

## SOME DYNAMIC FEATURES OF COLOUR VISION

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### INTRODUCTION

THERE is a body of evidence that temporal factors are important in colour vision (NELSON, 1971). It has long been known that a stimulus which, when viewed steadily, appears to be white can nevertheless produce sensations of colour when stimulation changes with time (e.g. in the case of Benham's top). PIÉRON has measured the rate at which chromatic saturation rises after switching on a monochromatic stimulus, and has found the rate of rise to be different for red, green and blue stimuli (PIÉRON, 1932, 1952). IKEDA and BOYNTON (1962) have shown that photopic spectral sensitivity, as measured by transient flash stimulation, depends on the duration of the flash; in the frequency domain KELLY (1961, 1962) has suggested that chromatic adaptation changes the shape of De Lange curves in ways which can be explained by assigning different time constants to different colour channels. DE LANGE (1957) reported that the residual brightness flicker in a heterochromatic flicker situation can be eliminated by adjusting the relative phases of the two chromatic components of the stimulus light; WALRAVEN and LEEBEEK (1964) later interpreted this finding as a reflection of latency differences between PITT'S (1945) fundamental colour channels. VAN DER HORST and MUIS (1969) have reported that the subjective hue of a stimulus of constant wavelength shows marked changes as a function of stimulus flicker frequency. More recently, GREEN (1969) has taken BRINDLEY *et al.*'s (1965) finding that the blue cone mechanism has a lower flicker fusion frequency than the red or green mechanisms and has shown that the modulation sensitivity of the blue mechanism is depressed over the entire frequency range from 1 Hz to the fusion point. Furthermore Green has shown that in the frequency range of 1 Hz to roughly 5 Hz there is a difference in shape between, on the one hand the De Lange curve for the green cone mechanism, and on the other hand that for the red and blue cone mechanisms.

The present study differs from the investigations mentioned above in that it is not concerned with the perception of *luminance changes* but with the temporal characteristics of the perception of *hue changes*, and specifically with the dynamics of wavelength discrimination. Our purpose in studying the temporal characteristics of the perception of wavelength-modulated and luminance-modulated light is to obtain clues to the different ways in which the human visual system handles information of wavelength changes and information of luminance changes, and particularly to obtain some insight into the neural mechanism which underlies the exquisite sensitivity of the visual system to differences of stimulus wavelength.

This paper is divided into three sections. Section 1 deals mainly with the effects of the surround field and modulation waveform on threshold vs. modulation frequency curves in

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the very low frequency region between 0.05 Hz and roughly 1 Hz. Section 2 compares De Lange curves with our analogous curves in which wavelength-modulation replaces luminance-modulation; these comparisons are made over a range of mean luminances in several spectral locations. Section 3 compares the classical bipartite-field wavelength discrimination curve with our dynamic wavelength discrimination curves measured at different frequencies.

## METHODS

The wavelength and luminance of a stimulus light were modulated in the manner described previously (REGAN and TYLER, 1971a).

A 2 deg bipartite field was required in the experiments of Section 3. This field was produced by means of a front-aluminized mirror from which a small semicircular area of aluminium had been removed. The mirror was arranged so that light from the wavelength modulator passed through the transparent semicircle; the reflecting part of the mirror was illuminated by a second beam which had been made monochromatic by passing through two interference filters, one of half-width 100 nm and the other of half-width 200 nm. In the experiments of Section 1 this same rough double monochromator was used to provide a steady equi-luminant surround field. Threshold was measured by the method of adjustments. All points shown in the figures are the mean of two settings, one in an ascending sequence and one in a descending sequence. All experiments reported and all controls were carried out by a single subject (40 experiments in all). All experiments and controls on which our conclusions are based were confirmed on one further subject who was judged to have normal colour vision on the basis both of her bipartite wavelength discrimination curves and the Ishihara test.

## SECTION 1

### THRESHOLD VERSUS FREQUENCY CURVES IN THE VERY LOW FREQUENCY REGION: THE EFFECT OF THE SURROUND FIELD

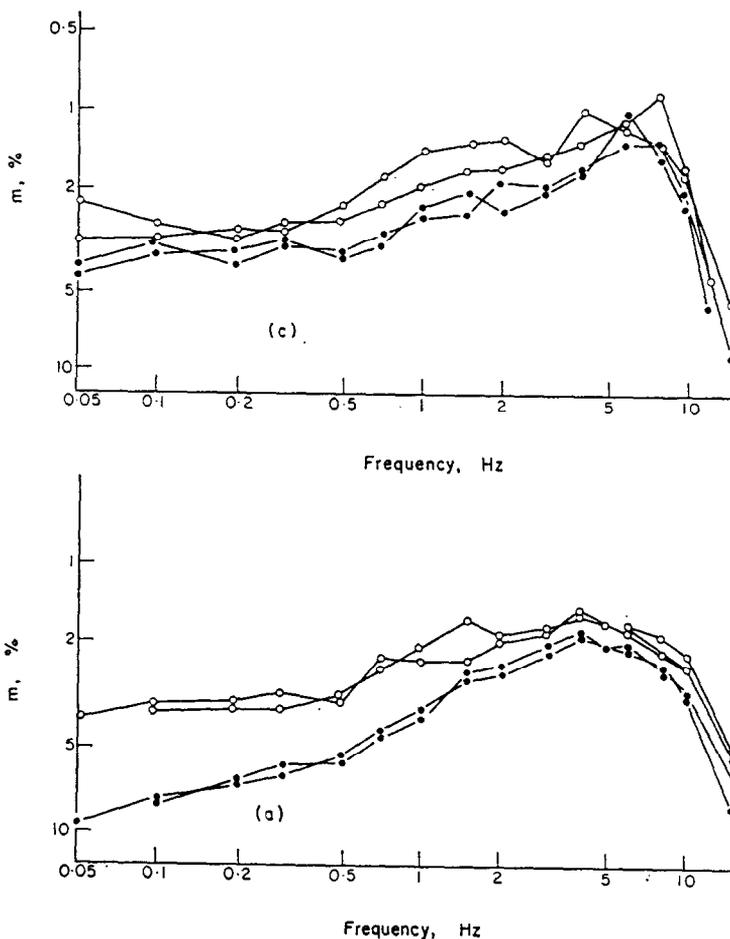
#### Introduction

In a previous paper, preliminary curves were presented of subjective sensitivity to flicker vs. stimulus modulation frequency for both luminance-modulated light and wavelength-modulated light (REGAN and TYLER, 1971a). The shapes of the curves were shown to be different throughout the whole of the frequency region studied, that is for frequencies between 1.0 Hz and 40 Hz. In the present section we report the ways in which subjective sensitivity to both luminance-modulation and wavelength-modulation vary with repetition frequency, modulating waveform and surround field, in the frequency range from 0.05 to 20 Hz.

#### Results

Figure 1 (a, b; lower curves) shows that for a 2 deg stimulus field with no surround, subjective sensitivity both to sinusoidal luminance-modulation and sinusoidal wavelength-modulation of the stimulus reached a maximum and then progressively fell as stimulus frequency was reduced. There was a broad maximum in subjective sensitivity for wavelength-modulated light centered on roughly 1 Hz (Fig. 1b). The subjective sensitivity to luminance-modulated light fell progressively as frequency was reduced below roughly 5 Hz. In contrast with the no-surround data, when a surround field of the same luminance and chromaticity as the test field was used the characteristic was approximately flat below roughly 2 Hz for light whose wavelength was modulated sinusoidally (Fig. 1d), and approximately flat below roughly 1 Hz for light whose luminance was modulated sinusoidally (Fig. 1c).

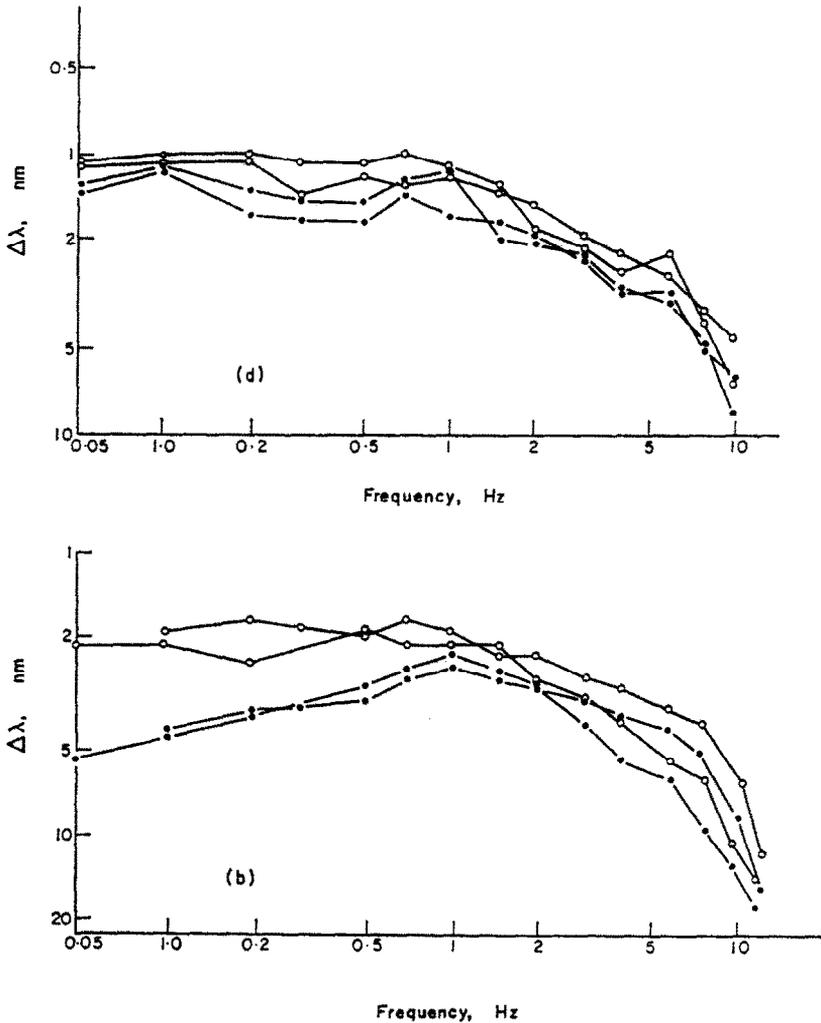
When squarewave modulation was used instead of sinusoidal modulation in the no-surround condition quite different results were obtained in the low frequency region, both for luminance-modulated light and for wavelength-modulated light. For squarewave



FIGS. 1c and 1a

modulation, the threshold vs. frequency curve was flat below 0.5 to 1 Hz for both types of stimuli (Fig. 1a, b, upper curves). At these low frequencies it was as if the steady-state conditions of higher frequencies were replaced by transient conditions in which the subject's threshold was not influenced by stimulus repetition frequency. Figure 1a also confirms De Lange's finding that for stimulus frequencies in excess of roughly 2 Hz, threshold seems to be determined by the amplitude of the (sinusoidal) fundamental component of the square-wave modulation. This conclusion follows from the observation that at threshold the peak-to-peak amplitude of the sinewave modulation was not significantly different from 1.27 times larger than the peak-to-peak amplitude of the squarewave modulation.

De Lange's curves were flat from a frequency of roughly 2 Hz to the lowest frequency he used (1 Hz). He suggested that when a dark surround was used the curve would progressively fall as the stimulus frequency was reduced from roughly 1 Hz. His prediction was based on the idea that as stimulus frequency fell below 1 Hz the state of adaptation of the eye would no longer be constant but would be able to follow the sinusoidal modulation to



FIGS. 1d and 1b

FIG. 1. Threshold vs. modulation frequency curves in the very low frequency region. Two degree field, 110 trolands, centre wavelength 527 nm. Each condition shows data obtained on two separate occasions. Both coordinates on logarithmic scales. (A) Thresholds sine (○) and squarewave (●) luminance modulation with a dark surround. (B) Threshold sine (○) and squarewave (●) wavelength modulation with a dark surround. (C) Threshold sine (○) and squarewave (●) luminance modulation with an equiluminant chromaticity-matched, steady 10 deg surround. (D) Threshold sine (○) and squarewave (●) wavelength modulation with an equiluminant, chromaticity-matched, steady 10 deg surround.

an increasing extent (the "slip-in" effect). This would have the effect of introducing negative feedback into the system which increased progressively as stimulus frequency was progressively reduced.

The curves shown in Fig. 1 show that De Lange's prediction is indeed fulfilled in that the dark-surround De Lange curves do fall progressively as stimulus frequency is reduced from roughly 1 Hz. If De Lange's suggestion is true that this progressive elevation of threshold as

stimulus frequency is reduced is due to the way in which the state of adaptation of the eye can more closely follow the sinusoidal modulation of the stimulus at low modulation frequencies, then the use of sinusoidal modulation with no surround field might reveal any differences between the temporal characteristics of adaptation of wavelength changes and to luminance changes. Our results suggest that at low frequencies (below 0.5 Hz or so) the slopes of the characteristics for wavelength modulation and luminance modulation are similar (Fig. 1a, b).

### *Discussion*

The present section reports the extension of threshold vs. frequency curves to frequencies as low as 0.05 Hz for both luminance-modulation and wavelength-modulation. When there is no surround field the threshold for sinusoidally modulated stimuli progressively rises as frequency falls below roughly 1.0 Hz in accord with DE LANGE'S (1957) prediction. This occurs for wavelength-modulated as well as luminance-modulated stimuli. Additionally, at frequencies below roughly 1 Hz the no-surround De Lange curves for sinusoidal modulation differ from the shapes of the corresponding curves for no-surround squarewave modulation. This difference could also be accounted for if it is assumed that there is a small overshoot in the visual system when squarewave modulation is used. An overshoot of this type would account for the slightly greater sensitivity to squarewave than to sinewave modulation. An alternative explanation is that for squarewave modulation of wavelength at frequencies near 1 Hz, some residual luminance modulation might also be expected from phase shifts between different colour channels (DE LANGE, 1957).

## SECTION 2

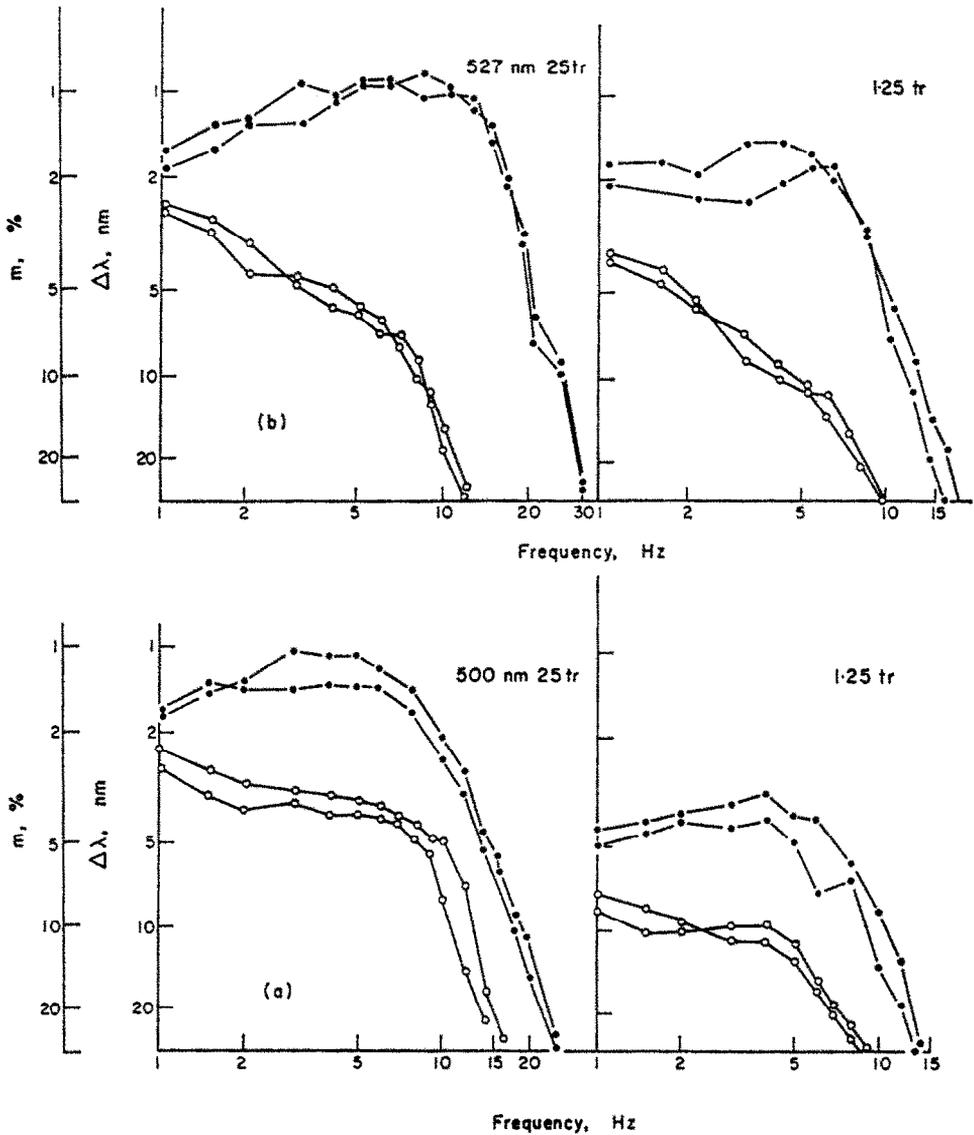
### THRESHOLD vs. STIMULUS FREQUENCY CURVES FOR LUMINANCE-MODULATED LIGHT (DE LANGE CURVES) AND FOR WAVELENGTH-MODULATED LIGHT

#### *Introduction*

The method, developed by DE LANGE (1957), of using the modulation *depth* of stimulus luminance as a parameter enables threshold conditions to be measured over a wide range of stimulus modulation frequencies. If it can be assumed that the subject's criterion for flicker detection is not a function of frequency, then a plot of threshold modulation depth vs. frequency can be regarded as a description of the way in which attenuation depends on stimulus frequency for the part of the visual pathway which precedes the flicker detection stage. Such De Lange curves related to the detection of subjective flicker due to modulation of stimulus luminance. We have compared classical De Lange curves with our analogous curves which relate to wavelength-modulation of the stimulus. One of our aims in comparing the dynamic characteristics of detection for luminance-modulated light and wavelength-modulated light was to find whether such measurements in the frequency domain might provide both (a) fresh discriminations between the neural processing of luminance changes and wavelength changes and (b) also give new clues to the nature and neuroanatomical locus of this neural processing.

#### *Results*

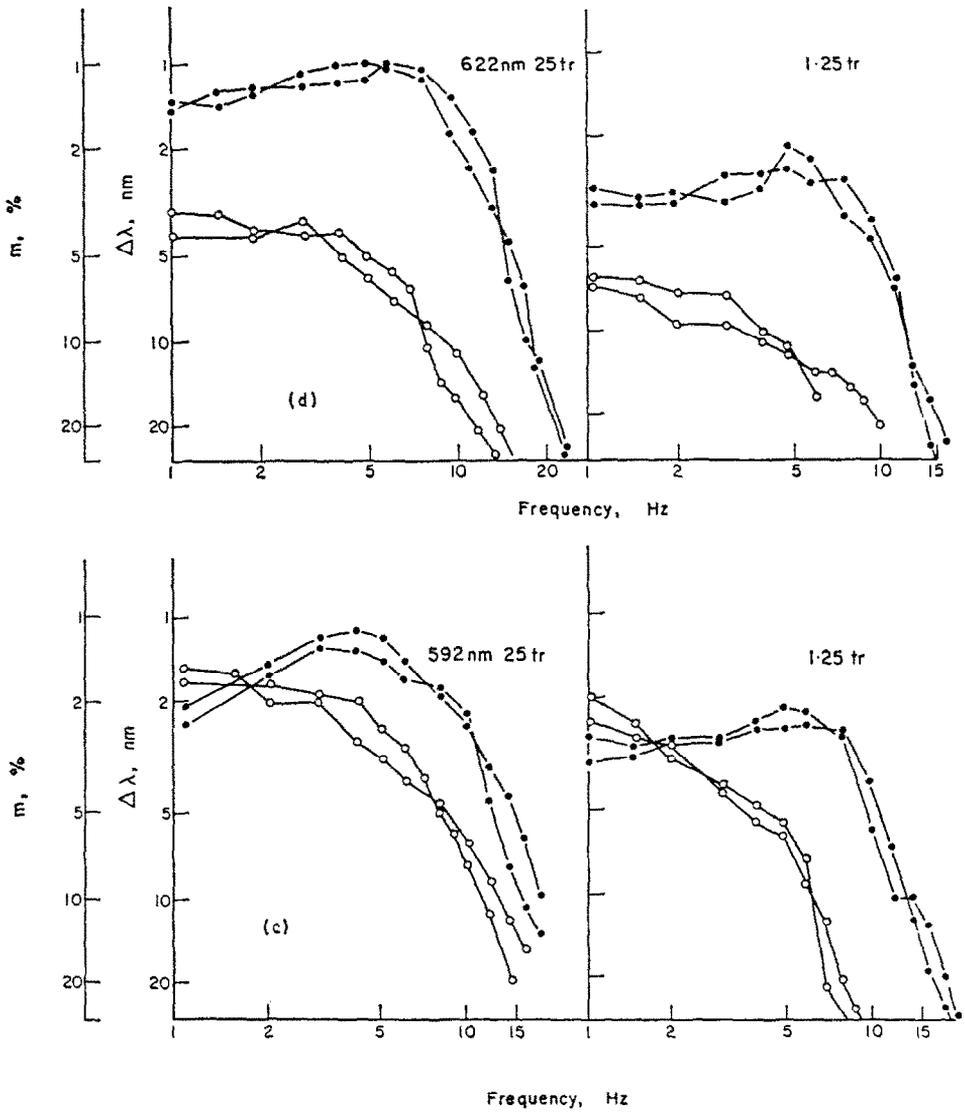
One subject (C.W.T.) measured threshold curves for luminance-modulated light and wavelength-modulated light for the whole range of centre wavelengths and retinal illumina-



FIGS. 2b and 2a

tions investigated. Measurements were made at centre wavelengths 500, 527, 592 and 622 nm, each at two luminances of 1.25 and 25 trolands. Each measurement was made both with increasing frequency and decreasing frequency and the results averaged. Two complete curves were obtained on different occasions. One further subject was used to confirm the main findings described below.

Figure 2 compares threshold vs. modulation frequency curves at two levels of retinal illuminance for luminance-modulated and wavelength-modulated light. Note that the relative positioning of luminance and wavelength modulation amplitude scales is necessarily



FIGS. 2d and 2c

FIG. 2. Threshold vs. modulation frequency curves for luminance and wavelength modulation, at two levels of luminance (25 and 1.25 trolands) and four centre-wavelengths. Two degree field with a dark surround. Luminance modulation (●) and wavelength modulation (○) are plotted on arbitrary-related scales of threshold luminance modulation depth (m%) threshold wavelength modulation amplitude (Δλ). Centre wavelength were 500 nm (2a), 527 nm (2b), 592 nm (2c) and 622 nm (2d). Each condition shows data obtained on two separate occasions.

arbitrary. The curves of Fig. 2 refer to wavelengths centred on 550 nm (Fig. 2a), 527 nm (Fig. 2b), 592 nm (Fig. 2c) and 622 nm (Fig. 2d). A 2 deg field with no surround was used and all stimuli were sinusoidally modulated. Luminances were matched by flicker photometry at 25 td.

Figures 2, a-d illustrates the finding that the shapes of the threshold vs. frequency curves for luminance-modulation (De Lange curves) differ in shape from the threshold vs. frequency curves for wavelength-modulation, and furthermore that the curves differ over the full range of retinal illuminations investigated. The most general difference is that the luminance-modulation curves show either a broad peak or a flat region between roughly 3 Hz and 12 Hz, whereas in contrast the wavelength-modulation curves fall continuously as stimulus frequency is progressively increased from 1 Hz.<sup>2</sup>

At constant retinal illuminance the shape of the De Lange (*luminance-modulation*) curves show little dependance on stimulus wavelength in the low frequency region (Fig. 2). This finding is more directly tested in the control experiment illustrated in Fig. 3a. Here the modulation depth of *luminance* at threshold is plotted vs. centre wavelength for a series of modulation frequencies between 0.5 Hz and 10 Hz. At no frequency has stimulus wavelength a significant systematic effect on threshold for luminance-modulation (Fig. 3a), contrary to DE LANGE's (1957) report (see above).

Our salient finding is that, in contrast to the luminance-modulation curves, the threshold vs. frequency curves for *wavelength-modulation* show changes in shape which depend

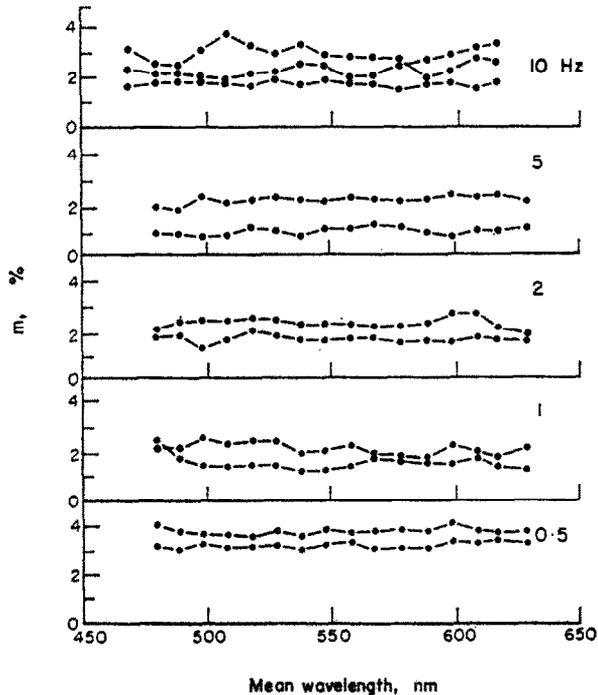


FIG. 3a

<sup>2</sup> In different experimental situations, and using different methods, VAN NES *et al.* (1967), VAN DER HORST and BOUMAN (1969) and VAN DER HORST (1969) noted this difference between De Lange curves and threshold differences of chromaticity.

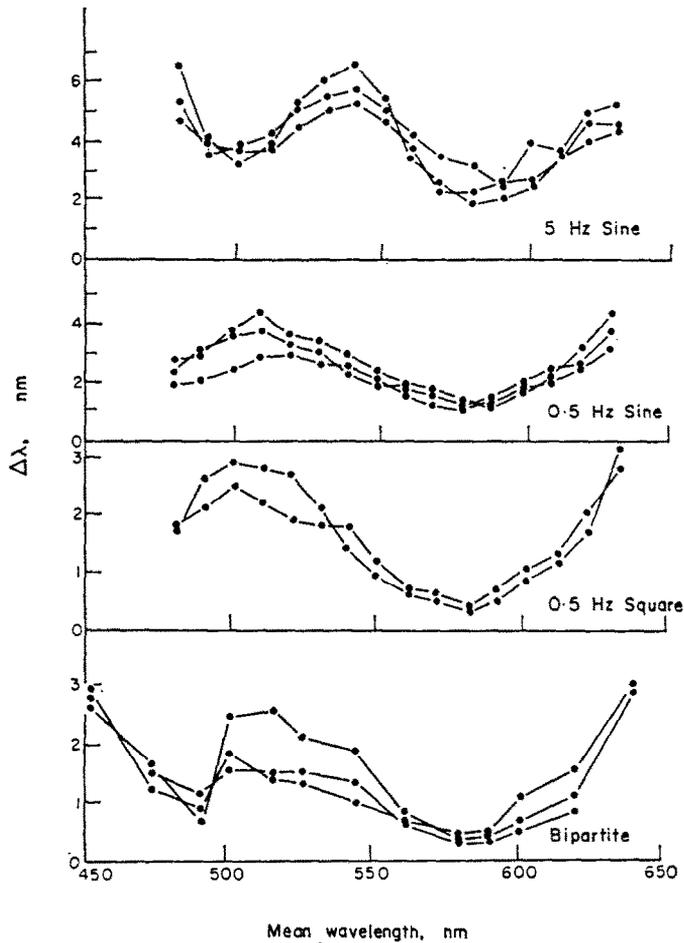


FIG. 3b

FIG. 3. Threshold modulation amplitude as a function of wavelength of the stimulus field (linear scales). (A) Sinusoidal luminance modulation threshold for five modulation frequencies (0.5, 1, 2, 5 and 10 Hz). Two degree field at 25 trolands with no surround. Each condition shows data obtained on two separate occasions. (B) Sinusoidal wavelength modulation threshold for two modulation frequencies of 0.5 and 5 Hz on three separate occasions (upper two graphs), and average squarewave modulation threshold at 0.5 Hz (third curve from top). Lowest graph shows wavelength discrimination curve measured with a bipartite field on three separate occasions. Note change of scale.

systematically on centre wavelength (Fig. 2; lower curves. See also Fig. 3b). Since the shapes of the luminance-modulation curves are comparatively unaffected by centre wavelength, the *differences* between the luminance-modulation and wavelength-modulation curves are a function of centre wavelength (e.g. compare Fig. 2b and d). A further difference between the luminance-modulation curves and the wavelength-modulation curves is that the shapes of the luminance-modulation curves are more affected by the mean luminance.

In the frequency region from roughly 5 to 1 Hz the luminance-modulation curves generally fall as frequency is reduced, whereas the wavelength-modulation curve continues to rise as frequency is reduced. The shapes of the two curves for still lower frequencies below

1 Hz are shown in Fig. 1, a and b for a centre wavelength of 527 nm. For sinusoidally modulated stimuli with no surround the luminance modulation curve falls progressively as frequency is reduced from roughly 5 Hz right down to 0.05 Hz. In contrast the no-surround curve for sinusoidal wavelength-modulation continues to rise as the stimulus frequency is reduced to roughly 1 Hz and thereafter progressively falls right down to a frequency of 0.05 Hz. (Note: this difference in low-frequency behaviour cannot be observed when a surround field is used, see above and Fig. 1.)

### *Discussion*

DE LANGE (1957), almost as an aside, demonstrated the feasibility of measuring subjective thresholds which were determined by modulation of stimulus chromaticity. His method, however, was similar to that used recently by VANDER HORST (1969), and suffers from limitations described previously (REGAN and TYLER, 1971a). De Lange found a small peak in the chromaticity-modulation curve which coincided in frequency with the major peak he had discovered in the luminance-modulation (DE LANGE) curve (DE LANGE, 1957, p. 88). We have been unable to find such a subpeak in wavelength-modulation curves for any of the centre wavelengths or levels of retinal illuminance we have used. Furthermore, the rather ill-defined change in slope which, for some centre wavelengths, can be observed in our wavelength-modulation curves does not seem to maintain a constant relation with the location of the peak in the luminance-modulation curve when either centre wavelength or retinal illuminance is changed (e.g. Fig. 2a, b). We conclude, therefore, that our evidence does not support De Lange's suggestion that the wavelength-modulation curves are related to the De Lange curves by a small additional number of simple stages of attenuation.

If a series of curves such as those shown in Fig. 2 were recorded throughout the spectrum, and stacked in sequence next to each other, then the dynamic wavelength discrimination curves of Fig. 3b could be obtained by slicing the stack in a direction perpendicular to the plane of the individual graphs. For example, cutting the stack through the 5 Hz point would give the 5 Hz dynamic wavelength discrimination curve of Fig. 3b. If a similar procedure were carried out for a series of luminance-modulation curves such as those of Fig. 2, then the curves shown in Fig. 3a would result. Figure 2 shows that in the low frequency region the threshold for the detection of luminance-modulation is not significantly affected by stimulus wavelength (in contrast with the threshold for wavelength modulation as illustrated in Fig. 2). The control experiment of Fig. 3a supports this result.

The wavelength-modulation curves of Figs. 2 and 3b represent two ways of presenting the same data, and since the two figures are based on separate experiments the curves can be used to validate each other. This cross-check has proved to be satisfactory. For example in the 622 nm (25 td) curve of Fig. 2d, threshold remains and fairly constant from 1 Hz up to roughly 5 Hz, whereas in the 527 nm (25 troland) curve of Fig. 2b threshold rises rapidly as stimulus frequency increases from 1 Hz, and by 5 Hz threshold has increased considerably.

In view of the known marked dependence of colour perception on the temporal characteristics of visual stimuli, we were surprised by our findings that the effect of mean wavelength on the shapes of the curves of threshold sensitivity vs. stimulus frequency was either inappreciable (for luminance modulation, Fig. 2) or no more than moderately striking (for wavelength modulation Fig. 2). This led us to search for effects of spectral location on the perception of transient pulses of wavelength change; such effects turned out to exist and to be comparatively striking (REGAN and TYLER, 1971b).

## SECTION 3

## DYNAMIC WAVELENGTH DISCRIMINATION CURVES: COMPARISON OF DYNAMIC CURVES WITH CLASSICAL (BIPARTITE FIELD) CURVES

*Introduction*

Wavelength discrimination has classically been described in terms of bipartite field data (WRIGHT, 1947). Bipartite field curves are obtained by adjusting the wavelength difference between the left and right halves of a stimulus field until a difference in hue can just be perceived (in the absence of any perceptible difference in luminance). If any effects of eye movements on wavelength discrimination can be neglected, then the bipartite field method can be regarded as providing a wavelength discrimination curve valid for static conditions. If on the other hand eye movements cannot be neglected (in fact they probably cannot be neglected (see MCCREE, 1957, 1958; BEELER, FENDER, NOBEL and EVANS, 1964), it is difficult to assess the relative importance of different frequency regions in the bipartite discrimination task. In order to investigate this problem we have measured a version of the wavelength discrimination curve under *dynamic conditions* and investigated the effect of the repetition frequency of wavelength changes on subjective sensitivity to such changes. The aims of this study were twofold: (a) to define the effects of frequency on wavelength discrimination, and (b) to look for fresh clues to the neural mechanism underlying wavelength discrimination.

At no point do the methods used in the present article rely on CIE spectral mixture data, so that our data could in principle be used to test hypotheses of relationship between such bipartite field CIE data and dynamic, homogenous-field data. This contrasts with a recent study on subjective sensitivity to chromaticity changes in which the method implicitly assumed the validity of spectral mixture data in the dynamic situation (VAN DER HORST, 1969). One point of difference between the present experiments and the experiments which form the basis of the CIE spectral mixture curves (WRIGHT, 1947) is that in the present study a 2 deg field was used whose luminance (or wavelength) changed uniformly over the whole field, whereas in the spectral mixture experiments the hue of two steadily-presented stimuli were compared across a sharp central boundary. In the present experiments, therefore, the subject's task was to detect temporal changes (whose frequency or time course could be varied). In contrast, when the bipartite field method was used, each point on the retina necessarily received an unvarying stimulus (neglecting eye movements) and was therefore in a constant state of adaptation.

In order to find whether the difference between the stimulus conditions described above had an important effect on the observed thresholds, the wavelength discrimination curve was determined by the bipartite field method, and the results compared with dynamic wavelength discrimination curves which were measured by modulating the wavelength of a homogeneous stimulus field.

*Results*

In both the bipartite field measurements and the dynamic measurements, we reduced luminance changes to such a level that subjective threshold was determined by wavelength changes. This was achieved by the method described by WRIGHT (1947) for the bipartite field experiments, and by the method described by REGAN and TYLER (1971a) for the dynamic experiments. A control for the dynamic measurements is shown in Fig. 3a. In this control, instead of the wavelength excursion, the luminance excursion which determined

threshold was plotted for wavelengths throughout the spectrum. Figure 3a shows that in our experiments the threshold for luminance-modulation was not significantly affected by stimulus wavelength for any of the modulation frequencies tested.

Figure 3b (lowest curve) shows wavelength discrimination curves determined by the bipartite field method. The field size was of 2 deg subtense, retinal illuminance was 25 trolands and there was no surround. The shape of the curve agrees with previous findings (WRIGHT, 1947; WRIGHT and PITT, 1934; JUDD, 1932) in showing prominent maxima of sensitivity near 490 nm and 580 nm. This result contrasts with the dynamic wavelength discrimination curves for stimulus repetition frequencies of 0.5 Hz and 5 Hz (Fig. 3b, upper graphs). These dynamic curves were constructed by plotting wavelength excursions (at threshold) vs. centre wavelengths for a series of stimulus modulation frequencies. The dynamic curves for all the repetition frequencies investigated differed in shape from the bipartite field curve. The most striking differences occurred in the blue-green. In this region the bipartite field curve showed a maximum subjective sensitivity centered on roughly 480 nm, whereas for the 5 Hz dynamic curve the corresponding point of maximum sensitivity was shifted to roughly 500 nm, and for the 0.5 Hz curve the corresponding point of maximum sensitivity was displaced to below 480 nm (measurements could not be carried out below 480 nm due to increasing non-linearity in the cancelling of luminance changes). The 5 Hz and 0.5 Hz dynamic curves differed most markedly in the 500–520 nm region, where a point of maximum sensitivity for the 5 Hz curve almost coincided with a point of minimum sensitivity for the 0.5 Hz curve. The point of minimum sensitivity located near 510 nm for both the bipartite field curve and the 0.5 Hz dynamic curve was displaced to near 540 nm for the 5 Hz dynamic curve.<sup>3</sup>The effect was progressive through 1 Hz and 2 Hz.

A dynamic curve was also measured using 0.5 Hz squarewave modulation of wavelength (Fig. 3b, centre graph). At this frequency the rate of stimulus repetition can be assumed to exert a negligible effect on threshold (Fig. 1b). The shape of this curve was also found to be appreciably different from the shape of the bipartite field curve in the blue-green region, although the locations of the points of maximum sensitivity seemed to be the same.

It was clear that for no wavelength did any of the dynamic curves show an absolute threshold lower than that for the bipartite field curve and that the general effect of an increase of frequency was to elevate the threshold (i.e. worsen wavelength discrimination).

Our finding that centre wavelength has no significant effect on the threshold for luminance-modulated light in the low frequency region conflicts with DE LANGE's (1957) report. This might be due to a difference in stimulus conditions. We used no surround while De Lange used the same white surround for all his different stimulus chromaticities.

The shape of the classical wavelength-discrimination curve obtained by the bipartite field method differed from the shapes of the dynamic curves recorded at frequencies between 0.5 Hz and 5 Hz even for 0.5 Hz squarewave modulation which might be regarded as providing the closest comparison between the bipartite and the dynamic stimulus situations (Fig. 3b) (on the grounds that separating the comparison fields by such a temporal transient has some formal analogy that the spatial transient which separates the comparison fields in the bipartite field case). One possible reason for this difference between the dynamic curves and the classical bipartite field data is that the dynamic measurements related to

<sup>3</sup> We are grateful to Professor M. A. Bouman (personal communication) for pointing out that this finding must be considered in conjunction with evidence that, for bar-patterned stimuli, the position of the blue-green sensitivity maximum depends on spatial frequency, and also with evidence that the position depends on luminance.

temporal changes of a spatially-homogenous field, so that the retina was in a constantly changing state of adaptation. In contrast the bipartite field data related to a retina which was in a relatively constant state of adaptation. A second possible reason for the difference between dynamic and bipartite-field data is that the dynamic data refer to specific stimulus repetition frequencies, whereas as a result of eye movements the bipartite field data may reflect a mixture of dynamic characteristics.

Our salient finding here is that the shape of the dynamic wavelength discrimination curve was frequency dependent. We observed three effects when we used sinewave modulation: (1) the psychophysical sensitivity to changes in stimulus wavelength was progressively degraded as the stimulus repetition frequency was raised (shown also in Figs. 1 and 2), (2) the location of the blue-green sensitivity maximum shifted from below 480 nm at 0.5 Hz to near 500 nm at 5 Hz. This shift was so marked that near 500 nm a *maximum* in sensitivity for 5 Hz stimulation almost coincided with a *minimum* in sensitivity for 0.5 Hz stimulation, (3) although the location of the yellow sensitivity maximum did not shift significantly as stimulus frequency was raised from 0.5 to 5 Hz, the dip in the curve broadened a little at the long-wavelength and short-wavelength sides.

It seems unlikely that the dynamic wavelength discrimination data of Fig. 3b is seriously contaminated by any effects of luminance changes since (a) in these experiments we used a procedure designed to ensure that threshold was determined by wavelength changes alone, and (b) in any case the control experiment of Fig. 3a showed that stimulus wavelength had no appreciable effect on the threshold for luminance modulation for any of the stimulus repetition frequencies used in the dynamic wavelength discrimination experiments.

The shapes of the wavelength discrimination curves measured by the dynamic and the bipartite-field methods are different for the situations which, it might be argued, are most closely analogous (0.5 Hz squarewave modulation). However, the locations of the points of maximum sensitivity do not differ in the two cases, so that although the sizes and shapes of the discrimination areas on the CIE chromaticity diagram might differ in the two cases, the same CIE diagram would seem to be applicable to both sets of data. On the other hand the locations of the blue-green point of maximum sensitivity depends on stimulus frequency. This suggests that either or both of the following two statements hold: (1) the CIE spectral mixture data would be frequency-dependent if measured under dynamic conditions, (2) the relation between CIE spectral mixture data and the shape of the dynamic wavelength discrimination curve is frequency-dependent. The finding that the location of the blue-green maximum depends on frequency confirms our suggestion (REGAN and TYLER, 1970a) that VAN DER HORST'S (1969) methods of investigating dynamic features of colour vision suffers from a limitation. This is that Van der Horst uses the CIE chromaticity diagram in order to translate his data into "chromaticity excursions". Since the relation between dynamic wavelength discrimination and the CIE data itself appears to depend on stimulus frequency, then Van der Horst's "chromaticity excursions" must be difficult to relate directly to the equivalent changes in cone excitation. This means that his data are correspondingly difficult to relate directly to underlying physiological mechanisms. Furthermore, since CIE trichromatic bipartite-field data are intimately involved in Van der Horst's presentation of data, it would also be difficult to use his data to test the applicability of the CIE data to the situation; for example in extrapolating theories of colour discrimination derived from CIE data (STILES, 1946, WALRAVEN and BOUMAN, 1966, etc.) to dynamic data such as that of Fig. 3b.<sup>4</sup>

The immediate objectives of this study were (a) to describe certain dynamic characteristics of the neural mechanisms which underlie the perception of wavelength changes and (b) to distinguish between these dynamic characteristics and the dynamic characteristics of the neural mechanisms which underlie the perception of luminance changes. If it were true that the neural representation of wavelength information is largely in the form of *temporal* structure, then the dynamic approach described here might prove to be of special value in

<sup>4</sup> See note added in proof.

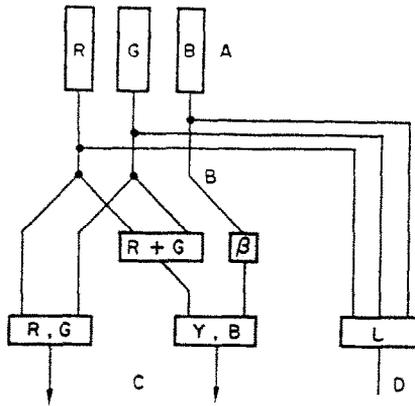


FIG. 4. Walraven's model of the luminance and chromatic channels in the visual system (from WALRAVEN and BOUMAN, 1966). R, G, B—red, green, and blue cones; L—brightness signal;  $\beta$ —weighting factor for blue signal in wavelength discrimination; R-G—site of generation of red-green chromatic signal; Y-B—site of generation of yellow-blue chromatic signal.

colour studies. The rest of this paper is a tentative attempt to relate our dynamic wavelength discrimination data to certain theories of colour vision.

Evidence for a separation between brightness and chromaticity channels has been reviewed by WALRAVEN (1962) who has proposed a model of the "zone" type (Fig. 4). In this model, both the chromatic and brightness mechanisms would share the stage AB (Fig. 4). On the basis of Walraven's model, one question which arises is to what extent the dynamic wavelength-modulation effects described in this paper are determined by the common section AB and what part is determined by the section BC which is specific to wavelength discrimination. Green has reported that the De Lange curves for luminance modulation differ for the three cone mechanisms (see Introduction). For frequencies above roughly 10 Hz. Green found that the modulation sensitivities of all three mechanisms fell off steeply and with similar slopes, whereas below 10 Hz the curves were either flat or rose with increasing frequency. We confirmed Green's general findings in a replication of Green's experiment in which we used a test-field luminance of 10 trolands, and an adapting field whose brightness was such that at 10 per cent modulation depth the test-field flicker was at threshold. These stimulus conditions were chosen so that the results of the dynamic wavelength discrimination experiments and the results of Green's procedure would be comparable. From the standpoint of the Walraven theory of colour vision (WALRAVEN, 1962; WALRAVEN and BOUMAN, 1966) Green's finding would predict that the influence of the section AB of Walraven's model (Fig. 4) on wavelength discrimination would be that: (a) dynamic wavelength discrimination would either be unaffected or improved as stimulus frequency was progressively raised from 1 to 10 Hz, and (b) for frequencies above 10 Hz discrimination would rapidly fall-off as stimulus repetition frequency was increased and fall-off in such a way that the wavelengths at which dynamic wavelength discrimination was most sensitive would not depend on stimulus frequency. The experimental data of Fig. 2 show that the sensitivity of dynamic wavelength discrimination does indeed fall off as stimulus frequency is progressively increased, but that the fall-off starts from frequencies much lower than 10 Hz, in conflict with the above prediction; by 10 Hz dynamic wavelength discrimination is already so

degraded that prediction (b) can hardly be tested. On the basis of Walraven's model and Green's data therefore, the greater part of the elevation of threshold to wavelength changes as stimulus frequency is increased (Figs. 2 and 3b) must be attributed to mechanisms specific to chromatic perception (BC in Fig. 4).

A marked feature of the dynamic wavelength discrimination curves (Fig. 3b) is the way in which one region of maximum sensitivity to wavelength changes shifts from below 480 nm at 0.5 Hz to 500 nm at 5.0 Hz. This contrasts with the way in which the location of the second region of maximum sensitivity remains in the vicinity of 580 nm as stimulus frequency is raised from 0.5 to 5.0 Hz and shows no more than a slight broadening of the maximum at both sides of the centre coupled with the general elevation of threshold common to all regions of the spectrum. Again the question arises whether the behaviour of the two sensitivity maxima reflect properties of the section AB or of the Section BC of Walraven's model. Two possibilities are evident: (1) Walraven's magnification factor ( $\beta$ ) (as in WALRAVEN and BOUMAN, 1966) for the *chromatic part* of the blue signal varies with stimulus frequency or (2) the differences between the shapes of the De Lange curves in the frequency region 1–5 Hz might indicate that the relative amplitudes of the red, green and blue signals entering the chromatic section of the Walraven model depend on stimulus frequency. Green's curves indicate that the sensitivity of the green cone mechanism rises relative to both the blue and red systems by a factor of 1.4–2.0 as stimulus frequency is raised from 1.0 to 5.0 Hz. One working prediction of how this might affect wavelength discrimination can be made by assuming that the threshold wavelength change is (for example near 490 nm) inversely proportional to

$$\left[ \left( \frac{dS_G}{d\lambda} \right) - \left( \frac{dS_B}{d\lambda} \right) \right]$$

where  $S_G$ ,  $S_B$  are the signals due to the green and blue cone mechanisms entering the chromatic section of Walraven's model. However, when trichromatic coordinate curves were derived from WALD'S (1964) cone sensitivity curves it was found that the change of sensitivity predicted by Green's data could *not* by any means explain the shift of the point of maximum sensitivity for wavelength changes from below 480 nm to 500 nm shown in Fig. 3b. On the other hand this line of argument did predict that the 580 nm sensitivity maximum should be shallower than the 490 nm maximum, that its location should not shift as stimulus frequency was raised from 1.0 to 5.0 Hz, but that it should broaden slightly at both sides of the centre at 5 Hz. All these three predictions are consistent with the data of Fig. 3b.

A second viewpoint is that of the Walraven theory of colour vision (WALRAVEN, 1962; WALRAVEN and BOUMAN, 1966). On this view a 2:1 change in modulation sensitivity of the green cone mechanism relative to the blue cone mechanism would result in either no shift of the blue-green maximum as frequency was raised from 1 to 5 Hz or a shift of roughly 5 nm (depending on whether Green's observation is attributed wholly to properties of the section AB or wholly to properties of the section BD respectively of Walraven's model (Fig. 4). The observed shift of the maximum is roughly four times greater than this prediction.

Green's data, which relates to section AD of Walraven's model, does not therefore on its own account for the shift to longer wavelengths of the 480 nm sensitivity peak as stimulus frequency is increased from 1.0 to 5.0 Hz. This suggests than an explanation should be sought in the properties of the chromatic section BC of Walraven's model. Walraven found it

necessary to postulate that blue chromatic signal is much more heavily weighted than the blue luminance signal, and introduced a multiplication factor  $\beta$  into his model to allow for this (WALRAVEN and BOUMAN, 1966). On the basis of Walraven's theory of colour vision and using Pitt's fundamental curves the shift in the point of maximum sensitivity shown in Fig. 3b can be explained if it is assumed that the weighting factor  $\beta$  (Fig. 4) rises from roughly 16 at 0.5 Hz to roughly 400 at 5.0 Hz (calculation based on data of WALRAVEN, 1962; WALRAVEN and BOUMAN, 1966).

We should emphasize that this attempt to relate our data to Green's data and to Walraven's modelling is speculative and is intended to do no more than indicate that the characteristics of dynamic wavelength discrimination as described in this paper may indeed prove to be of value in testing and sharpening hypotheses of colour vision.

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*Note added in proof*

Professor M. A. Bouman (personal communication) has pointed out since VAN DER HORST's (1969) study applies only to the yellow part of the spectrum his chromaticity formulations are probably sufficiently close to the spectrum locus to allow direct conversion into a wavelength-modulation formulation. In any case Professor Bouman states, VAN DER HORST's (1969) formulation in terms of the CIE X and Y components are closer to equivalent changes in cone excitation than a formulation in terms of wavelength modulation.

On the grounds of our finding that the spectral location of the yellow sensitivity maximum is relatively unaffected by stimulus modulation frequency, Professor Bouman's comment must carry weight for studies in the yellow region of the spectrum. It is our finding that the spectral location of the blue-green sensitivity maximum depends markedly on stimulus modulation frequency that is the basis for our general comment on the applicability of CIE data to studies of the steady-state dynamics of colour vision. On the face of it our comments might be expected to apply less strongly to the yellow region of the spectrum than to the blue-green region.

A second point is that we should explicitly point out that our criticism of VAN DER HORST's (1969) use of a CIE formulation is restricted here to studies in which stimulus chromaticity is modulated, and should not be taken to extend to studies in which stimulus purity only is modulated.

## REFERENCES

- BEELER, G. W., FENDER, D. H., NOBEL, P. S. and EVANS, C. R. (1964). Perception of pattern and colour in the stabilized retinal image. *Nature, Lond.* **203**, 1200.
- BRINDLEY, G. S., DU CROZ, J. J. and RUSHTON, W. A. H. (1965). The flicker fusion frequency of the blue-sensitive mechanism of colour vision. *J. Physiol., Lond.* **183**, 497-500.
- DE LANGE, H. (1957). Attenuation characteristics and phase shift characteristics of human fovea-cortex systems in relation to flicker-fusion phenomena. Thesis. Technische Hogeschool, Delft.
- DE LANGE, H. (1958a). Research into the dynamic nature of human fovea-cortex systems with intermittent and modulated light—I Attenuation characteristics with white and coloured light. *J. opt. Soc. Am.* **48**, 777-784.
- DE LANGE, H. (1958b). Research into the dynamic nature of human fovea-cortex systems with intermittent and modulated light—II. Phase shift in brightness and delay in colour perception. *J. opt. Soc. Am.* **48**, 784-789.
- IKEDA, M. and BOYNTON, R. M. (1962). Effect of test-flash duration upon the spectral sensitivity of the eye. *J. opt. Soc. Am.* **52**, 697-699.
- JUDD, D. B. (1932). Chromaticity sensitivity to stimulus differences. *J. opt. Soc. Am.* **22**, 72-108.
- KELLY, D. H. (1961). Visual responses to time dependent stimuli—II. Single channel model of the photopic visual system. *J. opt. Soc. Am.* **51**, 747-754.
- KELLY, D. H. (1962). Visual responses to time dependent stimuli—IV. Effects of chromatic adaptation. *J. opt. Soc. Am.* **52**, 940-947.
- MCCREE, K. J. (1960a). Colour confusion produced by voluntary fixation. *Optica Acta* **7**, 281-290.
- MCCREE, K. J. (1960b). Small field tritanopia and the effects of voluntary fixation. *Optica Acta* **7**, 317.
- NELSON, T. M. (1971). Stimulus intermittency and colour studies in review. *J. gen. Psychol.* (In press).
- PIERON, H. (1932). Les lois du temps du chroma. *Ann. Psychol.* **30**, 277-280.
- PIERON, H. (1952). *The Sensations*, Muller, London.

- PITT, F. H. G. (1945). The nature of normal trichromatic and dichromatic vision. *Proc. R. Soc. B.* **132**, 101.
- REGAN, D. and TYLER, C. W. (1971a). A wavelength modulated light generator. *Vision Res.* **11**, 43–56.
- REGAN, D. and TYLER, C. W. (1971b). Temporal summation and its limit for wavelength changes: an analogue of Bloch's law for colour vision. *J. opt. Soc. Am.* In press.
- STILES, W. S. (1946). A modified Helmholtz line-element in brightness-colour space. *Proc. Phys. Soc., Lond.* **58**, 41–65.
- VAN DER HORST, C. J. C. (1969). Chromatic flicker. *J. opt. Soc. Am.* **59**, 1213–1217.
- VAN DER HORST, G. J. C. and BOUMAN, M. A. (1969). Spatiotemporal chromaticity discrimination. *J. opt. Soc. Am.* **59**, 1482–1488.
- VAN DER HORST, C. J. C. and MUIS, W. (1969). Hue shift and brightness enhancement of flickering light. *Vision Res.* **9**, 953–963.
- VAN NES, F. L., KOENDERINK, J. J., NAS, H. and BOUMAN, M. A. (1967). Spatiotemporal modulation transfer in the human eye. *J. opt. Soc. Am.* **57**, 1082–1088.
- WALD, G. (1964). The receptors of human colour vision. *Science, N. Y.* **145**, 1007–1016.
- WALRAVEN, P. L. (1962). On the mechanisms of colour vision. Thesis, University of Utrecht.
- WALRAVEN, P. L. and BOUMAN, M. A. (1966). Fluctuation theory of colour discrimination in normal trichromats. *Vision Res.* **6**, 567–586.
- WALRAVEN, P. L. and LEEBEEK, H. J. (1964). Phase shift of sinusoidally alternating coloured stimuli. *J. opt. Soc. Am.* **54**, 78–82.
- WRIGHT, W. D. (1947). *Researches into Normal and Defective Colour Vision*, Mosby, St. Louis.
- WRIGHT, W. D. and PITT, F. H. G. (1934). The colour vision characteristics of two trichromats. *Proc. phys. Soc., Lond.* **47**, 207–208.

**Abstract**—These experiments are analogous with classical studies of threshold luminance perception, with wavelength changes replacing intensity changes. Throughout the spectrum the shapes of the sensitivity-vs.-frequency curves for the perception of wavelength modulation are quite different from the shapes of the analogous (De Lange) curves for luminance modulation. These curves are interpreted as descriptions of the different attenuation characteristics of the neural mechanisms which underlie the perception of threshold changes of stimulus wavelength and intensity respectively.

The classical bipartite-field method gives little information as to the dynamics of wavelength discrimination. We report that the shape of the wavelength discrimination curve is a function of stimulus repetition frequency. Although the yellow minimum is little affected, the blue-green minimum shifts from 500 nm to below 480 nm when stimulus frequency is reduced from 5 Hz to 0.5 Hz.

Tentative attempts are made to use the data as fresh tests of colour vision. Our data indicate that dynamic wavelength discrimination curves cannot straight forwardly be related to CIE data.

**Résumé**—On réalise des expériences analogues aux études classiques sur le seuil de perception de luminance, mais où les changements de longueur d'onde remplacent ceux d'intensité. Dans tout le spectre la forme des courbes de sensibilité en fonction de la fréquence pour la perception de la modulation en longueur d'onde est tout-à-fait différente de la forme des courbes analogues (De Lange) pour la modulation de luminance. On interprète ces courbes par des caractéristiques différentes d'atténuation dans les mécanismes nerveux sous-jacents à la perception des changements respectifs de longueurs d'onde et d'intensité du stimulus.

La méthode classique du champ bipartite donne peu d'information sur la dynamique de la discrimination en longueur d'onde. Nous trouvons que la forme de la courbe de discrimination en longueur d'onde est fonction de la fréquence de répétition du stimulus; tandis que le minimum dans le jaune varie peu, le minimum dans le bleu-vert se déplace de 500 nm à moins de 480 nm quand la fréquence du stimulus est réduite de 5 Hz à 0,5 Hz.

On tente d'utiliser ces données comme tests nouveaux de la vision des couleurs. Il semble que nos courbes de discrimination dynamique en longueur d'onde ne puissent pas être directement liées aux données de la CIE.

**Zusammenfassung**—Die Untersuchungen wurden analog den klassischen Versuchen zur Leuchtdichteunterschiedsschwelle durchgeführt. Diese wurde dabei durch die  $\Delta\lambda$  Schwelle ersetzt. Die Empfindlichkeitskurven sind über das ganze Spektrum völlig verschieden von den

entsprechenden (De Lange) Kurven für die Leuchtdichtemodulation. Diese Kurven werden als Beschreibung der Filtereigenschaften der neuronalen Mechanismen interpretiert, die der Wellenlänge und Leuchtdichteschwelle zugrunde liegen.

Die klassische Halbfeldmethode gibt nur wenig Information über die Dynamik der Wellenlängenunterscheidung. Wir fanden, daß die Form der Wellenlängenunterscheidungskurve von der Flimmerfrequenz abhängt. Das gelbe Minimum wird dabei wenig beeinflusst, dagegen verschiebt sich das blau-grüne Minimum von 500 nm bei 5 Hz auf unter 480 nm bei 0,5 Hz.

Es wird versucht, die Daten als neuen Test für das Farbsehen zu verwenden. Unsere Daten weisen darauf hin, daß die dynamischen Wellenlängenunterscheidungskurven nicht direkt mit den CIE Daten in Verbindung gebracht werden können.

**Резюме**—Эти эксперименты аналогичны классическим исследованиям порога восприятия яркости, только изменения интенсивности заменяются изменениями длины волны. По всему спектру формы кривых чувствительности против частоты восприятия модуляции длины волны значительно отличаются от формы аналогичных кривых (De Lange) модуляции яркости. Эти кривые истолковываются как изображение характеристик различных ослаблений нервных механизмов лежащих в основе восприятия изменений порогов волны раздражения и интенсивности соответственно.

Двусторонний классический метод дает очень мало информации о динамике различимости длины волны. Думают, что кривая дискриминирования формы длины волны является возбуждающим фактором частоты повторения; хотя, желтый минимум почти что не затрагивается, а сине-зеленый минимум сдвигается с 500 нм ниже 480 нм, когда частоту возбуждения снижают с 5 гц на 0,5 гц.

Предварительно пытаются использовать эти данные для определения цветного зрения. Наши данные указывают, что кривая различимости динамики длины волны не может быть непосредственно связана с данными CIE.