same before and after adaptation ($Y'_W = Y'_{W_A}$) and thus factored out.

The link with π mechanisms

After computing the von Kries coefficients that describe our data we tried to find out how these might be related to the retinal illuminance and the color of the background used. Recent work (Walraven, 1981) already suggested that the coefficients can be described in terms of attenuation or gain factors generated by mechanisms with the same action spectra and gain characteristics as Stiles' π mechanisms. The gain characteristic, by which we mean the relationship between attenuation factor (k) and input (x) to the gain box, is described by Stiles' functions $\zeta(x)$, which is tabulated by Wyszecki & Stiles (1967). It was assumed (cf. Walraven, 1981), that the quantity x, i.e. the effective quantum catch as "seen" by a given π mechanism, can be expressed in terms of the retinal illuminance of the background multiplied by the normalized π spectral sensitivity at the wavelength in question. We will refer to x as "selective" trolands. Thus, for example, a 1000 td blue (480 nm) background which stimulates, π_5, π_4 and π_1 in the ratio 0.328 : 0.474 : 0.198, will produce respectively 328, 427 and 198 selective trolands*.

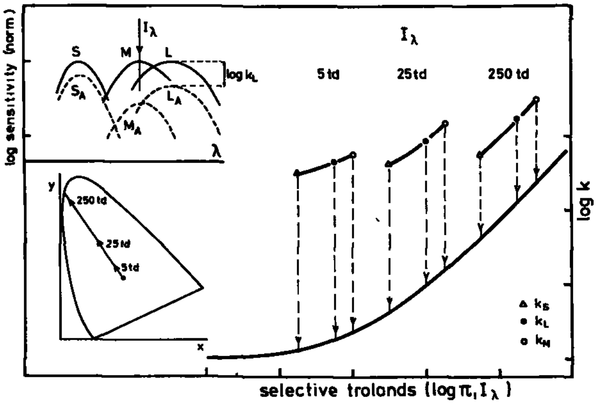

Fig. 6. Diagram illustrating the procedure in testing the model prediction that the von Kries coefficients that can be derived from the adaptive hue shifts of the white point (as shown at the left) can be described by Stiles' function $1/\zeta(x)$. That is, one should find for any given background I_λ, that plots of k_L, k_M and k_S as a function of selective trolands (i.e. $\pi_5 I_\lambda$, $\pi_4 I_\lambda$ and $\pi_1 I_\lambda$ respectively) can be made to fit $1/\zeta(x)$, merely by a vertical translation (*en bloc*), as illustrated by the dashed arrows. See text for further explanation.

To test whether the present results are consistent with the model proposed we proceeded as follows. First, using eq. (3), we calculated the von Kries coefficients that describe the shifts of the neutral point shown in Fig. 4. In Fig. 6, which will serve only as an illustration of what we did,

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* Boynton & Whitten (1972) computed a similar quantitity which they called effective troland. That term would have been preferred to the one used here were it not for the fact that it has already been formally defined in another way (Wyszecki & Stiles, 1967, p. 213).

the shifts in white point are shown (qualitatively) that result from adaptation to a green background, for each of the three adaptation levels (5, 25 and 250 td). Also shown are the attending reductions in cone spectral sensitivities (dashed curves) that belong, for example, to the 250 td background condition. Note that the vertical separations between the adapted and non-adapted cone (action) spectra define the von Kries coefficients. Also note, however, than an *en bloc* vertical shift of the three dashed curves would not affect the predicted adaptive shift of the white point (it would only connote a change in brightness of the test field). This implies that the von Kries coefficients as calculated with eq. (3) are only relative coefficients; each set of coefficients that belongs to a given background condition may be multiplied by a constant.

The next step was to draw the function $\zeta(x)$, as shown at the right in Fig. 6, i.e. the function that should describe the relation between von Kries coefficients and selective trolands. This was tested by plotting the von Kries coefficients as a function of the associated selective troland values, and then vertically translate each triplet (k_L, k_M, k_S) for a best fit with the function $1/\zeta(x)$. This procedure, which is indicated by the dashed arrows in Fig. 6, is justified (and necessary) because, as noted above each triplet relates to *relative* coefficients.

Some of the results obtained with the procedure outlined above are shown in Fig. 7. All values of k_M and k_L indeed fit the single function $1/\zeta(x)$, but the values of k_S are systematically laterally displaced. It should be mentioned in this respect that when vertically translating each

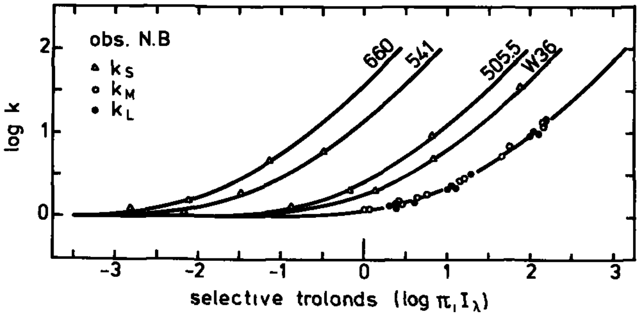

Fig. 7. Fit of the relative von Kries coefficients (as derived for four different backgrounds) to the function $1/\zeta(x)$. The solid curves represent the same template shifted along the abscissae to provide an optimal fit to the data points. Selective troland values were calculated on the basis of π_1, π_4, and π_5 for k_S, k_M, and k_L, respectively.

coefficient triplet for a best fit with $1/\zeta(x)$, we only strived for a fit with k_L and k_M, thus placing all the error on k_S, rather then dividing it equally. However, the systematic nature of the displacements suggests that the poor fit of k_S is not artificial, but rather might be due to an underestimation of the selective troland values assigned to the gain mechanism subserving the S cones. In other words, the π_1 action spectrum does not provide enough input to account for the gain changes we derived.

It was found, however, that a modified π_1 action spectrum, denoted by π_1^*, could bring k_S in register with $\zeta(x)$. It could be described by

$$\pi_1^* = a(\pi_1) + b(\pi_4 + \pi_5) \tag{4}$$

The resultant spectral sensitivity of this mechanism (Fig. 8) is equivalent to Stiles' π_1 for wavelengths below 500 nm, and to $\pi_4 + \pi_5$ for wavelengths above 520 nm, due to the fact that a >> b. Note again that the π values in eq. (4) relate to relative spectral sensitivities (i.e., $\pi_1 + \pi_4 + \pi_5 = 1.0$). The constants a and b were different for the two observers, as might be expected in view of their different achromatic point loci. For J.W. a = 6.70 and b = 0.09, whereas for N.B. a = 8.19 and b = 0.25. The need for the additional amplification of the gain system of the S cones was not entirely unexpected. It may be related to the complex nature of the short-wave adaptation sites (e.g., Pugh & Mollon, 1979; Pugh & Larimer, 1980), as well as to a general underestimation of the sensitivity of the short-wave system

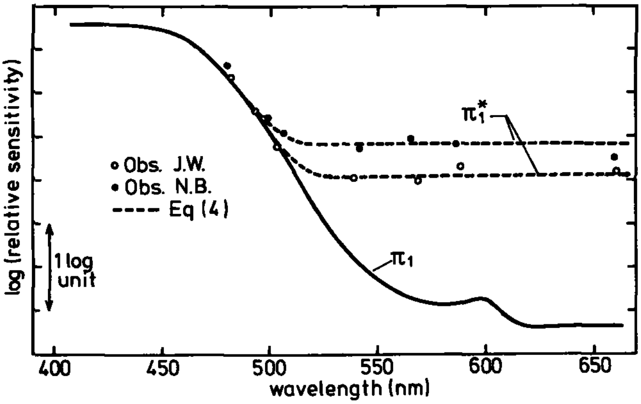

Fig. 8. Relative spectral sensitivity of π_1^*, as calculated with eq. (4), and π_1 (solid curve). The data points represent the π_1^* sensitivities that would bring k_S in register with k_M and k_L, when the latter are pinned to the function $1/\zeta(x)$, as in the sample shown in Fig. 7.

when employing flicker photometry. Boynton & Whitten (1972) made a similar assumption (they multiplied their calculated S cone response by a factor of 25) in modelling monkey late-receptor potentials.

The results of fitting the von Kries coefficients to $1/\zeta(x)$ but now employing π^*, rather than π_1, are shown in Fig. 9. The deviations from Stiles' function is generally less than 0.1 log unit.

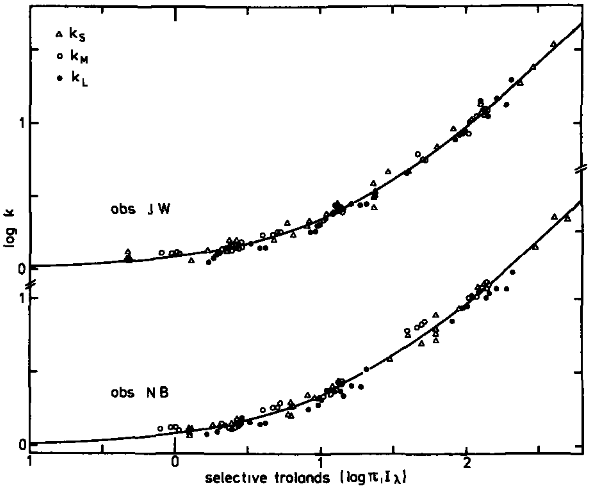

Fig. 9. Computed von Kries coefficients (k_S, k_M and k_L) as a function of selective trolands (π_1^* I_λ, π_4 I_λ and π_5 I_λ). Each set of coefficients (for a given I_λ) was translated vertically (cf. Fig. 6) for a best fit with the function $1/\zeta(x)$.

Data prediction

The results shown in Fig. 9 suggest already that the underlying model will adequately account for the shifts in chromaticity of the (adapted) white point. A more stringent test of the model is obtained, however, by trying to predict the data (as plotted in the conventional format shown in Fig. 2) on the basis of the model assumptions.

The first step was to calculate the von Kries coefficients for each condition according to

$$k_L = 1/\zeta(\pi_5\ I_{\lambda_A}) \quad (5a)$$

$$k_M = 1/\zeta(\pi_4\ I_{\lambda_A}) \quad (5b)$$

$$k_S = 1/\zeta(\pi_1^*\ I_{\lambda_A}) \quad (5c)$$

The $\zeta(x)$ function is tabulated by Wyszecki & Stiles (1967), but for computational purposes it was more convenient to use its close approximation (see Walraven, 1981).

$$\zeta(x) = \left[1 + \left(\frac{x}{x_o}\right)^{0.7}\right]^{-1/0.7} \qquad (6)$$

where x equals $\pi_i \ I_{\lambda_A}$ and x_o, the constant that defines the sensitivity at absolute threshold (the "dark" light), was set at 15 td.

The next step was to work backwards, retracing the steps outlined in Fig. 6. That is, starting from the computed von Kries coefficients using eq. (6), we derived the adapted (Vos-Walraven) cone spectral sensitivities, and from that, the adaptive shifts of the white point. We did that for a large number of backgrounds and thus generated contours of achromatic loci for the different contrasts and retinal illuminances tested.

The data predictions are shown in Fig. 10 by the dashed contours together with the complete sets of data for each observer. The fit between the

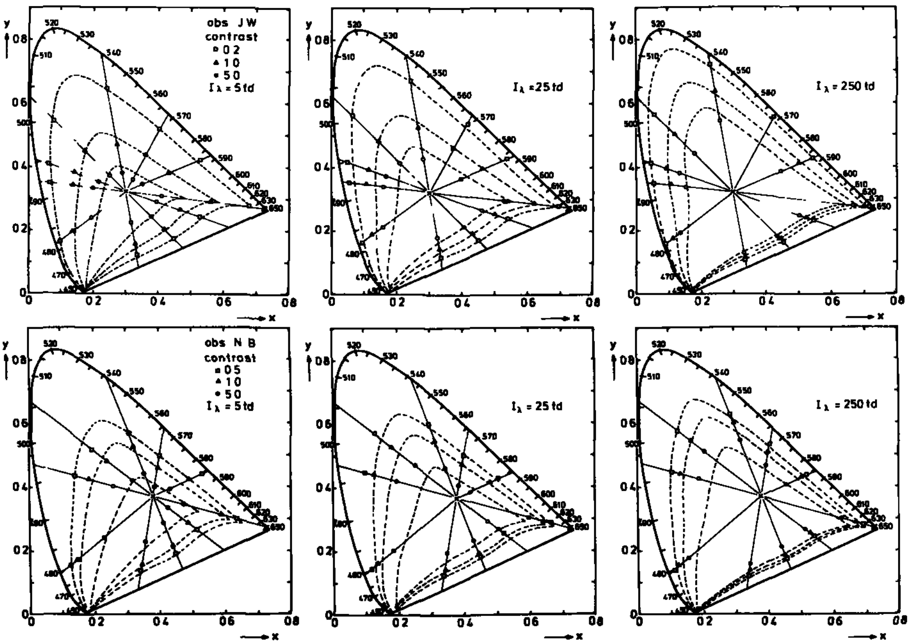

Fig. 10. Chromaticity coordinates of lights that were adjusted to appear achromatic under different conditions of chromatic adaptation (data from Fig. 2). Dashed lines represent achromatic contours predicted for the conditions tested according to procedures described in the text. Coordinates were calculated on the basis of the total stimulus configuration ($\Delta I_\lambda + \Delta I_\lambda' + I_\lambda$).

data and the model predictions is not perfect. However, it seems quite satisfactory when considering that the various parameters, S, M, L, π_1, π_4, π_5 and the $\zeta(x)$ function, all come from external sources, and thus do not necessarily provide the best estimates for our two observers.

Discussion

The present data, covering a broad range of background chromaticities but a limited range of background intensities, confirm the results of previous experiments (Walraven, 1981) that covered a limited range of background chromaticities, but a broad range of light levels. Taken together these results provide rather strong evidence for the model proposed. We are aware, however, that postulating cones with Vos-Walraven (1971) spectral sensitivities on the one hand, while assuming adaptation sites with (modified) π action spectra on the other hand does not make for the most parsimonious model. As was discussed already by Walraven (1981) the validity of the assumption of disparate spectral sensitivities of cone and gain systems is critically dependent on whether Stiles' function $\zeta(x)$ provides a valid description of the change in gain (or von Kries coefficient) as a function of (effective) light input. A gain function with a shallower slope, thus denying Weber's Law (except at very high light levels where pigment depletion is near-proportional with retinal illuminance), might provide a way out for trying to describe the results without introducing the π spectral sensitivities. Actually, this was our starting point for the data analysis. However, although we did by no means pursue this line of investigation exhaustively, we felt that this would lead to a less satisfactory description of the data. Moreover, the choice of Stiles' ζ-function seemed reasonable because it is well documented, both in threshold and supra-threshold experiments (Whittle, 1973), and also because our experimental paradigm is very similar to that used in the (increment threshold) experiments from which the ζ-function was derived. The only difference is that in our type of experiment the test flash probes sensitivity changes in three channels simultaneously, whereas in a two-color threshold experiment sensitivity is presumably measured in one channel at a time.

The modified π_1 action spectrum we introduced (π_1^*) is surprisingly flat in the spectral range beyond 530 nm. This result attests to the fact that the quantity (π_4 + π_5) in eq. (4) is constant for that range (to understand this, consider that π_1, π_4 and π_5 are *relative* sensitivities, summing to unity, and that π_1 is virtually zero in this range). This result implies that for

λ_A > 530 nm, the gain of the short-wave cone may be considered as being determined by the total effective quantum catch, that is, by a mechanism with the spectral sensitivity of the V_λ-function.

It is tempting to speculate that such a mechanism (possibly a luminance or achromatic channel) is also involved in controlling the gain of the L and M cones. It might explain, perhaps, the difference between cone and π spectra - assuming of course, that they are different (see Walraven (1981) for a discussion of this matter). A point of interest in this respect is that π_4 mainly deviates from the Vos-Walraven G-fundamental in the spectral range > 570 nm; similarly, π_5 deviates from the R-fundamental for wavelengths < 540 nm. Now recall that the π_4 and π_5 spectra describe the efficiency of a background (as a function of wavelength) in raising the threshold for seeing a green or red test flash, respectively. So, the afore-mentioned disparities relate to conditions in which there is a relatively large difference in the chromaticities of test and conditioning field. That is, green test flashes on reddish backgrounds (when measuring π_4), or vice versa (when measuring π_5). Consider now what happens when, for example, a green test flash is presented on a red background. It probably will be detected by the M cones, the L cones being desensitized by the conditioning field. If we assume, however, that the signals from the M cones may also be subjected to adaptation from other sources than those operating within the M cones (or cone system) themselves, then it should be kept in mind that, in this condition, the achromatic channel (a possible candidate in this respect) will mainly reflect the activity of the L cones rather than that of the M cones. The effect of such a "cross-talk" would be to enhance the π_4 sensitivity (relative to that due to the M cones alone) in the long-wave range of the spectrum. The same argument may be applied to explain the relatively high π_5 sensitivity in the middle and short-wave spectral range. Note, however, that when the green (red) test flash is presented on green (red) backgrounds - i.e. in homochromatic conditions - the cone system that detects the test flash is also largely controlling the gain (in both the cone-specific pathways and the achromatic channel). So, now the action spectra of gain (i.e. π) systems may indeed reflect those of single cone systems - and they do, over the spectral ranges in question.

It should be stressed that our success in demonstrating the kind of gain or volume control that was already enunciated by von Kries (but that has always been so difficult to isolate) was made possible by assuming that the "second process" in chromatic adaptation can be accounted for by discounting of the (steady) background signal, that is, non-additivity of the background. The non-additivity of backgrounds was also noticed in studies on perceived brightness by Whittle and collaborators (Whittle & Challands, 1969; Whittle, 1973; Whittle & Swanston, 1974), but has been contested by Shevell (1978). As has been shown by Walraven (1979), however, the discounting effect is also reflected in Shevell's (1978) own data (for the condition under concern). Recently, Shevell (1980) presented new results showing a small additive effect. This time he used a much smaller background, however, i.e. with a diameter of 2.7° instead of the 4° employed before (which is already rather small) thus leaving a separation of only 42' between test and background border . Walraven (1973, p. 1748) has shown that an additive effect develops with decreasing separation between test and background border. (Complete additivity will occur, of course, when the contours coincide.) It is quite possible therefore, that, due to the proximity of the background contour some of its color message was picked up at the test field border in Shevell's (1980) experiment.

The model proposed here is intended to account only for chromatic adaptation as manifested in our rather unnatural laboratory conditions. It does provide, however, some of the ingredients that may be incorporated in theories dealing with more complex visual stimuli as employed, for example, by Land and his associates (e.g., Land, 1964; McCann, McKee & Taylor, 1976). The relevance of the von Kries type of sensitivity control is self-evident, of course; it provides a mechanism for maintaining color constancy in spite of changes in the color of the illuminant. However, the fundamental significance of the discounting principle seems less obvious in this respect. It may actually work against color constancy, since it tends to make objects change color when viewed against different surrounds. We believe therefore, that the main function of this mechanism is to provide for economy in information processing (transmission of transients only) rather than to subserve color constancy. It may thus introduce "artefacts", as can be observed in demonstrations of simultaneous color contrast, but it also may provide the eye with important information. Gilchrist (1979, 1980) has pointed out that such a differencing mechanism is precisely what the visual system may need in order to be able to discriminate between "reflectance edges" and "illumination edges", that is, to separate reflectance distributions from illumination distributions.

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V. EPILOGUE

The work presented here provides some new answers to some very old questions. Still, it should be realized that the model we arrived at was developed to describe results obtained under particular conditions, and with a particular method. We have thus found some rules that apply to a visual micro-cosmos consisting of a yellow or white test patch in the centre of a coloured surround. There is nothing wrong with that, this being the only way to get "clean" data, but one should exercise great caution in extrapolating the conclusions to the real world situation. On the other hand, we did not study chromatic induction just for the purpose of explaining an intriguing phenomenon. Rather, we felt that induced colour was a manifestation of a basic principle in the processing of colour. In particular we believe, and in this we follow the gospel of Land (1959), that the visual system assigns colour on the basis of an analysis of the light distribution over the *total* field of view. Therefore, let us venture to make some generalizations.

With due reservation one might conclude from our results, then, that the spatial analysis the visual system performs amounts to a separation of common and differential components. That is, the retinal intensity profile is not treated as a mosaic, as has been the traditional view, but rather, sliced horizontally, into layers. The eye thus extracts edge information which not only makes for economy in processing, but may also aid in solving a problem that was already recognized by Koffka (1935). He pointed out that the visual system is confronted with the difficult task to separate spatial distributions of reflectances (that is, object properties) from inhomogeneities in the pattern of illumination (shadows and spots of light). Recently, Gilchrist (1977, 1980) has taken up this question again (see also Beck, 1965;

Bergström, 1977) and concluded that the first step in resolving this problem might be provided by the mechanism of background separation (or discounting) that was observed in our experiments.

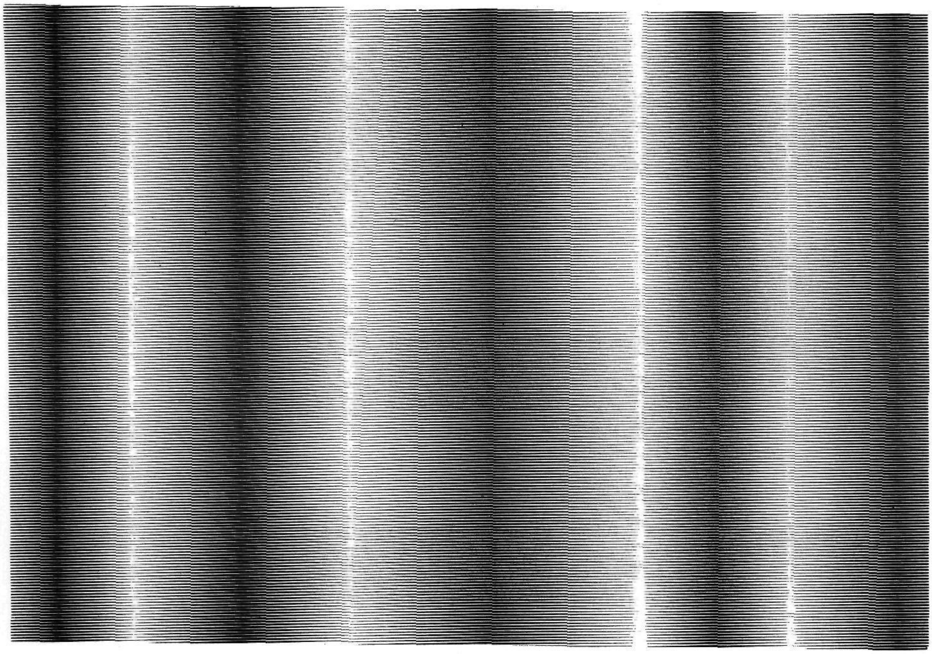
The same mechanism may also account for a hitherto unexplained negative result of the work of Land (1959a, b). Land has become famous for his demonstrations showing that a whole gamut of colors can be produced by a mixture of just two differently coloured lights (a white and a red for example). This was achieved by superimposing two projected images from photographic transparencies showing the same scene photographed through a long-wave and short-wave transmitting filter, called the long and the short record, respectively. There have been attempts to explain Land's results in terms of already existing formulae for "colour conversion" (e.g., Judd, 1960), but these fail to explain why not *any* patterned mixture of two colours produces the same colour gamut as observed in the Land demonstrations. For example, and this brings us to the afore-mentioned negative result, if one of the records is removed from the projectors, the resultant homogeneous light from that projector no longer seems to interact with the patterned image from the other projector, but only produces a desaturating "wash"; the scene is perceived as varying in a single hue. This is what we should expect if the visual system separates the "reflectance" pattern, as produced by the projector that contains the record, from the superimposed homogeneous illumination (the background) produced by the other projector. It can do this if it analyzes the retinal image profile in the way we proposed, that is, by horizontal slicing.

Land concluded from his work that each cone system makes its own reflectance record of the objects in the visual scene, normalized with respect to the highest reflectance present (as "seen" by the system in question). Thus each point in the field of view is assumed to be characterized by the three rank orders by which it is registered in the cone's reflectance records. This implies that colours may remain fairly constant despite changes in the colour of the illuminant, for rank orders of natural (i.e. broad-band) colours are quite resistant against changes in illumination. This hypothesis is certainly consistent with the high degree of colour constancy evidenced by Land's demonstrations. This hypothesis would also predict, however, that changes in sensitivity of the photoreceptors would not affect colour perception. For, altering the responsiveness of the receptors would not alter the rank order in their (normalized) reflectance records. So, there is actually no need for a von Kries type of adaptation mechanism in Land's theory. However, the results of our chromatic adaptation experiment, like those of others, show that colours do not remain invariant during adaptation, a result that can be accounted for by selective receptor attenuation, but only if we reject Land's hypothesis. We conclude, therefore, that Land's model has to be reconsidered, or anyway modified, in order to accommodate the findings from chromatic adaptation studies.

Turning now to the adaptation model we arrived at, we feel that some real progress has been made in showing that the von Kries coefficient rule seems to be valid after all, provided that allowance is made for the "second" process. Also the model's assumption that the mechanisms controlling the von Kries coefficients can be related to Stiles' π mechanisms is not without theoretical significance. For that very reason, however, it should be further tested.

It is hard to say to what extent this model may be generalized to predict perceived hue in more natural adaptation conditions than the ones we have studied. In the field of applied colour science there exist a number of adaptation formulae that were developed for exactly that purpose (e.g., McAdam, 1963; Richter, 1973; Bartleson, 1977; Takahama, Sobagaki & Nayatani, 1977). Sound criteria for evaluating the validity of the various propositions are lacking, however. In general the models are only suited (at best) for describing chromatic adaptation in the experimental conditions that produced the data from which they were derived. It is not surprising, therefore, that their predictions, even for relatively small variations in illuminant show but little agreement (cf. Bartleson, 1978). What is needed is a set of data obtained under conditions that are representative for a more normal viewing situation. Such a set might probably yield the kind of universal adaptation formula we are still looking for. The present formulations, and that includes our own (even if it is of a less empirical nature), are probably still too much "experiment oriented". This applies foremost, probably, to those derived from studies that did not employ surface colours (reflected light), but rather, self-luminous stimuli (aperture colours), as is true for our own studies.

The above reservations with respect to the extrapolation of our model to practical situations should not be taken as signifying that the mechanisms we have found are irrelevant for normal viewing conditions. Rather, we realize that there are probably more mechanisms involved in colour perception than those isolated in our experiments. That is to say, the system may employ sophisticated strategies that we are not aware of until we provide the kind of stimuli for which they have been evolved. In this respect we think in particular of mechanisms for evaluating the illuminant. Buchsbaum (1978) has shown how the visual system may be treated as an optimum recognizer, applying known principles from (statistical) communications theory for assessing the spectral parameters of the illuminant. It is thereby assumed that the visual system employs an internal model or template to arrive at some kind of null-hypothesis. That the eye may indeed resort to such guessing techniques can be illustrated by the picture below. It will be seen as a corrugated surface with more or less cylindrical folds with shining highlights. When turned around over 90°, however, one may see quite a different picture. The highlights have disappeared and the folds have been transformed into irregularly spaced ridges. It is a variation on the well-known relief-reversal phenomenon that occurs when pictures containing abiguous depth information (shadows) are viewed upside down. The phenomenon is explained in terms of the tendency of the visual system to put the (invisible) illuminant in the sky, as has been the best guess for a long time.



One may ask if such strategies, which can be traced to the visual system's perpetual problem of reconstructing a third dimension that is lost in the two-dimensional retinal image, may also play a role in colour vision. We think that this possibility should not be excluded, since any information that may be utilized by the eye to assess spatial relations may also be of help in achieving the miracle of colour constancy. The results of Gilchrist (1977), which show that the perceived lightness of a surface may vary from white to black, depending on whether it was seen monocularly (in two dimensions) or binocularly (in three dimensions), may be considered as a point in case. In this respect it should also be mentioned that induced colours are rarely seen in the natural (three-dimensional) image. Helmholtz (1911) already noted this and suggested that this has to do with our recognition of colour as belonging to objects, with implies therefore, the utilization of information obtained from the analysis of spatial structure. This may quite well be the case, but what remains to be explained is how the visual system is capable of sorting out objects (both opaque and translucent) from non-objects (patches of light, shadows, haze), that are all so thoroughly confounded in the retinal light profile. We know, of course, that the eye sometimes fails to solve this problem, as animals with spotted furs have found out to their advantage. Still, it is amazing how difficult it is to fool the visual system, as long as there is the slightest bit of information left. What that information is, and how it is extracted will keep psychophysicists busy for a long time to come.

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CONCLUSIONS

Since § 1.4 of Chapter I gives a concise survey of the various studies comprising this thesis, we shall avoid redundancy and just give here the conclusions, which may be summarised as follows:

- The simultaneous-contrast effect consists of two components. One, comprising the main effect, involves interactions in a narrow zone surrounding the test field, whereas the other seems to be independent of distance.
- The experimental paradigm used for measuring simultaneous contrast, can also be used for evaluating the spatial distribution of stray light. It was thus possible to define better the so-called glare function, and hence, the foveal point-spread function.
- The visual system separates common from differential information. That is, the retinal image profile is sliced horizontally, rather than vertically.
- The contrast flash data of Alpern et al. provide evidence - if properly analysed - for a model of visual adaptation incorporating the familiar sigmoid neural transducer function, followed by a gain control that resets steady signals to the level of the dark response.
- Chromatic adaptation can be described in terms of receptor-specific attenuation factors, consistent with the much disputed von Kries coefficient law.
- The adaptation sites that generate the adaptation coefficients have the same action spectra as Stiles' π_5, π_4 and (modified) π_1 mechanisms.
- The relation between adaptive input and adaptation coefficient can be described by Stiles' function $\zeta(x)$.

In Chapter V , the Epilogue, the relevance of these results is discussed with respect to problems in both the fundamental and applied field of vision research.

SAMENVATTING

In deze studie wordt getracht een antwoord te vinden op de vraag wat voor mechanismen ten grondslag liggen aan het verschijnsel van kleurinductie. Geïnduceerde kleuren ontstaan als gevolg van een interactie tussen de visuele stimulus en zijn directe omgeving. Men ziet dit geïllustreerd op de omslag van deze dissertatie waar de woorden "chromatic" en "induction" onderling in kleur verschillen, uitsluitend als gevolg van het verschil in omgevingskleur.

In de inleiding (Hoofdstuk I) wordt in kort historisch perspectief geschetst in welke richting de theorievorming zich heeft ontwikkeld van dit reeds door de klassieken beschreven kleurfenomeen. Een verklaring in termen van tenminste twee processen vormt waarschijnlijk het beste uitgangspunt voor een analytische beschrijving van dit verschijnsel. Daarbij wordt bij het eerste proces gedacht aan een effect dat gewoonlijk wordt aangeduid met chromatische adaptatie, d.w.z. selectieve gevoeligheidsveranderingen in de afzonderlijke kleurkanalen van het visuele systeem. Bij het tweede proces wordt gedoeld op een laterale wisselwerking tussen aangrenzende kleurvlakken, doorgaans aangeduid als simultaan-contrast.

De twee bovengenoemde processen veroorzaken kleurverschuivingen in dezelfde richting en zijn daardoor moeilijk van elkaar te scheiden. Met name bij de bestudering van het chromatische adaptatiemechanisme heeft onbekendheid met het effect (of zelfs het bestaan) van het tweede proces dikwijls geleid tot verdeeldheid over de geldigheid van bepaalde veronderstelde basiswetmatigheden, zoals b.v. de bekende coefficienten-wet van von Kries (zie later).

Het tweede proces, simultaan-contrast, laat zich gemakkelijker isoleren dan het eerste. Daartoe biedt men test- en inductiestimulus aan als een korte flits, kort genoeg om te voorkomen dat het oog zou afdwalen van de teststimulus en adapteren aan het licht van het naburige inductieveld. Men kan echter niet verhinderen dat het in de oogbol verstrooide licht, afkomstig van het inductieveld, een effect uitoefent ter plaatse van de teststimulus. Het gaat daarbij om maar weinig licht maar dat kan toch al effectief genoeg zijn om tot artefacten te leiden, met name wanneer men wil bepalen over welke afstanden inductie-effecten nog werkzaam kunnen zijn. Deze problematiek en de oplossing daarvoor, wordt behandeld in Hoofdstuk II. Daarin worden o.a. resultaten getoond die voor het eerst het volledig voor strooilicht gecorrigeerde effect van simultaan-contrast laten zien als functie van de spatiële parameters van het inductieveld. Uit deze resultaten blijkt dat het hoofdeffect zich afspeelt aan de grens tussen test- en inductieveld, maar dat daarnaast ook nog een mysterieus "contour" effect kan optreden dat over veel grotere afstanden kan opereren.

In hetzelfde onderzoek werd ook aangetoond dat bij continu aangeboden omgevingsvelden het inductie-effect volledig wordt veroorzaakt door het (adapterend) effect van strooilicht. Het was daardoor mogelijk uitspraken te doen over de strooilichtverdeling in het oog als functie van de afstand tot de (strooi)lichtbron, en wel tot op zeer korte afstand van de lichtbron (in hoekmaat ca. 5 boogminuten). Met de reeds bestaande (psycho)fysische technieken, zoals fundusreflectometrie en het meten van contrastdrempels, is het niet mogelijk om betrouwbaar te meten in het gebied tussen de 5 en 60 boogminuten. Met de nieuwe methode kon dus een leemte worden opgevuld in onze kennis betreffende de zgn. punt-spreidfunctie. In § 2 van Hoofdstuk II wordt besproken hoe deze functie inderdaad volledig kon worden gereconstrueerd uit de nieuwe en reeds bestaande gegevens.

In Hoofdstuk III worden een aantal resultaten beschreven die werden verkregen met een nieuwe configuratie van test- en inductieveld. In plaats van de teststimulus aan te bieden in een uitsparing van het inductieveld werd nu een veld zonder uitsparing gebruikt, d.w.z. een homogene achtergrond. De teststimulus werd hierop gesuperponeerd, zodat deze nu bestond uit een mengsel van het licht van test- en inductieveld. De proefpersoon had hierbij de taak, evenals trouwens in de voorafgaande experimenten, de kleur van de teststimulus op zuiver geel in te stellen. Hij kon dat doen door de verhouding van het rode en groene licht waaruit de teststimulus was samengesteld te variëren.

De resultaten van dit onderzoek leidden tot de verrassende conclusie dat de vermenging van het licht van de teststimulus met dat van de achtergrond, weer op de een of andere wijze wordt ongedaan gemaakt door het visuele systeem; de achtergrond wordt als het ware genegeerd. Anders gezegd, de kleur van de teststimulus wordt uitsluitend bepaald door de mengverhouding van het verschilsignaal (het increment).

Toegepast op de klassieke inductie-configuratie, d.w.z. een teststimulus in een omgevingsveld, voorspelt het bovengenoemde principe dat het licht dat de teststimulus gemeen heeft met dat van de omgeving, niet bijdraagt tot de kleurgewaarwording van de teststimulus. Er wordt dus als het ware licht onttrokken aan de teststimulus, en wel hetzelfde soort licht dat in de omgeving voorkomt. Hiermee zou dus een eenvoudige verklaring gegeven kunnen worden voor het verschijnsel van simultaan-contrast. Dat de hier gegeven interpretatie in overeenstemming is met de fenomologie van het simultaan-contrasteffect ziet men geïllustreerd aan het voorbeeld van de tekst op de omslag. Men ziet daar dat de purperen letters enigszins naar blauw zijn verschoven in de rode omgeving (er wordt rood onttrokken), en naar rood in de blauwe omgeving (er wordt blauw onttrokken).

Als logisch vervolg op het zojuist besproken onderzoek, waarbij er uitsluitend sprake was van positieve verschilsignalen (incrementen), werd aansluitend onderzocht hoe het gesteld is met de verwerking van negatieve verschilsignalen (decrementen). Daartoe werd nu de rode stimulus component (hetzelfde rood dat voor de achtergrond werd gebruikt), als een decrement in het intensiteitsprofiel van de achtergrond aangeboden. Vervolgens werd nagegaan wat de effectiviteit van dit rode decrement was, zoals gemeten aan de hoeveelheid groen stimuluslicht dat benodigd was om het rood te neutraliseren. Het bleek dat in alle gevallen, onafhankelijk van de intensiteit van het decrement, een uiterst geringe hoeveelheid groen licht (ongeveer twee maal de hoeveelheid die nodig was voor de contrastdrempel) al voldoende was om het rood te neutraliseren. Eerder was al gebleken dat, zelfs wanneer het decrement tot nul is gereduceerd, d.w.z. in het geval van een homogene achtergrond, het rode licht ineffectief is ter plekke van de teststimulus. Kennelijk kan dus het rood van de achtergrond zich uitsluitend dàn manifesteren (ter plaatse van het testveld) wanneer er sprake is van een increment in het (rode) lichtprofiel. Dit werd nog eens bevestigd in een experiment waarbij het centrum van de achtergrond, ter plaatse van het testveld, met een donker lijntje werd omcirkeld. Nu bleek dat de achtergrond zich wèl vermengde met de teststimulus en wel des te sterker naarmate het lijntje dieper in het rode intensiteitsprofiel was "uitgesneden".

Het afwezig zijn van een additief effect van de (homogene) achtergrond past goed in het beeld van een visueel systeem dat reageert op *veranderingen* in het retinale intensiteitsprofiel. Wanneer de veranderingen relatief gering zijn bijvoorbeeld bij de contrastdrempel, of bij een teststimulus die zich niet duidelijk van de achtergrond onderscheidt (in zowel tijd als ruimte), dan zou men kunnen verwachten dat een volledige scheiding tussen increment en achtergrond minder volledig zal zijn. Hierover gaat de laaste paragraaf van Hoofdstuk IV, waarin kritiek wordt weerlegd t.a.v. de genoemde niet-additiviteit van (continu aangeboden) achtergronden en een daarop gesuperponeerde testflits.

Voor wat betreft het "eerste" proces, chromatische adaptatie, waren de in Hoofdstuk III besproken resultaten ook van belang. Daaruit was immers geconcludeerd dat het effect van het "tweede" proces beschreven kon worden als het onttrekken van licht aan de teststimulus, nl. het licht dat deze gemeen heeft met de omgeving. Bij de hier gebruikte stimulusconfiguratie wordt dit effect van de achtergrond echter weer precies opgeheven doordat het licht van het omgevingsveld ook aan de stimulus wordt toegevoegd. (Dit is alleen maar een andere manier van zeggen dat de teststimulus op de achtergrond werd gesuperponeerd.) Daardoor kon dus het adaptatie-effect "sec" worden gemeten, d.w.z. al gecorrigeerd voor het contrasteffect.

Een bekend uitgangspunt voor de meeste adaptatietheorieën is de coëfficiëntenwet van von Kries. Volgens deze wet zou het effect van chromatische adaptatie te beschrijven zijn in termen van drie verzwakkingsfactoren (coëfficiënten tussen 0 en 1), één voor iedere klasse van fotoreceptoren (de kegeltjes). Tot nu toe leek de toepasbaarheid van deze wet echter zeer dubieus, een gevolg van onbekendheid met (of ontkenning van) het in dezelfde richting werkende effect van simultaan-contrast. De resultaten van het huidige onderzoek laten zich daarentegen zeer goed rijmen met de coëfficiëntenwet, waardoor de juistheid van deze belangrijke wet niet langer in twijfel behoeft te worden getrokken.

Een belangrijke vraag bij de gevoeligheidsregeling van de kleurkanalen van het oog is in hoeverre dit niet reeds begrepen kan worden uit een alineair verloop van de stimulus-respons functie (responscompressie bij toenemend lichtniveau). Over deze functie is echter uit de psychofysica maar weinig bekend. Eigenlijk is er o.i. maar één onderzoek dat hier mogelijk informatie over zou kunnen verschaffen, maar dat wordt helaas ontsierd door ongerechtvaardigde aannamen bij de data-analyse. De gegevens van het betreffende onderzoek leken op zich echter interessant genoeg voor een her-analyse hetgeen geleid heeft tot het in Hoofdstuk IV besproken onderzoek over de zgn.

"contrast-flash data". Uit de gegevens kon een eenvoudig model worden afgeleid - hierbij voortbouwend op wat uit eigen werk reeds was geconcludeerd - dat uitgaat van een uit de fysiologie bekende neurale responsfunctie, gevolgd door een gevoeligheidsregeling met een al even bekende karakteristiek, de zgn. Weber-Fechnerrelatie. Adaptatie is dus waarschijnlijk meer dan alleen maar responscompressie; het lijkt zelfs zeer aannemelijk dat een van de functies van het adaptatie-mechanisme is om te voorkomen dat de fotorespons van het systeem wordt gecomprimeerd (in de verzadiging geraakt).

Uit verder eigen onderzoek bleek dat chromatische adaptatie zich ook goed laat beschrijven met de Weber-Fechnerrelatie. In § 2 van Hoofdstuk IV wordt aannemelijk gemaakt dat deze relatie beschrijft hoe de receptor-specifieke verzwakkingsfactoren toenemen met het lichtniveau. Daarbij gaat het om het licht zoals dat "gezien" wordt door de betreffende regelsystemen. Voor de hand zou liggen dat deze systemen dezelfde spectrale gevoeligheden zouden hebben als de receptoren waarvan ze de signaalsterkte regelen. De resultaten suggereren echter dat dit niet het geval is. Veeleer lijkt het erop dat deze regelmechanismen dezelfde golflengte-afhankelijkheid vertonen als de systemen die men kan afleiden uit metingen van contrastdrempels met gekleurde testflitsen op gekleurde achtergronden, de bekende (maar onbegrepen) π mechanismen van Stiles. Hiermee is mogelijk een eerste aanzet te geven tot een verklaring van de oorsprong en functie van de π mechanismen.

In de laatste van de in Hoofdstuk IV besproken studies wordt het uit het voorgaande werk naar voren gekomen model getest op zijn voorspellende waarde voor het gehele kleurdomein. Aanvankelijk was namelijk vermeden het kleurkanaal te stimuleren dat het kortgolvige gebied van het spectrum bestrijkt (het "blauw"-systeem), een en ander om te voorkomen dat te verwachten complicaties (het is een enigszins afwijkend kleursysteem) een vruchtbare analyse in de weg zouden staan.

Inderdaad bleek dat bij het blauw-systeem een uitbreiding van het model nodig was, en wel in die zin dat aangenomen moest worden dat, meer nog dan bij de andere systemen, er sprake was van interacties tussen de receptoren voor wat betreft de gevoeligheidsregeling van de kleurkanalen. Deze interacties laten zich echter vrij eenvoudig beschrijven en het model is er dan ook niet veel gecompliceerder door geworden. Uiteindelijk bleek dat met slechts twee vrij te kiezen constanten (beide betrekking hebbende op het blauw-systeem) een redelijk goede beschrijving kon worden verkregen van de wijze waarop het (subjectieve) witpunt zich door de kleurenruimte verplaatst als functie van kleur en intensiteit van de adaptatie-stimulus.

In de Epiloog (Hoofdstuk V) worden de belangrijkste conclusies van het onderzoek nog eens vermeld en wordt in kort bestek ingegaan op de relevantie daarvan voor zowel fundamenteel als toegepast onderzoek op dit terrein. Er wordt daarbij o.a. gewezen op het feit dat bij laboratoriumexperimenten bij voorkeur eenvoudige stimuli worden gebruikt. Daardoor zal dus extrapolatie naar de praktijksituatie, waar het visuele systeem geconfronteerd wordt met een veel complexere taak, met de nodige voorzichtigheid moeten geschieden. Dit geldt met name voor het huidige onderzoek waarin, zoals gebruikelijk bij dit soort onderzoek, werd gekeken naar een zelf-lichtend stimuluspatroon. In de natuurlijke waarnemingssituatie komt dit maar zelden voor en heeft men bijna altijd te maken met een lichtbron, gewoonlijk "wit" licht, en ontstaan de kleuren door reflectie van dit licht aan (gekleurde) voorwerpen. Het is nog steeds een raadsel hoe het oog in staat is in de chaos van het op het netvlies vallende licht een scheiding aan te brengen tussen lichtvariabelen enerzijds, zoals intensiteit, kleur en lichtverdeling (schaduwen en lichtvlekken), en voorwerpsvariabelen anderzijds, d.w.z. de reflectie-eigenschappen en de vorm. Hier ligt een rijk terrein voor toekomstig onderzoek, zowel in de fundamentele als toegepaste sector.

CURRICULUM VITAE

De schrijver werd geboren in het voormalige Nederlands Oost-Indië, waar hij tijdens de oorlogsjaren zijn eerste onderwijs genoot op het kampschooltje van zijn zuster. Na de repatriatie, in 1947, begon hij drie jaar later aan zijn middelbare schoolopleiding op het Coornhert Lyceum te Haarlem. In 1956 werd het einddiploma behaald waarna nog in hetzelfde jaar een aanvang werd gemaakt met de studie in de biologie aan de Rijksuniversiteit te Leiden. Na het candidaatsexamen (K') werden drie onderzoeken gedaan, respectievelijk in de plantenanatomie, de oecologie en de ethologie. In 1965 werd het doctoraalexamen afgelegd en werd aansluitend begonnen met de vervulling van de dienstplicht, waarvan het laatste jaar werd doorgebracht als gedetacheerde op het Instituut voor Zintuigfysiologie. In die tijd werd psychofysisch en fysiologisch onderzoek gedaan onder leiding van Dr. R.L. DeValois die zijn "sabbatical" doorbracht op het Instituut. Deze samenwerking werd na afloop van de diensttijd nog een jaar in Amerika voortgezet, als research assistant (Indiana University, Bloomington). Na zijn terugkeer in 1967 trad de schrijver in dienst bij het Instituut voor Zintuigfysiologie waar hij zich specialiseerde op het gebied van het kleurenzien (contrast en adaptatie mechanismen), met als neveninteresse het ruimtelijk zien.

STELLINGEN

I

Het visuele systeem analyseert het netvliesbeeld in termen van spatio-temporele verschilsignalen.

Dit proefschrift, Hoofdstuk III

II

Chromatische adaptatie kan beschreven worden met receptor-specifieke verzwakkingsfactoren, welke zich laten berekenen met de psychometrische functies die door Stiles werden afgeleid uit zijn metingen aan hetero-chromatische contrastdrempels.

Ibid., Hoofdstuk IV

III

De beneden-grens(hoek) voor de toepasbaarheid van de strooilichtformule van Vos, ca. 1°, kan door de toevoeging van een constante worden teruggebracht tot 0,15°.

Ibid., Hoofdstuk II

IV

Het door Wyszecki aangevoerde bewijs voor de stelling dat de coëfficiëntenwet van Von Kries volgt uit diens persistentie-wet kan worden aangemerkt als een geval van petitio principii.

Wyszecki, G. (1954) Beitrag zur valenzmetrischen Untersuchung der Umstimmung. *Die Farbe 3*, 93-104.

V

De kosten van toegepast psychofysisch onderzoek worden ruimschoots teruggewonnen uit de besparingen die op grond daarvan mogelijk zijn.

Walraven, J. and Lotens, W.A. (1975) Optimal flash characteristics for lighted buoys; an experimental evaluation. *I.A.L.A. Bulletin 64*, 8-15.

Walraven, J. (1976) A random-dot depth perception test for the selection of range-finder operators. In: *Introduction to Human Engineering* (Eds.: Kraiss, K.F. and Moraal, J.) Verlag TüV Rheinland GmbH, Köln.

VI

Van de gangbare hulpmiddelen voor de vroegtijdige opsporing van amblyopie, het z.g. "luie oog", voldoet de TNO-dieptezientest het best aan het gestelde doel.

Walraven, J. (1975) Amblyopia screening with random-dot stereograms. *Am. J. Ophthalmol. 80*, 893-900.

Cashell, G.T. and Durran, I.M. (1980) *Handbook of orthoptic principles*, Churchill Livingstone, London, New York.

VII

Het effect van subjectieve beeldvergroting c.q. afstandsverkleining dat kan worden opgewekt met een door prisma's geïnduceerde convergentie-afname, wordt door Ogle ten onrechte aangevoerd als argument voor de veronderstelling dat convergentie niet of nauwelijks bijdraagt tot de ruimtezin.

Ogle, K.N. (1962) The visual space sense. *Science 135*, 763-771.

VIII

De verbetering in spraakverstaanbaarheid (in geroezemoes) die resulteert bij binaurale lokalisatie van de spreker, het z.g. cocktailparty-effect, heeft een visueel pendant.

IX

Goethe's kritiek op Newton als onderzoeker en als mens is vrijwel volledig op hemzelf van toepassing.

Goethe, J.W. von (1810) *Zur Farbenlehre*, Cotta, Leipzig.

X

Het door Koenderink et al. voorgestelde visuele adaptatie-mechanisme laat zich moeilijk rijmen met het verschijnsel van chromatische adaptatie.

Koenderink, J.J., Grind, W.A. van de, and Bouman, M.A. (1972) Opponent color coding: a mechanistic model and a new metric for color space. *Kybernetik* 2, 78-99.

XI

Bij de preventie van verslaving aan verdovende middelen zou de overheid een actiever beleid kunnen voeren door een professioneel gebruik van de media.

XII

Het linkse nivelleringsstreven zou waarachtiger overkomen wanneer daarbij vermeld zou worden wat het te verwachten nuttig effect zou zijn voor de lagere inkomens.

XIII

De in rechtse kringen veel gepropageerde stelling dat bij een verdere daling van de (hogere) inkomens de prikkel tot werken zou worden weggenomen, gaat voorbij aan de reële mogelijkheid dat men voor de terugval in inkomen zal trachten te compenseren door juist harder te werken.

XIV

Fleming's suggestie, bij monde van zijn creatie de geheimagent James Bond, dat men zich moet wachten voor autorijders met een hoed op achter het stuur, kan worden aangemerkt als een interessante bijdrage tot het profiel van de brokkenmaker.

Fleming, I.L. (1955) *Moonraker*, Pan Books Ltd., London.

Stellingen bij: Chromatic induction - psychofysical studies on signal processing in human colour vision.

J. Walraven

Utrecht, juli 1981