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Reversed effect of adapting stimuli on visual sensitivity

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The sensitivity of the eye to incremental stimuli normally decreases as the intensity of a steady background field increases. We examine here a range of conditions under which an added field anomalously *increases* sensitivity. If the threshold intensity for violet ($\lambda = 423$ nm) test flashes is measured on a blue ($\mu_1 = 473$ nm) field of $10^{9.7}$ quanta s^{-1} deg^{-2} and if then yellow ($\mu_2 = 575$ nm) fields of increasing intensity are added to the background the threshold may fall by 0.3–0.4 logarithmic unit.

The facilitation occurs whether yes/no or forced-choice procedures are used (experiments 1, 2), is abolished when the blue and yellow fields are presented dichoptically (experiment 5) and varies in magnitude with the duration of exposure to the composite adapting field (experiment 6). The intensity of the yellow field required for maximal facilitation (*a*) increases as the intensity of the blue field increases and (*b*) is typically that intensity required to render the composite field achromatic (experiments 1, 3).

The results imply that the sensitivity of the psychophysically defined blue mechanism is not controlled merely by photons absorbed in the short-wavelength receptors. We hypothesize that signals originating in the short-wavelength receptors are confined to opponent-colour channels (assumption 1) and that any opponent-colour channel is most sensitive to input perturbations when at an intermediate value of its response range (assumption 6). We relate the latter principle to line-element analyses of colour discrimination.

Variation of μ_2 allows us to estimate the action spectrum of the long-wavelength input to the putative opponent channel (experiment 4). This spectrum resembles the photopic luminosity function, V_λ ; but for $\mu_2 > 600$ nm the facilitation is less than for $\mu_2 \approx 575$ nm.

We discuss the implications of the present results for the π mechanisms of Stiles. If detection were by opponent channels, might Stiles's field sensitivities be contaminated by variation in post-receptoral sensitivity when field wavelength was varied or when an auxiliary field was added? Although hindsight does suggest that the large and long targets used by Stiles would favour detection by opponent channels, an unappreciated advantage of the two-colour method may be that the monochromatic field desensitizes opponent channels and ensures that detection is via a non-opponent pathway whose (post-receptoral) sensitivity varies little in the course of field-sensitivity measurements. Stiles's own checks and other evidence suggest that π_4 and π_5 are little distorted by opponent processes and even for the blue mechanism, where the use of long-wavelength

auxiliary fields would be likely to modulate the sensitivity of opponent channels, the relative field sensitivity for $\mu < 500$ nm is probably that of the receptors. The present results do suggest that Stiles's two-colour method can, with care, be extended to the study of chromatically opponent channels in the visual system.

INTRODUCTION

We describe in this paper a noteworthy exception to the commonly accepted properties of visual adaptation. The detectability of a violet test flash on a steady blue field is found to increase when yellow light is added to the blue field so as to yield a composite field that appears white.

The procedures of the present experiments are adapted from the two-colour increment-threshold method of W. S. Stiles and the theoretical context is his model of independent π mechanisms (Stiles 1953, 1978; Wyszecki & Stiles 1967); but the results require a basic modification of the classical model. Each of the π mechanisms, as originally defined, has a unique spectral sensitivity, which should be the same whether it is a 'test sensitivity', derived by varying the wavelength of the test flash (λ), or a 'field sensitivity', derived by varying the wavelength of the adapting field (μ). The sensitivity of a given mechanism is assumed to be independent of that of other mechanisms and to decrease monotonically as the intensity of an adapting field is increased. The present experiments suggest that neither of these assumptions can be correct for the blue-sensitive mechanism; but they equally suggest that Stiles's field-sensitivity method can be extended to the study of chromatically opponent processes.

The blue-sensitive mechanism† differs in a number of properties from π_4 and π_5 , Stiles's green- and red-sensitive mechanisms: its contrast sensitivity and its spatial and temporal resolution are poorer; it is disproportionately vulnerable to some retinal diseases; and it is subject to several anomalies of adaptation (for discussion and references see Willmer (1961), Trezona (1970), Mollon (1977, 1979), Stiles (1978), Boynton (1978*a*), Pugh & Mollon (1979)). Nevertheless, although the present experiments are concerned exclusively with the blue mechanism, the phenomenon that we describe should not necessarily be regarded as a peculiarity of the blue mechanism. Provided that conditions are carefully chosen, analogues of this phenomenon (and perhaps of other 'anomalies' of the blue mechanism) may well be demonstrated for the other mechanisms. Sternheim *et al.* (1978) have described a very similar phenomenon when detection depends on the red-sensitive mechanism: a 633 nm grating of low spatial frequency (1 cycle/deg) was presented

† Stiles distinguished three blue-sensitive mechanisms, π_1 , π_2 and π_3 (Stiles 1953). It is argued elsewhere (Mollon & Polden 1976; Pugh & Mollon 1979) that π_1 and π_3 do not represent independent mechanisms. In the present paper, when we refer to the blue mechanism we intend only that the reader should understand that the psychophysical response is controlled by signals originating in the short-wavelength cones.

on a 615 nm field of $10^{3.7}$ td† and the detection threshold was found to be lowered when a 565 nm field was added to the first field. The phenomenon was not observed when the grating was of higher spatial frequency (see also Sternheim *et al.* 1979).

Since π_4 is approximately as sensitive to blue light as is the blue mechanism, a long-wavelength adapting field is conventionally used to isolate the blue mechanism. It was in the nature of our experiments that we wished to isolate the blue mechanism without resort to such a field. To this end we drew upon the known factors that favour detection by the blue mechanism: the target was large and long, so as to exploit the greater spatial and temporal integration of the blue mechanism, and it was delivered to the parafovea, where the blue mechanism is more sensitive than in the fovea (Stiles 1949; Brindley 1954; Mollon & Polden 1977*b*); the test wavelength (423 nm) was chosen to maximize the difference in sensitivity of the blue and green mechanisms, whereas the primary adapting wavelength (473 nm) was chosen to have an adapting effect on π_4 that was equal to, or greater than, its effect on the blue mechanism.

A note on terminology

In preliminary reports (Mollon & Polden 1977; Mollon 1977, 1979), we have used the term 'negative masking' for the phenomenon examined in the experiments described below; we here abandon this term, since the double negative has not recommended it to others and since it is used in the existing literature to refer to a heterogeneous class of facilitatory effects (see below). We propose instead the specific term *combinative euchromatopsia* for the enhancement of hue discrimination that occurs when certain adapting fields are combined. This term is compatible with our present operational knowledge of the phenomenon. The formation *euchromatopsia* ('good colour discrimination') has had earlier usages, but has been in general disuse for many years.

In the choice of symbols for stimulus parameters we follow Stiles (Wyszecki & Stiles 1967): II_i is used to indicate the field spectral sensitivity of the *i*th of the cone mechanisms postulated by Stiles; π_i is used for test spectral sensitivity and is also used to refer to the hypothesized neural mechanism that gives rise to the measured sensitivities (Wyszecki & Stiles 1967, p. 574).

METHODS

Apparatus

All measurements were made with a three-channel Maxwellian-view system. The apparatus, and the calibration procedures, are described in detail in an earlier paper (Mollon & Polden 1977*b*). A 2 mm artificial pupil was used throughout.

† 1 td (troland) is the retinal illumination when a luminance of 1 cd/m² is seen through a pupil of area 1 mm². For light of wavelength 580 nm, transmission losses being taken into account: 1 td \approx 0.003 lm/m² \approx 10⁷ quanta s⁻¹ mm⁻².

Except in experiment 2, the adjustment of stimulus intensity and the recording of responses were performed by a laboratory computer.

For the forced-choice measurements (experiment 2), a liquid-crystal cell of the twisted-nematic type (Mollon *et al.* 1977) served as a secondary shutter. An electro-optic shutter of this type recommended itself by its total silence but had too long a recovery time to serve as the primary shutter.

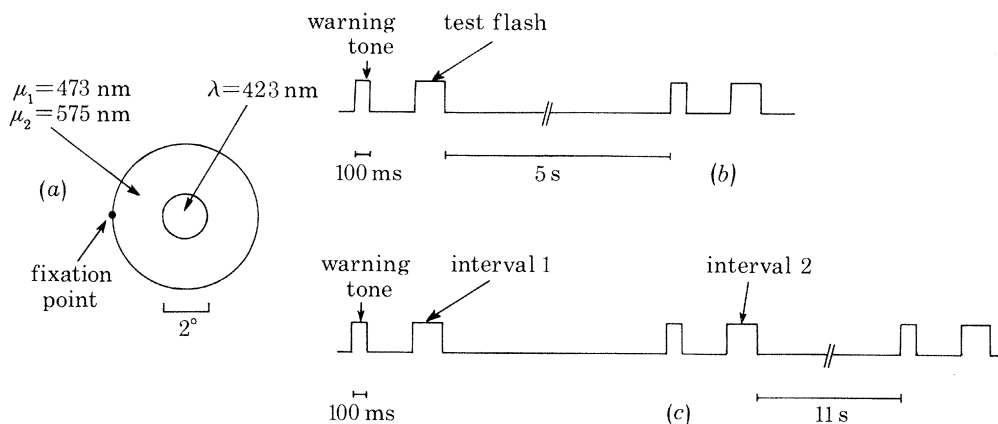


FIGURE 1. (a) Spatial arrangement of stimuli for all experiments. (b) Temporal sequence of stimuli for experiments 1 and 3-6. (c) Sequence of stimuli for experiment 2.

Stimuli

The spatial and temporal arrangement of stimuli is shown in figure 1. In all experiments the target subtended 2° and was presented 3.25° to the right of a fixation point. Its duration was 200 ms and its wavelength (λ) was 423 nm, except when λ was an independent variable.

The two, congruent, adapting fields subtended 6.5° and were concentric with the test flash. The fixation point lay on the left-hand perimeter of the composite field. The wavelength (μ_1) of the primary adapting field was 473 nm. The wavelength (μ_2) of the second field was 575 nm, except in experiment 4, where μ_2 was an independent variable. The wavelength 575 nm was chosen because it is approximately the complementary of 473 nm (with respect to CIE Illuminant C). The full bandwidths at half-height of the 473 nm and 575 nm fields, measured *in situ*, were 22 nm and 12 nm respectively.

Procedure

Except in experiment 2, thresholds were measured by a randomized double-staircase procedure (Cornsweet 1962) and the observer responded 'yes' or 'no' by means of push buttons. A test flash was presented every 5 s. A 100 ms warning tone began 400 ms before the onset of the test flash. A block of trials consisted of

50 flashes; but the estimate of the threshold was based only on responses made after the first crossing of two staircases. The observer maintained fixation throughout a block of trials. Except in experiment 6, 4 min of adaptation preceded each determination of threshold. Since the effects upon the blue mechanism of long-wavelength fields dissipate very slowly (Pugh 1976; Augenstein & Pugh 1977), an interval of at least 15 min was allowed between individual determinations of threshold.

Observers

All observers are emmetropic males and perform normally on the Farnsworth-Munsell 100-hue test and on the Nagel anomaloscope. CS and GM were not told of the purposes and results of the experiments.

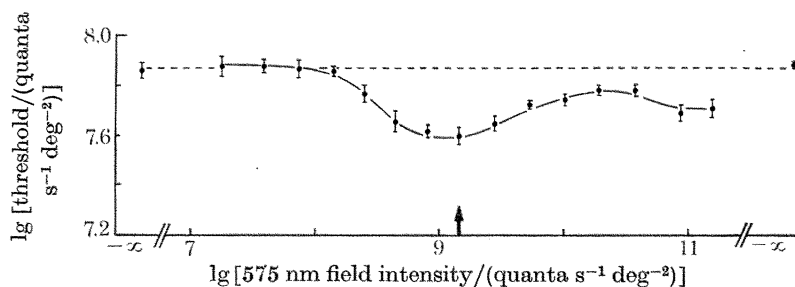


FIGURE 2. Lg (incremental threshold) for 423 nm test flashes presented on composite fields consisting of a 473 nm field of fixed intensity ($10^{9.2}$ quanta s^{-1} deg^{-2}) and a 575 nm field of which lg (intensity) is indicated on the abscissa. The vertical arrow marks the value of the 575 nm field at which the composite field appeared white. The horizontal broken line represents the mean of the two thresholds measured on the 473 nm field. Observer: AS.

RESULTS

Experiment 1. Basic phenomenon

Figure 2 shows for observer AS the threshold for the violet test flashes on composite adaptation fields. The intensity (M_1) of the blue field remained fixed at $10^{9.2}$ quanta s^{-1} deg^{-2} ; a series of yellow fields of increasing intensity was added to the blue field and it is the logarithm of the intensity (M_2) of the added yellow field that is plotted as the abscissa of figure 2. Each data point represents the mean of eight runs, performed on separate days, and the error bars correspond to ± 1 s.e.m. (as calculated from the eight independent estimates). The threshold on the blue field alone was measured at the beginning and at the end of each day's run; the mean values for these two thresholds are plotted separately, as the leftmost and rightmost points respectively.

The horizontal broken line in figure 2 (and in later figures) represents the mean of the two thresholds measured on the 473 nm field alone. It will be seen that, as yellow fields of increasing intensity are added to the blue field, the threshold systematically falls and then rises again. For this observer, under these conditions,

the change in sensitivity, $\lg \Delta N$ ($= \lg$ [threshold on 473 nm field] $- \lg$ [threshold on composite field]), has a maximum value of 0.28. (We do not yet know whether the secondary fall in threshold shown by AS for $M_2 > 10^{10.8}$ quanta $\text{s}^{-1} \text{deg}^{-2}$ is a general result.)

What makes this 'combinative euchromatopsia' especially remarkable is that the composite field yielding maximal sensitivity has a much greater luminance than has the blue field alone and does indeed appear much brighter. In the present case, the troland values (calculated from the radiometric measurements) of the blue field and of the composite field giving maximal sensitivity were 150 and 1150 respectively.

We required AS to record the appearance of the field and of the test flash immediately after each threshold measurement in each experimental session. His reports varied little from day to day and his typical responses are tabulated in table 1 for each value of M_2 , together with the value of ΔN . The most interesting finding is that the combination of M_1 and M_2 described as white is that yielding the largest value of ΔN . (The corresponding value of M_2 is indicated by a vertical arrow in figure 2.) It is noteworthy that imperfections in the adapting fields that passed unnoticed when the fields appeared blue or yellow revealed themselves as faint variegations when the field was close to white; this observation may reflect the very phenomenon of combinative euchromatopsia. It may also be significant that a liminal test flash appears clearly coloured when ΔN is maximal and is without colour at the extreme values of M_2 . Less formal phenomenological reports obtained from other observers are similar to those of AS.

One possible artefact requires consideration. We have reported elsewhere (Mollon & Polden 1977*a*) that the blue mechanism shows evidence of saturation, in that the increment-threshold function has a slope greater than unity when increasingly intense short-wavelength fields are added to an auxiliary long-wavelength field. Could it be that the strong yellow fields added in the present experiment had no direct effect upon the blue mechanism but caused a constriction of the pupil that attenuated the blue field and the test flash concomitantly? Under conditions where Weber's law held, an effect of this kind would pass undetected; but under conditions where \lg (threshold) was increasing more rapidly than $\lg M_1$, a spurious recovery of sensitivity might be recorded if test flash and field were attenuated by the same factor. To eliminate this possibility we have checked that combinative euchromatopsia still occurs when a 1 mm artificial pupil is used. The dichoptic measurements of experiment 5 provide further evidence against an artefact of this type, in so far as the consensual pupil reflex ought to have acted to produce euchromatopsia, if the latter were a pupillary artefact.

Experiment 2. Forced-choice

Under the conditions of experiment 1 the appearance of the test flash at threshold varies as the adaptational conditions vary (table 1) and there is thus a possibility that combinative euchromatopsia merely reflects a change in the observer's

TABLE 1. EXPERIMENT 1: PHENOMENOLOGICAL OBSERVATIONS

lg [intensity of 575 nm field/(quanta s ⁻¹ deg ⁻²)]	lg (ΔN)	appearance of composite field	appearance of test flash at threshold	appearance of test flash above threshold
$-\infty$		blue	translucent disturb- ance of field	violet blue
7.25, 7.59	0.00	blue	translucent disturb- ance of field	violet blue
7.87	0.01	blue 'with tinge of white'. Less satur- ated at end of 4 min adaptation	translucent disturb- ance of field	bluish violet
8.15	0.02	whitish blue	translucent disturb- ance of field	bluish violet
8.40	0.11	whitish blue, less saturated	translucent disturb- ance of field	bluish violet, more saturated
8.65	0.22	bluish white, less saturated	translucent disturb- ance of field	violet pink or lilac
8.91	0.26	white with tinge of blue; variegation apparent after 4 min	translucent violet or pink	violet pink or lilac
9.16	0.28	white; faint blue and yellow variegations apparent after 4 min	violet pink	saturated violet pink or lilac
9.45	0.23	white with tinge of yellow	pink	pink lilac
9.73	0.15	very pale yellow	pink	pink lilac
10.01	0.13	pale yellow	whitish pink	pink
10.28	0.09	bright, desaturated yellow	white	desaturated pink
10.58	0.09	bright desaturated yellow becoming less intense after 4 min	white	greyish pink
10.94	0.18	bright yellow, becoming less intense after 4 min	white	whitish grey
11.19	0.16	intense saturated yellow, becoming less intense after 4 min	white	pinkish grey

criterion. A two-interval temporal forced-choice experiment was therefore undertaken for PGP and CS. Thresholds were measured on the 473 nm field alone and on the composite field that yielded the minimum threshold in yes/no measurements for these observers. M_1 remained $10^{9.2}$ quanta s⁻¹ deg⁻² and M_2 had a value of $10^{9.65}$ quanta s⁻¹ deg⁻². Eight independent estimations of the threshold were made for each adaptational condition. The adaptational conditions were alternated.

The sequence of an individual trial is shown in figure 1c. A 200 ms test flash

was presented in one of two intervals. A warning tone occurred 400 ms before each interval and the two intervals were separated by 1.5 s. Successive pairs of intervals were separated by 11 s. The primary shutter opened during both intervals of a given trial, giving an audible signal, but only during one interval was the silent secondary shutter open. The threshold for 75% correct responses was determined by the b.u.d.t.i.f. ('block up-and-down, two-interval forced-choice') method (Campbell & Lasky 1968): during a block of eight trials the stimulus intensity was held constant and at the end of each block it was increased by 0.1 logarithmic unit if performance was poorer than 75% correct and was decreased by 0.1 logarithmic unit if performance was better than 75% correct. Titration began at a supra-threshold level (identical for the two adaptational conditions) and the estimate of the threshold was based on the six blocks following the first reversal.

TABLE 2. RESULTS OF EXPERIMENT 2

observer	lg [threshold on 473 nm field/(quanta s ⁻¹ deg ⁻²)]	lg [threshold on composite field/(quanta s ⁻¹ deg ⁻²)]	lg (ΔN)	<i>p</i>
PGP	7.97 (s.d. 0.080)	7.63 (s.d. 0.079)	0.34	< 0.01
CS	8.04 (s.d. 0.068)	7.76 (s.d. 0.074)	0.28	< 0.05

Table 2 shows the mean thresholds and standard deviations, and the significance values given by a two-tailed *t*-test. It is clear that the phenomenon survives when forced choice is used.

Feedback was used in the present experiment to ensure that observers reached their optimum performance; but we have obtained similar results in a forced-choice experiment in which feedback was not given.

Experiment 3

The purpose of this experiment was to place the phenomenon in context, by exploring a matrix of combinations of M_1 and M_2 and defining the region of stimulus space in which euchromatopsia occurred. We were additionally concerned to relate our results to those of Pugh (1976), who had found that long- and short-wavelength fields were superadditive rather than cancellative in their effects on the sensitivity of the blue mechanism. Pugh used 430 nm fields in the range 10^6 – $10^{7.8}$ quanta s⁻¹ deg⁻² and long-wavelength fields in the range 10^8 – 10^{10} quanta s⁻¹ deg⁻²; when such fields were combined, the threshold rose more than would be expected if the sensitivity of the blue mechanism depended simply on the total rate of quantum catch in a single photopigment.

In the present experiment, M_1 ($\mu_1 = 473$ nm) varied between experimental sessions but within a session took a fixed value in the range of $10^{8.2}$ – $10^{10.7}$ quanta s⁻¹ deg⁻². Two sessions were devoted to each value of M_1 and the order of sessions was randomized. At the beginning of each session the threshold was measured on

the blue field alone; a 575 nm field was then added and measurements were made at increasing values of M_2 , in the range 10^7 – $10^{11.3}$ quanta $s^{-1} \text{ deg}^{-2}$; finally the threshold on the blue field alone was remeasured. Ancillary threshold: intensity curves for $\lambda = 423 \text{ nm}$, $\mu = 473 \text{ nm}$, were obtained in separate sessions, measurements being made for increasing values of M_1 within a session. On the basis of pilot studies, slightly different ranges of M_1 and M_2 were examined for the two observers, PGP and GM.

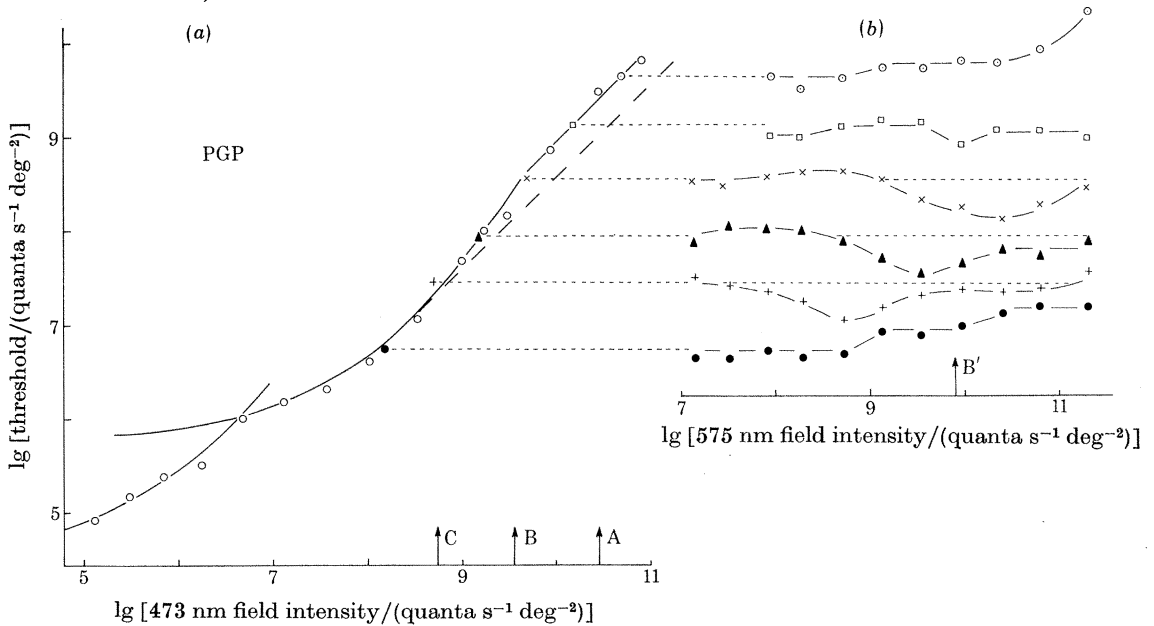


FIGURE 3. (a) Lg (incremental threshold) for 423 nm test flashes as a function of the Lg (intensity) of a 473 nm field alone. The vertical arrows refer to conditions used in experiment 3a. Observer: PGP. (b) Lg (incremental) threshold for 423 nm test flashes presented on composite fields consisting of (i) a 575 nm field of the intensity indicated on the right-hand abscissa and (ii) a 473 nm field that has a fixed intensity for any one set of symbols. A broken line connects the set of data obtained for a given 473 nm field with the threshold (identified by the same symbol and plotted to the left) obtained when only the 473 nm field was present; the intensity of the 473 nm field is indicated on the left-hand abscissa.

Results are plotted in figures 3 and 4. To the left of each figure is shown the conventionally obtained threshold: intensity curve (\circ) for the violet targets on the blue field alone. Since the measurements were made outside the centre of the fovea, the lowermost branch is to be attributed to the rods. We show below (experiment 3a) that the next branch is attributable to the blue mechanism. The curve for PGP has a significant feature: for $M_1 \approx 10^9$ quanta $s^{-1} \text{ deg}^{-2}$ the function has a slope greater than 1, recalling the 'saturation' of the blue mechanism that we have reported elsewhere (Mollon & Polden 1977a). The final part of the function has a slope of 1 and is probably attributable to π_4 (see below).

To the right in figures 3 and 4 is shown how the threshold varies when M_1 is held constant and M_2 is varied. Each point represents the mean of estimates obtained in two sessions. A broken line connects the set of data obtained for a given value of M_1 with the threshold (estimated in the same session and identified by the same symbol) obtained when only the blue field is present; these latter values are plotted to the left, in their correct position with respect to the left-hand abscissa.

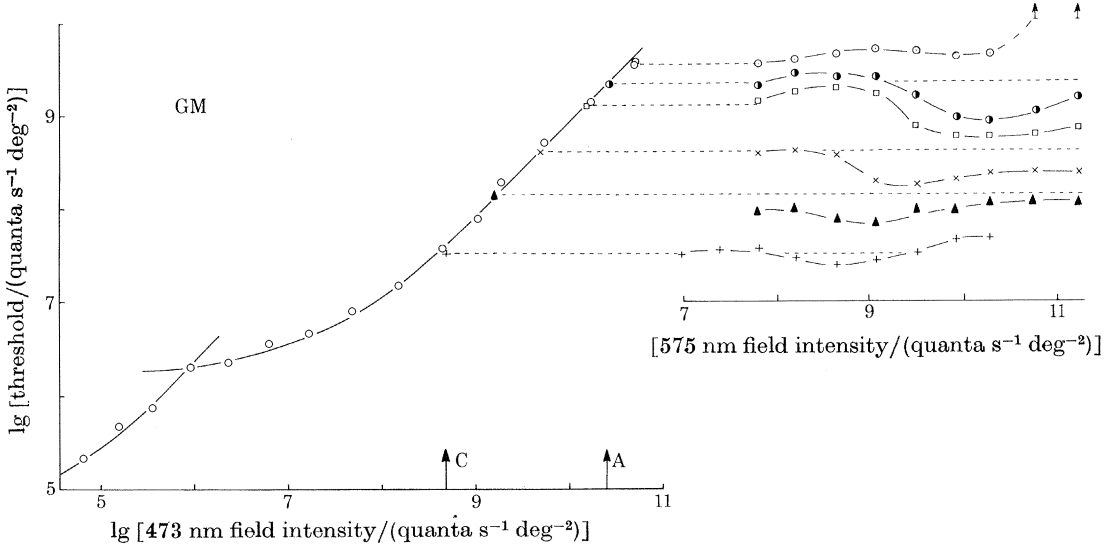


FIGURE 4. As for figure 3. Observer: GM.

The results for the two observers are qualitatively similar, although they differ quantitatively. A ΔN of greater than 0.4 logarithmic unit is found for PGP in the range $M_1 = 10^{8.7}-10^{9.7}$ quanta s^{-1} deg^{-2} and an effect of greater than 0.3 log unit is found for GM in the range $10^{9.7}-10^{10.5}$ quanta s^{-1} deg^{-2} . At lower values of M_1 the effect weakens and at the highest values it is absent. For both observers the value of M_2 needed to produce a maximal value of ΔN increases as M_1 increases. Notice that yellow fields that produce an increase in threshold at low values of M_1 may reduce thresholds at higher values of M_1 . It is significant that under conditions where an observer showed combinative euchromatopsia the values of M_1 and M_2 yielding maximum sensitivity were those that gave the composite field classified by the observer as most nearly achromatic.

It is now clear that there is no contradiction between the super-additivity found by Pugh (1976) and the combinative euchromatopsia represented in figures 3 and 4. The conditions for securing the two effects differ both in the absolute value of M_1 and in the ratio M_1/M_2 . If we assume that I_3 (Stiles 1978, tbl. B) represents the spectral sensitivity of the blue cones, we calculate that Pugh's maximum 430 nm field of $10^{7.8}$ quanta s^{-1} deg^{-2} would be equivalent in its effects on the

short-wavelength cones to a 473 nm field of $10^{8.1}$ quanta $s^{-1} \text{ deg}^{-2}$; this value is close to the lowest value of M_1 used for PGP (•, figure 3), where no facilitation is apparent but where 575 nm fields of greater than 10^9 quanta $s^{-1} \text{ deg}^{-2}$ cause the threshold to rise. Super-additivity is found when the blue field contributes negligibly to the appearance of the composite adapting field. In Pugh's experiments a 570 nm auxiliary field of $10^{8.63}$ quanta $s^{-1} \text{ deg}^{-2}$ was always present, and the observers 'were virtually unable to detect the presence of the $\mu_1 = 430$ nm field when it was added to the $\mu_2 = 590$ nm field' (Pugh 1976). Combinative euclimatopsia is found when M_1/M_2 is much greater and the field appears achromatic.

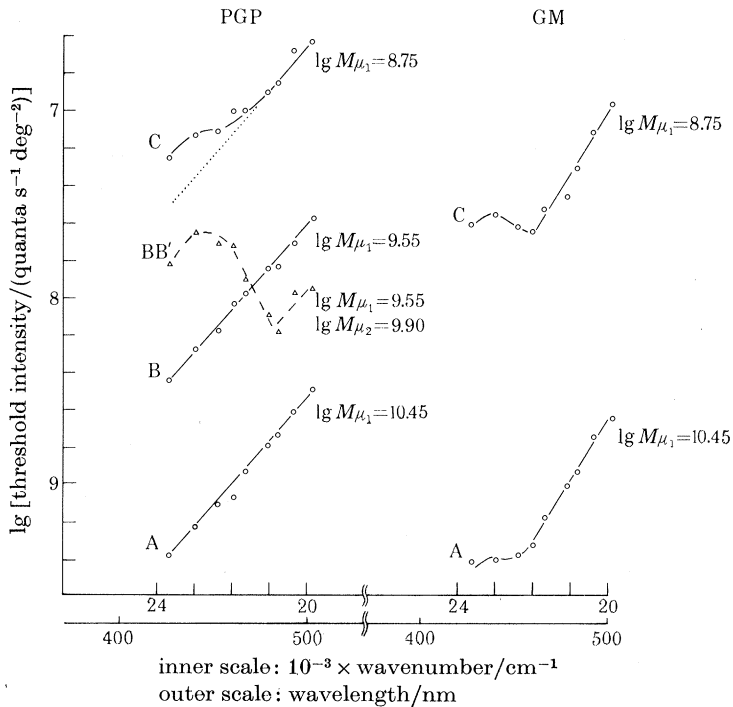


FIGURE 5. Results for experiment 3a: test spectral sensitivities (threshold:wavelength curves) for intensities of 473 nm field as indicated. The conditions used are identified by the same letters on this plot and on the abscissae of figures 3 and 4; $\mu_1 = 473$ nm, $\mu_2 = 575$ nm. In one case (BB', triangles) for PGP a 575 nm field was also present. The solid line fitted to the data for conditions A and B for PGP has been displaced upwards to form the dotted line for condition C.

Experiment 3a. Test sensitivities

To check our interpretation of the threshold:wavelength curves of figures 3 and 4, we have sampled test spectral sensitivities (threshold:wavelength curves) under several of the adapting conditions of experiment 3. The abscissa values used are marked by capital letters in figures 3 and 4 and the same letters are used in figure 5 to identify the corresponding threshold:wavelength functions.

These ancillary measurements were made after the completion of experiment 3. The adaptational condition remained constant within a session and two sessions were devoted to each condition. In one session λ was successively increased in the range 423–505 nm; in the other session, measurements were made in the reverse order. By this stage we were aware of a slow decline in the size of ΔN when adaptation was prolonged (a phenomenon examined formally in experiment 6) and therefore the observer rested for 10 min and then readapted for 4 min before beginning measurements at each fresh value of λ .

Results are plotted in figure 5. We have not attempted to fit to our data the π_3 and π_4 functions of Stiles, since the latter are for the central 1° of the fovea whereas the present results are for 2° targets centred 3.25° from fixation; the spectral band examined here is the one where macular pigmentation would alter the threshold:wavelength function markedly.

When the 473 nm field is relatively weak ($M_1 = 10^{8.75}$ quanta $s^{-1} \text{ deg}^{-2}$; condition C in the figures), a short-wavelength hump in the threshold:wavelength function for both observers suggests that violet flashes are detected by the blue mechanism. At higher values of M_1 ($10^{9.55}$, $10^{10.45}$ quanta $s^{-1} \text{ deg}^{-2}$) the hump disappears from the function for PGP, reflecting the apparent 'saturation' of the blue mechanism seen in figure 3; we are led to conclude that the uppermost thresholds of the threshold:intensity curve of figure 3 (left plot) are determined by π_4 and that the further upward deviation of the blue-mechanism threshold is thereby obscured. For GM the short-wavelength lobe is very prominent at the lower value of M_1 and is attenuated though not absent, when $M_1 = 10^{10.45}$ quanta $s^{-1} \text{ deg}^{-2}$.

Especially instructive are the results obtained for PGP when both the adapting fields are present and M_1 and M_2 have similar quantal values (condition BB', figure 5). A clear peak is then present at 430–440 nm. Sensitivity at these shorter wavelengths has risen relative to that obtained when only a 473 nm field was present, whereas sensitivity at longer wavelengths has fallen, no doubt because the added yellow field acts directly to adapt π_4 and π_5 . These results offer a particularly happy illustration of the phenomenon of combinative euchromatopsia.

A provisional theory

At this stage we introduce a provisional theory that has guided our further experiments. Several of its elements are incorporated in the qualitative model of figure 6. A formal account of a theory of this type is published elsewhere (Pugh & Mollon 1979).

Operationally, Stiles's two-colour method requires the observer to make an intensity discrimination. The essence of our proposal is that in practice the task may be either one of intensity discrimination or one of hue discrimination and that our anomaly arises under stimulus conditions where hue discrimination is the more sensitive.

Assumption 1. Liminal signals originating in the short-wavelength receptors have access only to the chromatic channels of the visual system, that is, to channels receiving inputs of opposite sign from different classes of receptor.

Such a proposal has been made explicitly by Guth *et al.* (1968) and Boynton (1971). Walls (1955), in his 'branched-pathway schema' for colour vision, had earlier suggested that the contribution of the blue cones to his (single) non-opponent channel was very slight. Such suggestions are traditionally supported by the fact that changes in the intensity of the short-wavelength primary in colour-matching experiments can produce large changes in hue while having negligible effects on brightness. Whittle (1973, 1977) has shown directly that flashes seen only by π_1 cannot be consistently matched in brightness to flashes detected by the long-wavelength mechanisms (although Marks (1974) found that observers could rank suprathreshold π_3 flashes according to some quality)†.

For our present purpose we need not exclude the possibility that suprathreshold signals from the short-wavelength receptors have some access to non-chromatic channels. We must assume only that when euchromatopsia is observed the chromatic channels offer a pathway for detection that is significantly more sensitive than any non-chromatic channel.

Assumption 2. Many of the anomalous properties of the psychophysically defined blue mechanism are properties not of the short-wavelength receptors themselves but of the chromatic channels to which their signals are confined.

This proposal was made by Mollon & Krauskopf (1973) and now seems particularly pertinent to the explanation of the adaptive anomalies. The P535 and P565 cones enjoy access to a variety of pathways and only under certain conditions are their liminal signals detected by chromatically opponent channels (King-Smith & Carden 1976; Sternheim *et al.* 1978). Thus we propose that the adaptational 'anomalies' of the blue mechanism (such as transient tritanopia, saturation, combinative euchromatopsia) reveal general properties of opponent channels, properties that are concealed when non-opponent channels provide alternative means of detecting signals originating in the P535 and P565 cones.

Assumption 3. The signal originating in the short-wavelength receptors may be attenuated or masked at two successive sites.

Assumption 4. At the first site, the attenuation produced by background fields depends only on the rate of isomerizations in the short-wavelength cones themselves.

† Blue cones certainly contribute little or nothing to *luminance*, as measured by flicker photometry or the minimally distinct border (see Boynton (1978a) for a review), but such evidence cannot properly be brought to bear on assumption 1, since only a mechanism able to follow high temporal and spatial frequencies could influence measurements of luminance and we do not yet know for certain whether the large space and time constants of the psychophysically defined blue mechanism are the cause or the consequence of the exclusion of short-wavelength cone signals from the non-opponent channels.

Assumption 5. At the second site the sensitivity depends on antagonistic signals from (a) the short-wavelength cones and (b) one or other or both of the middle- and long-wavelength cones.

There have been recurrent suggestions that the sensitivity of the psychophysically defined blue mechanism is in part controlled by signals from the red and green cones (De Vries 1948, 1949; Stiles 1959; Brindley 1960; Mollon & Polden 1975; Pugh 1976). The accumulated evidence consists of (a) the long-wavelength lobe of π_1 ; (b) the lack of correlation between the sensitivities of a given observer's blue mechanism at short and long wavelengths (Stiles 1946; see also Mollon & Polden 1977*b*); (c) non-additivities in the effects on π_1 of short- and long-wavelength fields (Pugh 1976); (d) differences in the time constants of adaptation of the blue mechanism to short- and to long-wavelength fields (see, for example, Augenstein & Pugh 1977); (e) the absence of the π_1 lobe and of transient tritanopia in blue-cone monochromats (Daw & Enoch 1973; Hansen *et al.* 1978); (f) the variation with field wavelength of the optimal point of pupil entry for II_1 and the similar values of the directional sensitivity parameter ρ for II_1 and II_5 at long wavelengths (Alpern & Zwas 1979). For further discussion, see Mollon & Polden (1976, 1979), Stiles (1978), and Boynton (1978*b*). That the interaction is opponent in nature was suggested by Mollon & Polden (1977*b, c*), Pugh (1977), Augenstein & Pugh (1977) and Stromeyer *et al.* (1978); for detailed discussion see Pugh & Mollon (1979).

The 'first site' (assumption 4) is probably to be identified with the outer segments of the blue-sensitive cones; we leave unspecified the anatomical basis of the second site (but see experiment 5).

Assumption 6. A chromatically opponent channel is most sensitive to input perturbations when it is at an intermediate value of its response range.

Assumption 7. The latter point corresponds to a phenomenal neutral point, i.e. for a 'blue-yellow' channel, to a sensation that is neither yellowish nor bluish.

Assumption 6 is crucial. Combinative euchromatopsia is probably the most direct evidence in its favour. It can be illustrated by reference to the model of figure 6. Signals from the adapting fields and from test flashes reach the opponent site via the same pathways and detection of a test flash depends on a criterion perturbation in the output of the channel. The output of the opponent site (V_2) is a sigmoid function of the difference of the input signals ($V_B - V_Y$): when the field combination is such that $|V_B - V_Y|$ is small, the input perturbation (ΔV_B) resulting from a given short-wave test flash yields a relatively large change in V_2 , but when $|V_B - V_Y|$ is large, ΔV_B must be greater for the same change in V_2 (see right-hand inset of figure 6). Note that this channel would be little sensitive to *white* flashes, since the concurrent increments in V_Y and V_B would tend to cancel. We shall speak of the channel as *polarized* when $|V_B - V_Y|$ is large.

In the present experiments we suppose that the 473 nm field impairs sensitivity both by reducing the gain of the short-wavelength receptors and by polarizing the

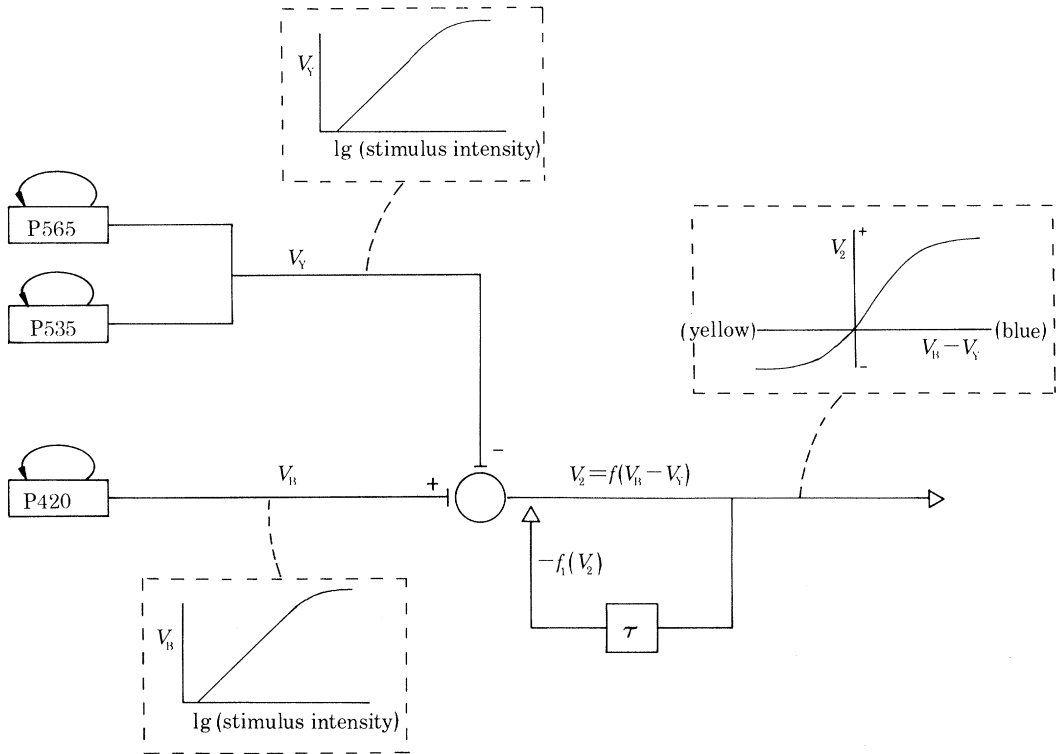


FIGURE 6. Qualitative model of the blue mechanism. The short-wavelength receptors deliver a signal V_B to a chromatically opponent site where V_B is opposed by a signal V_Y , which originates in the long- and middle-wavelength receptors. The receptor signals (inset) are asymptotic functions of stimulus intensity, being limited by bleaching and possibly by additional response compression. The output of the opponent site (V_2) is a sigmoid function of the net input signal $(V_B - V_Y)$ (see inset). When $|V_B - V_Y|$ is small, a small change on the abscissa produces a large change in V_2 , but, when $(V_B - V_Y)$ assumes a large positive or negative value, a much larger change on the abscissa is required for the same change in V_2 . Values for the peak sensitivities of the receptors are based on recent microspectrophotometric measurement (Bowmaker *et al.* 1978; Bowmaker *et al.* 1979, 1980) but are consistent with accumulated psychophysical evidence. The asymmetry of our sigmoid function and the association of blue with positive values of V_2 are speculative, but are based on psychophysical evidence that the number of j.n.ds between yellow and white is much less than that between blue and white (Wright 1946, ch. 13) and on electrophysiological evidence that in the primate retina it is much more common to record blue ON-centre ganglion cells than it is to record blue OFF-centre cells (Malpelli & Schiller 1978; Zrenner & Gouras 1979). To account for transient tritanopia a restoring force is postulated, which acts to reduce the polarization of the opponent site and which here is represented as a function of V_2 (integrated over a long time sample). See Pugh & Mollon (1979) for a full treatment of this aspect of the model.

second site, whereas the long-wavelength fields primarily act to alter the polarization of the second site. Depending on the value of M_1 , the addition of a yellow field of a given intensity may increase or decrease the polarization of the second site. When polarization is reduced, euchromatopsia is observed.

If the short-wavelength receptors have approximately the spectral sensitivity of Π_3 , then 575 nm field that produces maximal facilitation under the conditions of experiment 1 will add less than 0.1% to the number of photons absorbed by these receptors from the 473 nm field. Thus the conditions of the present experiments are analytically attractive, since they allow us to manipulate the state of the second site while producing negligible change at the first.

The means by which sensitivity is altered at the second site is not yet known. In the model of Pugh & Mollon (1979) a gain control is postulated that is analogous to that conventionally postulated for the first site; but the changes in sensitivity might equally be achieved by response compression or by masking without attenuation of the signal. Moreover, polarization of the second site in one direction may not reduce sensitivity in the same way as does polarization in the other.

Experiment 4. Action spectrum for combinative euchromatopsia

The purpose of this experiment was to establish whether the facilitation occurs for values of μ_2 removed from the complementary of μ_1 and to identify the source of the antagonistic, long-wavelength signal that acts at the postulated second site. The latter signal might originate in the green-sensitive cones alone or in the red-sensitive cones, or might represent a weighted sum of their outputs. The first possibility has been suggested by Gouras (1972) and the second by Abramov (1968); many authors have favoured the third. (It is always just possible that the long-wavelength mechanism controlling the sensitivity of the blue mechanism has an otherwise unknown spectral sensitivity, one unlike those of the photopigments responsible for direct visual excitation.) The procedure of the present experiment was to measure the action spectrum of the facilitatory effect, i.e. to hold constant the 473 nm field and discover for different values of μ_2 the intensity of the added field needed to bring the threshold to its minimum.

Throughout the experiment, M_1 remained fixed at $10^{9.2}$ quanta $s^{-1} \text{ deg}^{-2}$, the value used in experiments 1 and 2. Two sessions were devoted to each value of μ_2 and the order of sessions was randomized; μ_2 remained constant within a session and the procedure was as for a single session of experiment 3. Values of μ_2 were defined by a set of narrow-band interference filters in combination with blocking filters; full bandwidths at half height for the combinations, measured *in situ*, were in the range 6–13 nm.

The results are shown in figure 7 (upper panel) for PGP and in figure 8 for CS. The parameter is μ_2 , the wavelength of the added field. Since the function relating threshold to M_2 is shallow and the minimum is very indeterminate, the only feasible way of deriving an action spectrum is to take into account all the data points for a given value of μ_2 . Each set of data in figure 7 has been fitted by eye with the same

template, which is represented by the solid line and which has no *a priori* significance. The horizontal displacements of this template have been used to obtain a first approximation to an action spectrum (the derivation is represented graphically

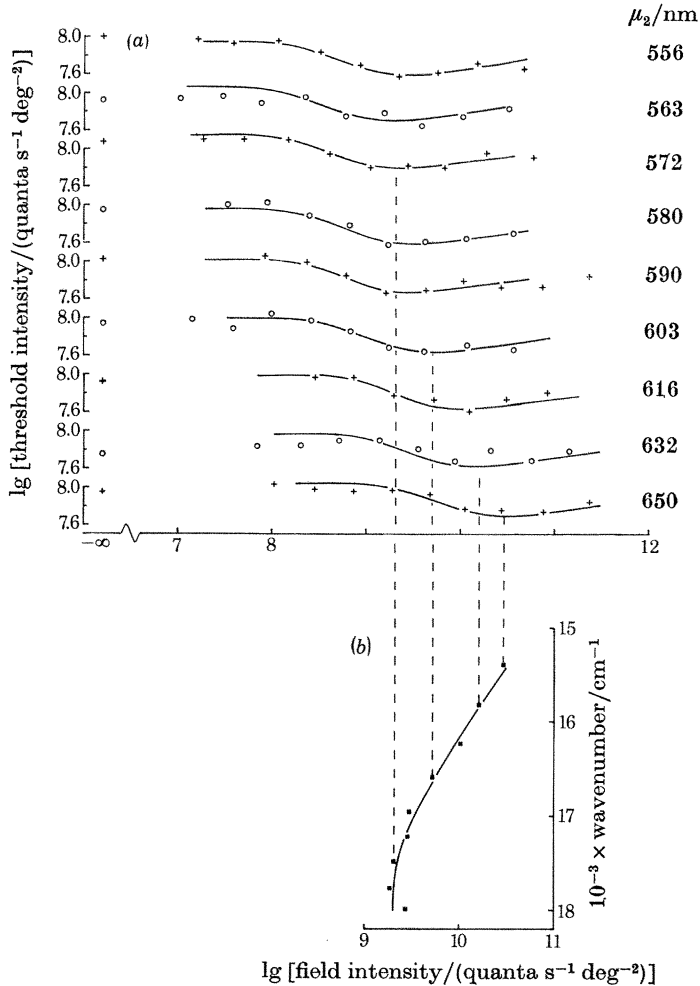


FIGURE 7. Results of experiment 4. Observer: PGP. (a) \lg (incremental threshold) for 423 nm flashes presented on composite fields consisting of (i) a 473 nm field of fixed intensity ($10^{9.2}$ quanta $s^{-1} \text{ deg}^{-2}$) and (ii) long-wavelength fields of the \lg (intensity) shown on the abscissa and the wavelength shown to the right; the same arbitrary template (solid line) has been fitted to each set of data. (b) Action spectrum for combinative euchromatopsia, i.e. \lg intensity of long-wavelength field required to produce maximal facilitation plotted as a function of wavenumber.

in the lower panel of figure 7). As μ_2 increases above 590 nm the template has to be shifted to the right: higher values of M_2 are required to bring the threshold to its minimum. These criterion values of M_2 are plotted against $1/\mu_2$ in the lower panel and constitute an action spectrum for combinative euchromatopsia. In terms

the theory outlined above, this derived function would represent the spectral sensitivity of V_Y , the long-wavelength input to the second, opponent, site. The solid line drawn through the data is close to the photopic luminosity function, V_λ .

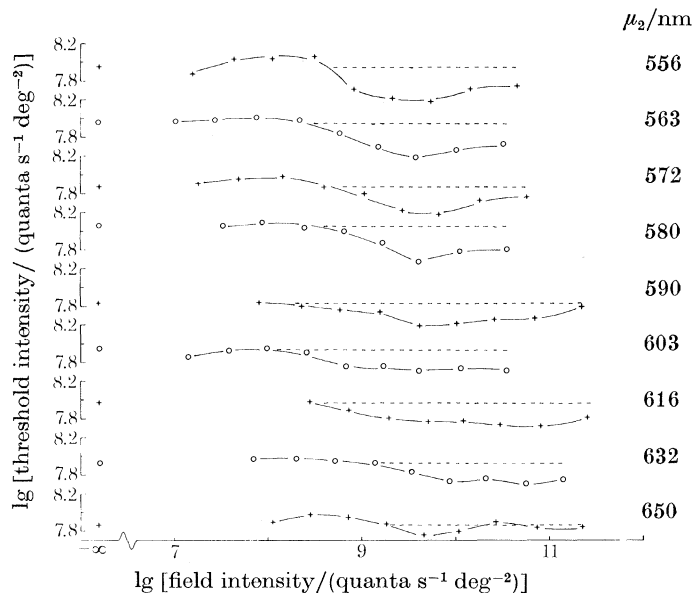


FIGURE 8. Results of experiment 4. Observer: CS. Lg (incremental threshold) for 423 nm flashes presented on composite fields consisting of (i) a 473 nm field of fixed intensity ($10^{9.2}$ quanta s^{-1} deg^{-2}) and (ii) long-wavelength fields of the lg(intensity) shown on the abscissa and the wavelength shown to the right. The broken line (and the leftmost of each set of symbols) represent the threshold on the 473 nm field alone.

For CS (figure 8) the data sets cannot realistically be fitted by a single template. For values of μ_2 between 556 and 580 nm, the function has a form similar to that for PGP and $\log \Delta N$ has maximal values in the range 0.35–0.38; but as μ_2 increases, the function becomes shallower, until at 650 nm there is no clear evidence of facilitation. The same trend can in fact be seen in the data for PGP (figure 7): for $\mu_2 = 580$ nm, $\log \Delta N$ has a maximal value of 0.42, for $\mu_2 = 632$ and 650 nm the values are 0.15 and 0.24 respectively.

Experiment 4a

The experiments described immediately above took several weeks to complete for each observer; only one set of measurements at one value of μ_2 could be obtained in a day, owing to the need to allow adaptation to recover between measurements. In the light of the results of experiment 4, we therefore concentrated measurements for a third observer (AS) at two values of μ_2 most likely to answer questions of interest: 575 and 650 nm. Bandwidths at half height for the two fields were 12 nm and 8 nm respectively. On each experimental day, measurements were obtained

at both values of μ_2 , the order of the two runs being alternated on successive days. Calibrations were made at the beginning and end of each run and variations of more than 5% in the maximum output of any channel were not tolerated. After

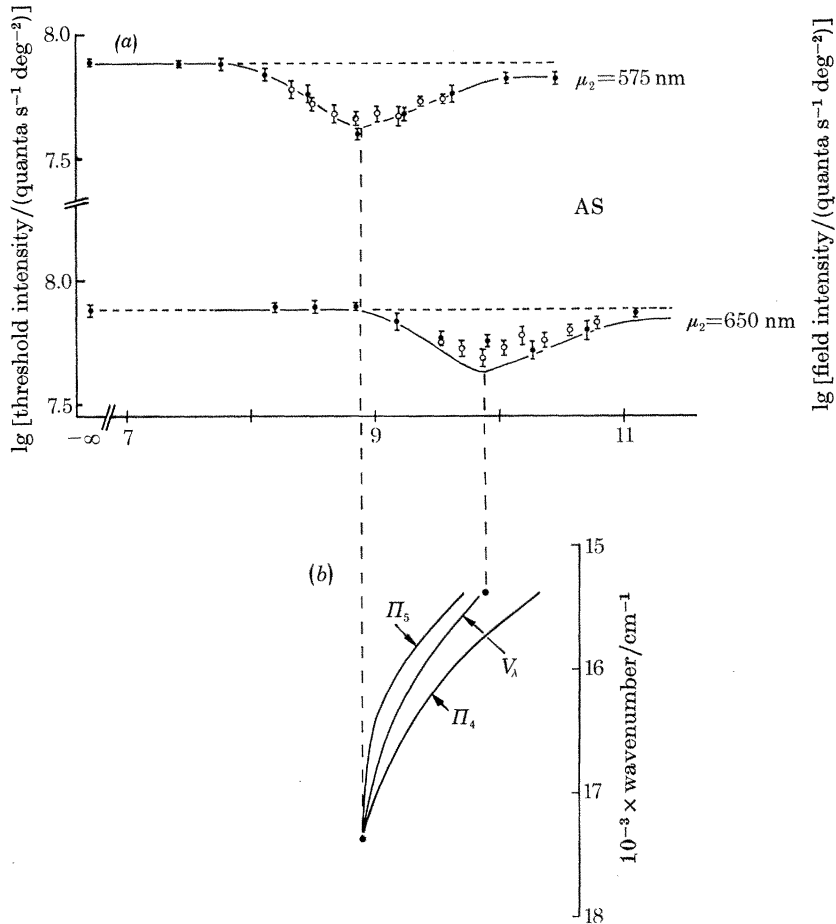


FIGURE 9. Results of experiment 4a. Observer: AS. (a) Lg (incremental threshold) for 423 nm flashes presented on composite fields consisting of (i) a 473 nm field of fixed intensity ($10^{9.2}$ quanta s^{-1} deg^{-2}) and (ii) either a 575 nm (upper set of data) or a 650 nm field (lower set of data) of the lg (intensity) shown on the abscissa; \bullet , \circ first and second series of measurements respectively. The broken line (and the leftmost filled symbol) in each case represents the threshold on the 473 nm field alone. (b) Comparison between (\bullet) intensities of 575 nm and 650 nm fields required to produce maximum facilitation and (—) relative intensities predicted by Π_4 , Π_5 and V_λ .

eight separate runs had been completed for each value of μ_2 , a further series of eight runs was undertaken for values of M_2 concentrated near the minimum of each function.

Results for experiment 4a are shown in the upper panel of figure 9. Solid circles

correspond to the first series of eight runs, open circles to the second. Error bars indicate ± 1 s.e.m. An arbitrary curve has been drawn through the upper set of data, which is for $\mu_2 = 575$ nm. This template has then been fitted to the lower data points ($\mu_2 = 650$ nm), being laterally adjusted to minimize the sum of the squared vertical deviations; no vertical adjustment was allowed. In the lower panel, the lateral shift required is represented graphically, and is compared with those that would be required if the facilitatory effect had the action spectrum of Π_4 , Π_5 or V_λ .

The results for AS confirm the two trends of the results for PGP and CS: (a) as far as an action spectrum can be derived, it lies between those of Π_4 and Π_5 ; and (b) the maximal value of ΔN is smaller for $\mu_2 = 650$ nm than for $\mu_2 = 575$ nm. There is now microspectrophotometric (Bowmaker *et al.* 1978, 1980; Bowmaker & Dartnall 1980) and psychophysical (Estévez & Cavonius 1977; Pugh & Sigel 1978) evidence that the field sensitivities Π_4 and Π_5 are close to the sensitivities of the middle- and long-wavelength cones and thus finding (a) does suggest that the signal V_Y originates in both the red and the green cones; but in adopting this provisional conclusion we place rather more weight on the finding for all three observers that a single template will not fit the data for all values of μ_2 . For if V_Y originated in a single class of cones that obeyed the principle of univariance (Rushton 1972) and if, as argued above, V_B were unaffected by long-wavelength fields in the relevant range of intensity, then a single template ought to fit all sets of data. Changing the value of μ_2 would merely change the probability that a given photon from the long-wave field would lead to an isomerization; and thus the threshold function would merely be displaced bodily along the abscissa.

Our provisional conclusion that V_Y originates in both red and green cones is consistent with our earlier finding that transient tritanopia occurred in both a protanope and a deuteranope (Mollon & Polden 1977*b*), with the fact that there is not a unique ratio of two long-wavelength fields that will minimize transient tritanopia when one field is substituted for the other (Mollon & Polden 1979) and with the finding of Boynton (1978*b*) that long-wavelength lights that equally impair discriminations based on blue cone signals are lights of equal troland values. But a difficulty remains. It is true that if the long-wavelength signal represented the weighted sum of signals from *two* classes of cone, a fixed template would not necessarily be expected to fit the data at each value of μ_2 ; for as μ_2 increases, the sensitivities of the red- and green-sensitive cones diverge and thus there may well be a change in the function relating the sum of their signals to field intensity. Nevertheless, provided that the individual signals are related monotonically to intensity, there ought always to be some value of M_2 at which the sum of the red and green signals is such as to yield the full facilitation. And this is not so, as is shown, for example, by the difference in the depths of the minima of the data curves for $\mu_2 = 575$ and 650 nm in figure 9. It is as if *any* residual colour in the field prevents the blue mechanism attaining its highest sensitivity. Two possibilities present themselves. (a) The sensitivity of the blue mechanism may be

additionally controlled by a signal itself dependent on the difference of the red and green signals. (b) There may be more than one opponent channel to which the blue cones contribute signals. To be specific, there may be channels receiving inputs of one sign from blue and green cones or from blue and red cones and receiving an antagonistic signal from the remaining class of cone, as well as the classically postulated channel in which signals from red and green cones are opposed to signals

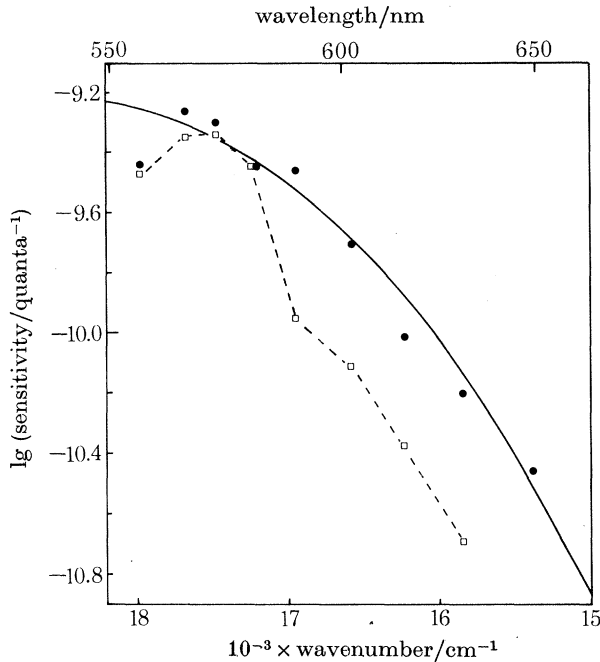


FIGURE 10. Results of experiment 4b compared with those of experiment 4 for observer PGP; ●, action spectrum for euchromatopsia replotted from figure 7; ◻, lg (reciprocal intensity) of long-wavelength fields required to cancel blueness of fixed 473 nm field of $10^{9.2}$ quanta $s^{-1} \text{ deg}^{-2}$.

from blue cones. De Monasterio *et al.* (1975) report all three such combinations of inputs to retinal ganglion cells in *Macaca mulatta*. If then the short-wavelength cones contribute to several opponent channels, the overall psychophysical sensitivity may be maximal only when all the channels are brought close to their neutral point; and this may happen only when μ_2 is close to the complementary of μ_1 .

Experiment 4b. Chromatic cancellation

If the chromatically antagonistic channel that we have postulated to account for combinative euchromatopsia is to be identified with the blue-yellow system of classical opponent-process theory (Hurvich & Jameson 1957), it would be appropriate to compare the action spectrum for euchromatopsia with the 'yellow chromatic function' derived by adding a blue stimulus to various long-wavelength

stimuli and finding the intensity of the blue field at which the composite stimulus appeared neither yellowish nor bluish. In figure 10 our action spectrum for PGP (●; replotted from figure 7, lower panel) is compared with the 'yellow chromatic function' of observer H of Hurvich & Jameson (—). However, little weight can be placed on the good agreement between the two, since the 'yellow chromatic function' is subject to large individual differences; thus our data are a poor fit to the function for observer J of Hurvich & Jameson. We therefore sought to obtain a yellow chromatic function for our own observer PGP. We adapted the method of Hurvich & Jameson to our own conditions.

To approximate better the procedure of experiment 4, we held constant the short-wavelength field and titrated the intensity of long-wavelength fields to establish the values at which the composite fields appeared neither yellowish nor bluish. Thus the intensity of the 473 nm field was fixed, as before, at $10^{9.2}$ quanta $s^{-1} \text{ deg}^{-2}$. The wavelengths and bandwidths of the long-wavelength fields were also those of experiment 4 (although we proved not to have enough radiance to measure a data point at 650 nm). The size and position of the composite stimulus were, however, those of our standard *test* stimulus (2° diameter, 3.25° eccentricity), since this region of the background field would presumably be most relevant in our primary experiments.

Each blue–yellow neutral point was obtained by a randomized double-staircase procedure under computer control. For 5 min before a block of trials and for 10 s between individual trials, the observer adapted to a screen coated with magnesium oxide and illuminated by CIE Illuminant C. The screen was not seen in Maxwellian view and was mounted to one side of the main optical system. At the end of each inter-trial interval a tone instructed the observer to apply his eye to the Maxwellian system and to judge the hue of the steadily presented target. He was required to respond within 2 s, indicating 'bluish' or 'yellowish' by means of push buttons. The computer then adjusted the intensity of the long-wavelength field for the next trial. Two blocks of 50 trials were devoted to each wavelength and the order of blocks was randomized.

The neutral points so obtained are shown as open squares in figure 10. No vertical adjustment of the points has been made. In the region of 575 nm (the wavelength complementary to 473 nm) there is good absolute agreement with the solid points, which are derived from experiment 4 and represent the action spectrum for euchromatopsia. This result formally demonstrates that (when μ_2 is close to 575 nm) the composite fields yielding maximal values of ΔN are those that appear most nearly achromatic (cf. assumption 7, above).

For $\mu_2 > 590$ nm, however, the phenomenological blue–yellow equilibrium points do not coincide with the values of M_2 that yield maximal values of ΔN for the same observer. For this and earlier reasons, we hesitate to identify the classical 'blue–yellow' channel of opponent-process theory with the channel that underlies combinative euchromatopsia in the present experiments.

Experiment 5. Dichoptic preservation

In this experiment the two adapting fields were presented dichoptically. The apparatus was modified so that the 575 nm field was presented to the left eye while the 473 nm field and the test flash were presented to the right eye as before. M_1 had a value of $10^{9.2}$ quanta s^{-1} deg^{-2} . The observers were PGP and CS, both of whom show a reliable facilitation at this value of M_1 when fields are combined monocularly (figures 4, 7, 8).

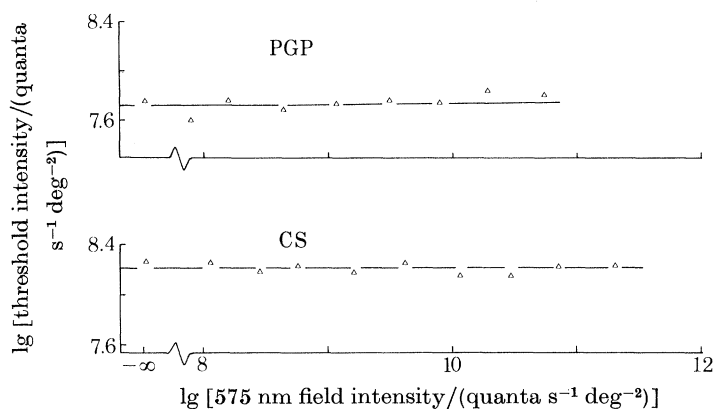


FIGURE 11. Lg (incremental threshold) for 423 nm flashes presented on a dichoptic field consisting of (i) a 473 nm field of fixed intensity ($10^{9.2}$ quanta s^{-1} deg^{-2}) presented to the same eye and (ii) a 575 nm field of the lg (intensity) shown on the abscissa and presented to the contralateral eye.

CS reported binocular rivalry between the blue and yellow fields, whereas PGP found that they fused to give a stable binocular field, which, at intermediate values of M_2 , appeared as achromatic as a composite field viewed monocularly. Neither observer showed any evidence of euchromatopsia (figure 11). Similarly, Sternheim *et al.* (1979) found that detection of a flickering 620 nm target on a 615 nm field was not facilitated when a 548 nm field was presented to the contralateral eye.

We conclude that the postulated opponent site does not receive inputs from the two eyes. This conclusion is consistent with the demonstration of transient tritanopia at the level of the retinal ganglion cell (Gouras 1968) and the b-wave (Valeton & Norren 1979), and with the absence of transient tritanopia when field and target are presented dichoptically (Mollon & Polden 1977*b*, expt 7).

Experiment 6. Temporal variation

In earlier experiments we had become aware of temporal variations in the size of ΔN when a composite adapting field was steadily observed for some minutes; and we were therefore careful to hold constant the period of adaptation preceding

threshold measurements. In experiment 6 we formally examined the time course of the effect.

After dark adapting for 4 min, the observer adapted either to a 473 nm field of $10^{9.2}$ quanta $s^{-1} \text{ deg}^{-2}$ or to this field in combination with a 575 nm field of $10^{9.7}$ quanta $s^{-1} \text{ deg}^{-2}$. The temporal variation of the threshold following the onset of the field was tracked by means of a single-staircase procedure (Cornsweet 1962), the step size being 0.15 logarithmic unit. The starting intensity of the test flash

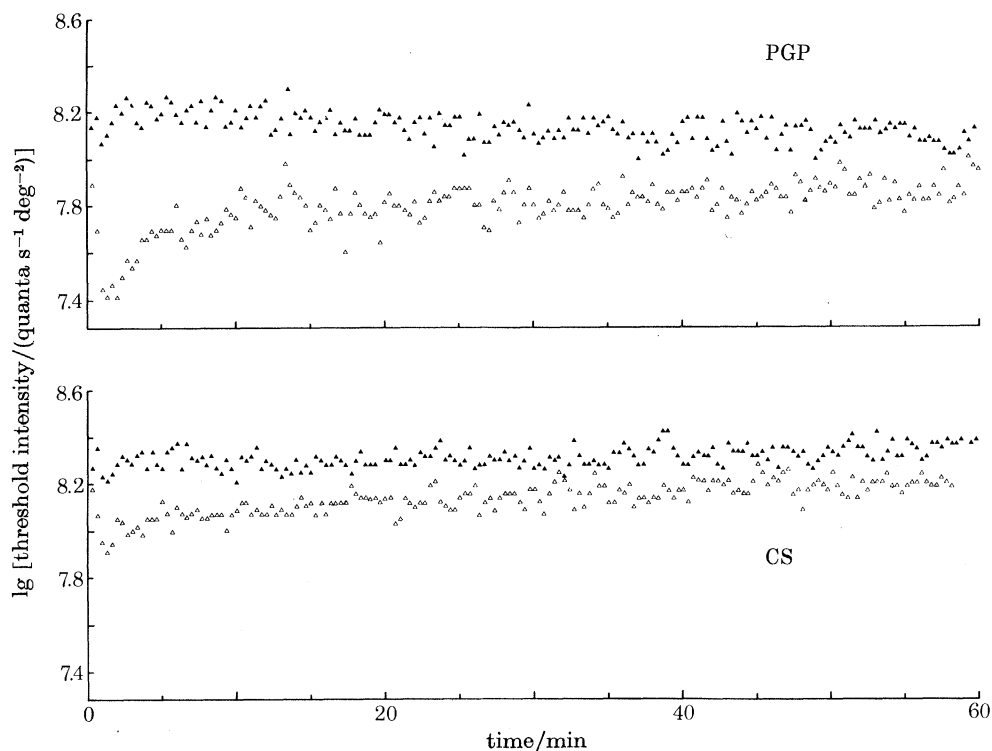


FIGURE 12. Lg (incremental threshold) for 423 nm flashes as a function of time since onset of adapting field; ▲, thresholds on 473 nm field of $10^{9.2}$ quanta $s^{-1} \text{ deg}^{-2}$; △, thresholds on this field in combination with a 575 nm field of $10^{9.7}$ quanta $s^{-1} \text{ deg}^{-2}$.

was the same for the two conditions of adaptation and was chosen on the basis of pilot measurements. Test flashes occurred every 5 s. Measurements were continued for 1 h without interruption of adaptation. Four separate runs were devoted to each condition of adaptation. The conditions were alternated and successive experimental runs were separated by a minimum interval of 1 h.

For each run the mean intensity level visited was calculated for each successive 20 s interval. These values were in turn averaged across the four runs for a given condition and the resulting values are plotted in figure 12. The most curious feature of the data is the increase and then decrease in ΔN during the first few

minutes of adaptation. This feature is particularly marked for PGP, who shows a facilitation of almost 0.8 logarithmic unit during the second minute of adaptation to the composite field. (When higher values of M_1 and M_2 are used, the initial oscillation of sensitivity is even greater in amplitude and is more rapid, and after several minutes the threshold may be higher than it was immediately after the onset of the fields (Mollon & Polden 1978, 1980; Stromeyer *et al.* 1979).) After 1 h the threshold is still lower on the composite field, but ΔN is reduced.

The slow loss of sensitivity with maintained exposure to the composite field recalls the loss of sensitivity to frequently presented targets that was described by McFarland *et al.* (1942) and, independently, by Frome *et al.* (1976) and by Baker & Bargoot (1977). But our interflash interval was long by the standards of these authors and, if the present phenomenon is to be identified with the 'visual habituation' that they describe, an *ad hoc* hypothesis is necessary to explain why the habituation is most marked in the presence of the composite field; there is only a slight drift in threshold when only the blue field is present and the trend is in opposite directions for PGP and CS. *Prima facie* these facts are equally difficult to explain in terms of the two-site model outlined above. In the specific version of the theory formalized by Pugh & Mollon (1979) a restoring force, ρ , with a long time constant acts to reduce the polarization of the second site. The force ρ increases as the polarization increases. The threshold ought to be most stable when the field is chromatically neutral. We suspect therefore that the variation in sensitivity during adaptation to the composite field reflects a variation in the signal delivered to the second site from the long-wavelength receptors and thus a variation in $|V_B - V_Y|$; in this context we note that a 575 nm field of $10^{9.7}$ quanta $s^{-1} \text{ deg}^{-2}$ has a troland value of $10^{3.55}$ and would produce some bleaching in the long-wavelength receptors. Evidence for this position will be published elsewhere.

DISCUSSION

In the sections that follow, we demonstrate some results that can be drawn out by further analysis of our data, examine the implications of combinative euchromatopsia for Stiles's two-colour method, and relate our results to those of others.

Saturation

We have shown elsewhere (Mollon & Polden 1977*a*) that the blue mechanism, unlike the other cone mechanisms, can be 'saturated' by steady adapting fields, in that the increment-threshold function on logarithmic ordinates has a slope much greater than unity when short-wavelength fields of increasing intensity are added to a fixed yellow auxiliary field. In figures 3 and 5 (above) we have seen that a similar saturation occurs for PGP in the presence of a blue field alone, although in the absence of an auxiliary field the upwardly deviating function cannot be followed far, owing to intrusion by π_4 .

In the theory of Pugh & Mollon (1979), the 'saturation' occurs when the polarization of the second site is increasing at the same time as sensitivity is being reduced at the first site. As blue light of increasing intensity is added to the yellow auxiliary field in the experiments of Mollon & Polden (1977*a*), adaptation at the first site

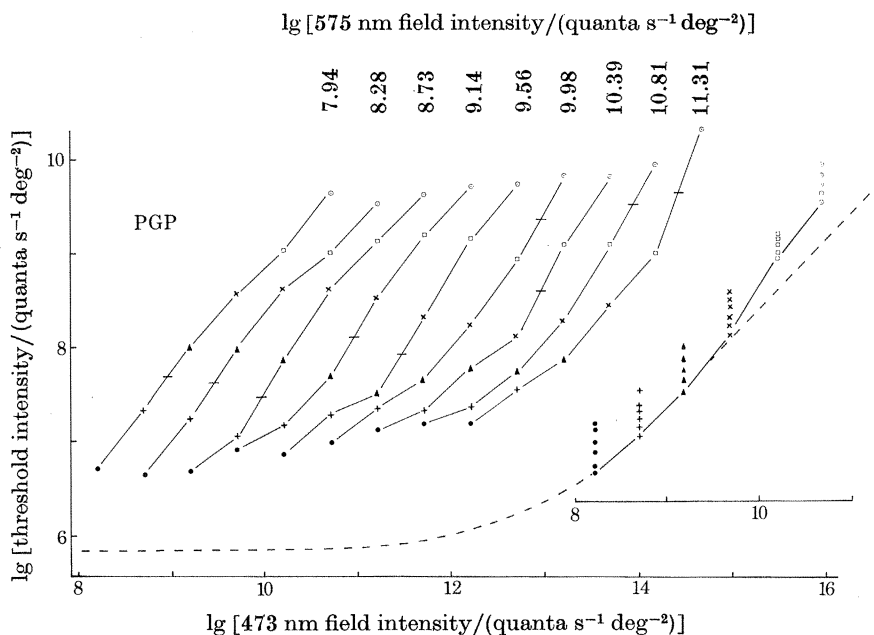


FIGURE 13. Data replotted from right-hand panel of figure 3. (Observer: PGP.) Solid lines link thresholds for one intensity of the 575 nm field and varying intensities of the 473 nm field. The abscissa indicates \lg (intensity) of the latter fields and is correct only for the leftmost set of data, data sets for more intense 575 nm fields being displaced successively 0.25 log unit to the right. Cross-bars indicate the steepest segment of each function. (In all cases these segments have a slope greater than unity.) Corresponding thresholds are represented by corresponding symbols in this figure and figure 3. On the extreme right of this figure the data have been collapsed and plotted against a single absolute abscissa representing the \lg (intensity) of the 473 nm field. The solid line connects the lowest data point for each value of the 473 nm field and thus represents the set of conditions under which the blue mechanism is empirically most sensitive. Different values of the 575 nm field are required for maximal sensitivity at different values of the 473 nm field. The broken line represents Stiles's function $\zeta(x)$ (Stiles 1978, p. 17) and is placed so that the absolute threshold for the blue mechanism coincides with that implied by figure 3 (left-hand panel).

will increase monotonically while the polarization of the second site will first decrease, will pass through its minimum and will then increase. When the last occurs, when, that is, sensitivity is falling at both sites as field intensity increases, the increment-threshold function will deviate upwards from the Weber line.

A clear prediction derives from the theory of Pugh & Mollon: since the polarization of the second site depends on the difference of the long- and short-wavelength

signals, the intensity of the short-wavelength field needed to produce a deviation from the Weber line will increase with the intensity of the long-wavelength auxiliary field (provided that the latter is not so intense as to saturate the red and green cone signals). A transformation of the data of experiment 3 shows that this prediction is confirmed.

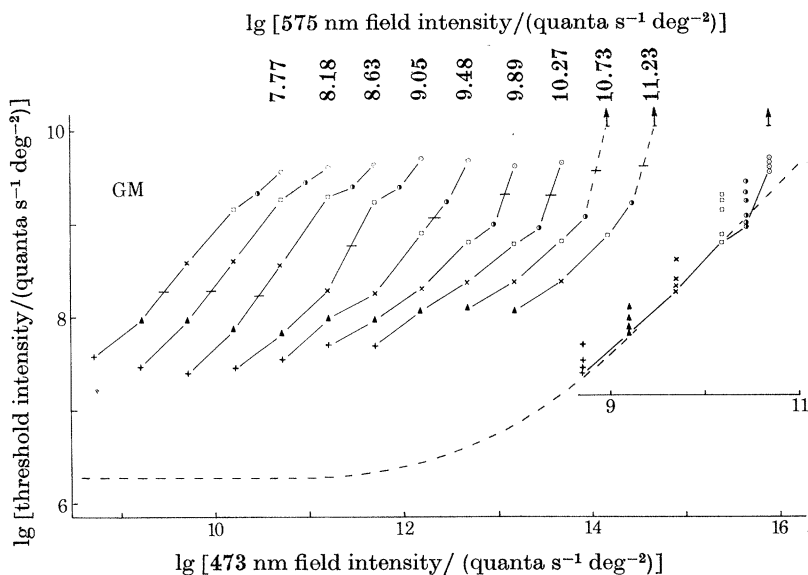


FIGURE 14. Data replotted from right-hand panel of figure 4. (Observer: GM.)
Details as for figure 13.

In the right-hand panels of figures 3 and 4, thresholds for a given intensity (M_1) of the 473 nm field are plotted against the intensity (M_2) of the 575 nm field; these plots reflect the way in which the data were gathered. Suppose for a moment, however, that we deem the yellow fields to be a series of auxiliary fields and that for each value of M_2 (now the intensity of the 'auxiliary' field) we plot thresholds against M_1 . This is equivalent to taking a vertical slice through the data of the right-hand panels of figures 3 and 4. Thresholds replotted in this way are shown in figures 13 and 14 for PGP and GM respectively. The solid lines connect a set of thresholds for a given 'auxiliary' field and the log intensity of the latter (in quanta $s^{-1} \text{ deg}^{-2}$) is shown above each function. In these reconstructed threshold: intensity curves we are connecting data points obtained on different days, since M_1 was constant within a session; but we remind the reader that successive threshold measurements within a session were in any case more independent than usual, being separated by a minimum interval of 15 min.

In figures 13 and 14 we have identified with cross-hatches the steepest part of each threshold: intensity curve. (In every case the slope is greater than one.) There is clearly a systematic relation between the value of M_2 and the position of the

hatch: as the 'auxiliary' field is made more intense the upward deviation is deferred to higher values of M_1 . This is seen clearly in figure 15, where reconstructed threshold:intensity functions for two different 'auxiliary' fields are superimposed on the same absolute ordinates: when the 473 nm field is weak, the more intense 'auxiliary' field is associated with the higher threshold, since the 'auxiliary' field is presumably then the primary determinant of the threshold,

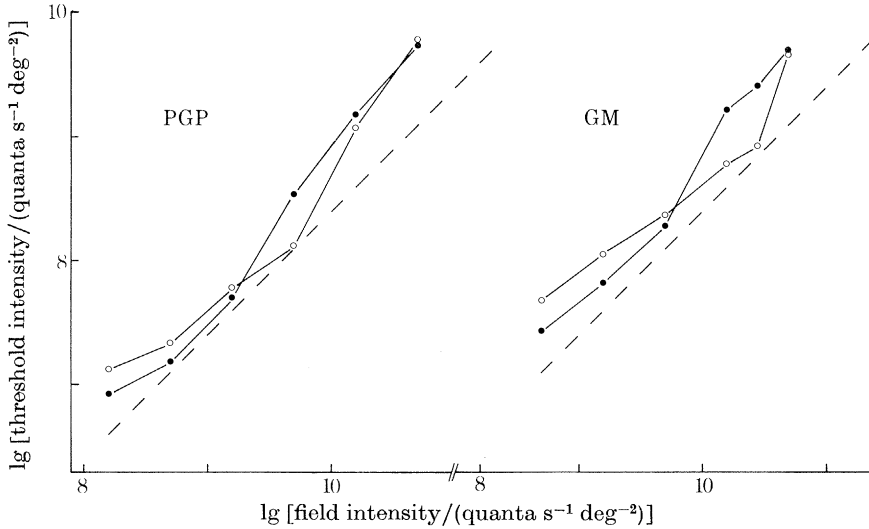


FIGURE 15. Data replotted from figures 3 and 4 to show threshold:intensity curves reconstructed for different values of a yellow 'auxiliary' field. For PGP $M_2 = 10^{9.14}$ (●) and $10^{10.39}$ (○) quanta $s^{-1} \text{ deg}^{-2}$; for GM, $M_2 = 10^{9.05}$ (●) and $10^{10.27}$ (○) quanta $s^{-1} \text{ deg}^{-2}$. The abscissa represents the lg (intensity) of the 473 nm field. The broken line has a slope of unity and represents Weber's law.

but as M_1 increases, thresholds rise more rapidly on the weaker 'auxiliary' field and the two functions cross. (In figures 13–15 several of the threshold:intensity functions for the weaker 'auxiliary' fields show a downward inflexion at the highest values of M_1 ; we do not yet have measurements of test sensitivity under these conditions and so cannot say whether these inflexions represent intrusion by π_4 .)

Weber fraction

Stiles (1939, 1953) reported that the Weber fraction was greater for the blue mechanism than for the green and red mechanisms, being 8.7% for π_1 and π_3 and 1.9 and 1.8% for π_4 and π_5 respectively. A Weber fraction must, of course, always be arbitrary, being dependent on the temporal and spatial parameters of the target and the integrative properties of the mechanism, but the present results show that the field conditions must also be considered. Stiles (1953) derived the Weber fraction for the case where $\mu = \lambda =$ the wavelength of peak sensitivity of

the mechanism. Auxiliary fields were used for π_1 and π_3 (Stiles, personal communication, and see next section) but were not of course chosen with the intention of maximizing the sensitivity of a putative opponent site.

We believe that experiment 3 provides conditions under which the blue mechanism approaches its maximal sensitivity and it is therefore of interest to derive the limiting Weber fraction. The reader will recall that the parameters of the test flash were already chosen to favour the blue mechanism. The addition of long-wavelength fields brings a further gain in sensitivity. On the right-hand side of figures 13 and 14 we have plotted on the same absolute abscissa the several threshold values obtained for a given value of M_1 , thus collapsing the left-hand data, which are plotted separately for each value of M_2 . The solid line forming the lower envelope of these points connects the minimum thresholds for different values of M_1 . As far as data points on this 'limiting envelope' correspond to combinations of M_1 and M_2 that yielded a nearly achromatic field, the solid line constitutes a threshold: intensity curve for conditions of chromatic cancellation and thus, in terms of our model, may represent the adaptive behaviour of the first site alone; but to avoid begging theoretical questions we emphasize that we have connected the empirical minima.

Our data were not obtained for $\lambda = \mu$. To estimate minimum Weber fractions from figures 13 and 14 we therefore need to know the ratio of sensitivities at 423 and 473 nm for the blue mechanism. The logarithm (base 10) of this ratio is 0.2 at the fovea and 0.1 at an eccentricity of 8° (Stiles 1978, pp. 18 and 207). Taking these values as possible limits for our own case of 3.25° eccentricity, we derive minimum Weber fractions of 3–4 % for PGP and 5–6 % for GM, values less than that classically obtained but still larger than those for π_4 and π_5 . Since the experiments were not started with the purpose of obtaining minimum Weber fractions, our estimates are provisional. Experiment 6 shows that still smaller Weber fractions are to be obtained under transitional conditions.

For both observers the limiting envelope deviates upwards at high values of M_1 . Does this mean that some saturation of the blue mechanism can occur even when the opponent site is unpolarized? This may be so, but another possibility is that after 4 min there is no value of M_2 that will yield from the (bleached) long-wavelength receptors a signal at the second site that is large enough to cancel the short-wavelength signal produced by these values of M_1 .

Status of π mechanisms. Use of auxiliary fields

The derivation by Stiles of the π mechanisms rests on the assumption that the sensitivity of a given mechanism is independent of that of other mechanisms. The present results show that this assumption of adaptive independence *can* be false. May analogous effects have contaminated the original derivation of the π mechanisms?

Cumulating evidence suggests that detection via chromatically opponent channels is favoured when the stimulus contains energy at low spatial and temporal

frequencies (see, for example: Regan & Tyler 1971; King-Smith & Carden 1976; Sternheim *et al.* 1978). Thus, from a retrospective vantage point, it looks as if Stiles settled on the wrong stimulus parameters for isolating the cones: his standard target was large (1°) and long (200 ms). Yet Π_4 and Π_5 are close to linear transformations of colour-matching functions (Estévez & Cavonius 1977; Pugh & Sigel 1978) and, when appropriate corrections are made, resemble the microspectrophotometrically measured sensitivities of the middle- and long-wavelength primate cones (Bowmaker *et al.* 1978, 1980; Bowmaker & Dartnall 1980). The present results, and the model to which they point, suggest why Π_4 and Π_5 may be close to the cone sensitivities: in the two-colour procedure the monochromatic field will typically polarize chromatic channels, and thus desensitize them. Detection will then depend on non-opponent pathways that apparently do not vary greatly in their sensitivity as μ is varied in a field-sensitivity experiment. These latter pathways might be of the 'Young-Helmholtz' type, receiving input from a single class of cone, or might be a.c.-coupled to both P535 and P565 cones, transmitting transients that arise in either but not being influenced by the steady signal from the class of cones that is being suppressed in a typical field-sensitivity experiment.

Presenting flashes of varying λ on a *white* field, Stiles & Crawford (1933) themselves obtained multiply peaked luminosity functions, often with a clear peak in the region 600–620 nm, a finding replicated by Grether (1939), by Sperling *et al.* (1968) and by King-Smith & Carden (1976) and now known to depend on the luminance of the white field. Stiles did not return to the case of a white field, but the long-wavelength peak is often too marked to be plausibly reconstructed from the envelope or the weighted sum of the mechanisms π_4 and π_5 , derived from increment thresholds on coloured fields. This discrepancy can now be understood if we suppose that the white field brings all opponent channels close to the centres of their response ranges and that one of these channels is more sensitive to targets in the range 600–620 nm than to those of slightly shorter wavelengths. When monochromatic fields are used (as in the determination of the π mechanisms), contamination by opponent processes may be rare, except where the field is least saturated; and here we may have the explanation for the notorious flattening of Π_5 in the region 570 nm, since the latter is the least saturated region of the spectrum (Wright 1946, ch. 13). It is telling that Sternheim *et al.* (1978), using as their target a 633 nm grating, found a field-sensitivity function with a flattened top when the spatial frequency of the target was 2 cycle/deg; with targets of 12 or 20 cycle/deg the function was more sharply peaked.

An interesting complication is introduced by the use of auxiliary fields. In the simpler, original form of Stiles's two-colour method the single background field (of wavelength μ) serves two functions: (a) to suppress the mechanisms not currently under investigation, and (b) to provide a measure of the spectral sensitivity of the mechanism thus isolated, a measure that is independent of the 'test sensitivity' obtained by manipulating λ . This 'field sensitivity' method is well suited to examining spectral sensitivity at wavelengths removed from the peak sensitivity

of the isolated mechanism, when the other mechanisms will be more sensitive to the field; but the isolation becomes inadequate when μ approaches the wavelength of peak sensitivity. De Vries (1946*b*) and Stiles (1953) therefore introduced the *auxiliary field method*, in which the two original functions of the adapting field are dissociated. An auxiliary field of fixed wavelength and intensity remains present throughout the measurements and is chosen to have its greatest adaptive effect on the mechanisms not under examination. 'Main' fields of varying μ are added to the auxiliary field and it is assumed that, when the threshold is raised to a criterion level, the isolated mechanism is absorbing quanta from the total background at the same fixed rate whatever the value of μ and that the auxiliary field simply accounts for a small fixed fraction of the total effective absorption.

The present results show that the auxiliary field is not the straight-forward tool originally supposed: in addition to producing a fixed rate of absorptions in the receptors responsible for detection of the test flash, the auxiliary field will modulate sensitivity in a way that will vary with the wavelength and intensity of the main field. In the terms of our model, it will increase or decrease the polarization of the opponent site, according to the values of μ_1 and M_1 ; it may thus alter the absolute field sensitivity and distort the relative spectral sensitivity function.

To what extent are Stiles's field sensitivities (Stiles 1978, tbl. B) likely to be in error for ' II_1 ' and ' II_3 ', the two cases where auxiliary fields were systematically used? Stiles's own account of his procedures (Stiles 1978, pp. 19–20) suggests that serious error is unlikely in the case of II_1 . To examine the latter, he used a yellowish-green auxiliary field (effective wavelength 555 nm) 'of sufficient intensity to raise the threshold on to the lower part of the π_1 branch', but the auxiliary field was not present for all values of μ . In one series of measurements, μ varied from 404 to 533 nm and the auxiliary field was used; in a second series, the auxiliary field was absent and the absolute field sensitivity was obtained for values of μ from 494 to 702 nm. The relative values of II_1 obtained at short wavelengths were converted to absolute values by multiplying them by a single factor chosen to give best agreement in the 40 nm range of μ where both relative and absolute sensitivities were known. Thus any error would be confined to short wavelengths and would have to consist of a distortion of the relative spectral sensitivity. Yet the excellent agreement at short wavelengths (410–500 nm) between test and field sensitivities for the π_1 branch (Stiles 1953) suggests that the relative field-sensitivity function is not in fact distorted.

We have suggested above that π_1 and π_3 do not represent distinct mechanisms; and in the model developed by Pugh & Mollon (1979) the field sensitivities of these branches at short wavelengths depend on the sensitivity of the same short-wavelength receptors. Yet the absolute field sensitivity of π_3 is approximately 0.5 decadic unit less than that of π_1 at 440 nm. At least part of this discrepancy may be due to the use of an auxiliary field, since for π_3 an auxiliary field was present for all but the two highest values of μ and there was no band of overlap between absolute and relative determinations (Stiles 1978, p. 20). The orange auxiliary field

was 'just sufficient to bring the threshold on to the initial flat range of the π_3 branch of the t.v.i. [threshold:intensity] curve'. Although Stiles's stimuli differ from ours in several ways, the results of figures 3 and 4 (above) are quantitatively compatible with the possibility that Stiles was working in the region of stimulus space where combinative euchromatopsia occurs: in the terms of our figures, M_1 would have a value of *ca.* $10^{9.4}$ quanta $s^{-1} \text{ deg}^{-2}$ (reciprocal of field sensitivity of π_3 at 473 nm, from Stiles (1978); no correction made for differences in macular pigmentation) and M_2 would be *ca.* $10^{10.4}$ quanta $s^{-1} \text{ deg}^{-2}$ (intensity of a 575 nm field needed to raise the threshold to the level of the estimated 'absolute threshold' of π_3 ; calculated from our unpublished measurements for these conditions and observers). These values of M_1 and M_2 place PGP clearly in a region of facilitation, but GM less clearly so.

However, to ask what is the true field sensitivity of π_3 is to ask a doubly meaningless question, since π_3 is probably not a distinct mechanism and since theoretical and practical considerations will determine whether the experimenter wants the sensitivity on a monochromatic field or that under conditions of chromatic cancellation. We wish to emphasize primarily that the value obtained will depend on the auxiliary field.

We are led to the following conclusions on the status of the π mechanisms. Although hindsight suggests that Stiles's spatial and temporal parameters were not ideal and that auxiliary fields may nullify one of the unappreciated strengths of the two-colour method (polarization of opponent channels), nevertheless Stiles's own checks and the ancillary evidence suggest that Π_1 , Π_4 and Π_5 may be close to the sensitivities of the cones and only locally contaminated by opponent processes. There would be value in a systematic redetermination of the π mechanisms with targets of high spatial and temporal frequencies and perhaps with auxiliary fields chosen so as to increase rather than to decrease the saturation of the background, although the adoption of these changes might limit the ability of Stiles's method to separate mechanisms.

Previous studies of field additivity

The first use of the field-additivity experiment to test the assumption of adaptive independence was probably in the neglected study of De Vries (1946*a*, 1949), who presented 480 nm targets on mixtures of blue (455 nm) and green (550 nm) fields and asked his observers to adjust the intensity of one field until the target was at threshold, the other field and the target remaining fixed in intensity. For lower values of the green field (his conditions *e-i*), where detection appeared to be by the green mechanism, total calculated excitation of the green receptors by the field remained constant as the components of the composite field were varied; for more intense green fields (his conditions *b-d*) the amount of blue light required became constant, presumably because detection was then by the blue mechanism and the green field could be varied over a large range without significantly changing the total absorption in the P420 receptors. Thus, within the conditions tested,

additivity appeared to hold for both green and blue mechanisms. More extensive measurements and systematic discussion were published by Boynton *et al.* (1966). The latter authors found that the pairs of fields that they used were often supra-additive in their adaptive effects and Boynton & Das (1966) were led to advance the general rule that the most efficient adapting stimulus is one that is dispersed in space, time and wavelength. The present results demonstrate that the Boynton–Das rule can fail and in retrospect it is interesting that one of the two observers (RMB) in Boynton *et al.* (1966, fig. 7*b*) showed sub-additivity when 600 nm targets were presented on intermediate combinations of 527 and 625 nm fields, fields that would probably appear a desaturated yellow and would place opponent channels near the centres of their response ranges. Conversely, a particularly marked supra-additivity was found for mixtures of 667 and 456 nm fields (Boynton & Das 1966), which would appear strongly coloured in all combinations.

The field additivity experiments of Pugh and of Sternheim *et al.* have been discussed above.

Chromatic discrimination

We should like briefly to relate the present results, and those of Sternheim *et al.* (1979), to earlier analyses of colour discrimination, since combinative euclimatopsia suggests that colour discrimination will not be well described by line elements that correspond to independent processes with fixed Weber fractions.

In his classical analysis of the MacAdam ellipses, Le Grand (1949) re-expressed MacAdam's x , y data in terms of estimated cone responses, R , G and B . Two different estimates of the latter were calculated by means of two sets of fundamental sensitivities, both derived from dichromatic matching data, one by König's hypothesis and one by Fick's. When the calculated thresholds (ΔR) of the red system, for different ellipses, were plotted against the ratios of the calculated red and green signals (R_0/G_0) the function showed a minimum when R_0 and G_0 were approximately equal. This result, which was obtained whichever set of fundamentals was used, is consistent with assumption 6 (above). The long axes of the ellipses proved to correspond to modulation of the blue cones alone and Le Grand concluded that the latter act independently in detection. This latter conclusion does not contradict our own results: MacAdam's data were gathered at constant luminance and thus V_Y (in our terms) is held constant while absorption in the short-wavelength receptors varies by more than 10^2 ; conditions such as ours, where absorption in the short-wavelength receptors is approximately constant while V_Y varies and where detection depends only on the putative B–Y channel, will seldom occur in conventional experiments on colour discrimination.

In the line-element model of Friele (1961) the sensitivity of the red–green differencing mechanism is maximal near the middle of its response range:

$$(\Delta c_{r-g})^2 = \frac{1}{\beta^2} \left[\frac{\Delta R}{R} - \frac{\Delta G}{G} \right]^2,$$

$$\text{where } \beta = 0.015 \frac{R^2}{R^2 + G^2} \text{ for } R > G,$$

$$\text{and } \beta = 0.015 \frac{G^2}{R^2 + G^2} \text{ for } G > R.$$

The effect of β is explicitly that incorporated in our assumption 6. In Friele's second differencing mechanism a blue signal is subtracted from a yellow signal compounded from r and g signals, but the sensitivity of this mechanism is made to depend on the ratio G/B , independently of R (see Stiles (1971) for a review).

In a recent analysis of wavelength discrimination, Boynton (1979) uses the Smith-Pokorny fundamentals to calculate the change in the red cone response per unit wavelength but finds it necessary (p. 268) to introduce a factor J to shift the estimated minimum threshold from 600 nm to coincide with the empirical minimum at 580 nm. Boynton himself suggests that J might be interpreted in terms of 'the extra brightness produced by R and G cones via the r-g channels', but, without reference to brightness, J could be interpreted in terms of assumption 6 and a model of the type shown in figure 6; and we note that elsewhere (p. 265) Boynton explicitly suggests that 'a threshold change in r-g differences depends upon the initial value of r-g'.

Combinative euchromatopsia places in a new light the observation by Stiles (1955) that the precision of colour matches to monochromatic stimuli in the range 420–460 nm was unacceptably poor and could be improved by desaturating the stimuli, that is, by adding his green primary (526 nm) to both sides of the colorimetric field. Stiles's effect may prove to be essentially the same as that examined here.

Other 'reversals of Weber's law'

The phenomenon reported here is unusual in the context of Stiles's procedure, but is not unique in sensory science. There does exist a class of scattered phenomena that constitute 'reversals of Weber's law'. Subliminal and supraliminal 'pedestals' have been reported to improve the detection of both simple increments (see, for example: Baumgardt & Smith 1966; Leshowitz *et al.* 1968) and gratings (Nachmias & Sansbury 1974; Stromeyer & Klein 1974). Bender & Ruddock (1974) have described an unusual subject whose incremental threshold for 1° red targets falls as the intensity of a red field increases. Yoon (1970) reported an odd ganglion cell in the cat retina that became absolutely more sensitive to increments as a steady field was intensified. An auditory example is provided by one instance of 'binaural unmasking': a signal and masking noise are first delivered to one ear only and the monaural threshold is measured; if then the noise is additionally presented to the other ear, the threshold falls (for a review, see Moore (1977), pp. 190–202). However, it is crucial that the noise should be correlated at the two ears and the phenomenon probably depends on specialized mechanisms of binaural localization. A second psychoacoustic example is provided by the 'lateral suppression' that occurs in forward masking (Houtgast 1974): if say, a 1 kHz tone is masked by a

preceding 1 kHz masker, the signal can be rendered audible again if a band of noise or a tone of adjacent frequency is added to the masking tone. There is a strong resemblance between our figures 3 and 4 and the middle panel of Houtgast's figure 7.1; but we note that this 'lateral suppression' does not occur when masker and signal are simultaneous.

Do these operationally similar phenomena constitute a single class open to one general explanation? We think not. An explanation applicable to several cases is that the pedestal or secondary mask increases the observer's certainty as to the spatio-temporal position of the target, but this explanation is hardly appropriate here. The present phenomenon suggests a special property of opponent sensory systems and its value lies in allowing the use of Stiles's field-sensitivity method in the study of chromatically opponent processes.

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