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On the Nature of Models of Colour Vision

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

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

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

1. The nature of a satisfactory model

1.1: Models as analogues

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

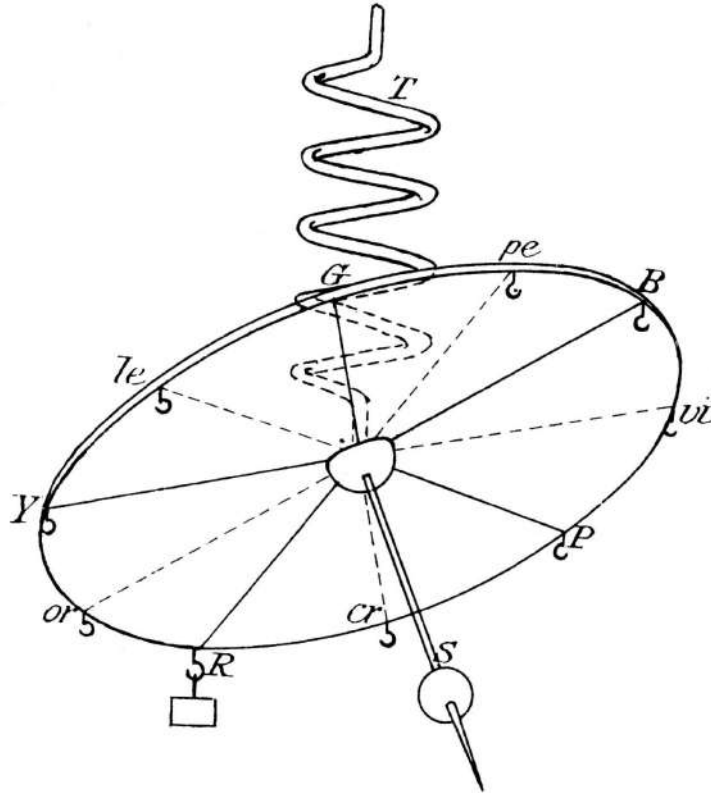* *Department of Experimental Psychology, University of Cambridge (UK)*

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

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

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

1.2: Models as schemata. Requirements for a model

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

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

Between the optical stimulus and the generation of the signals that control our behavioural responses, there intervene, we believe, a number of stages or sub-mechanisms or computational levels. By each sub-mechanism, or at each computational level, the input signals may be transformed. The relationship between particular sub-mechanisms may be a parallel or a serial one; and there may be recursive loops within the system. A model then is a schema of the sub-mechanisms and their relationships.
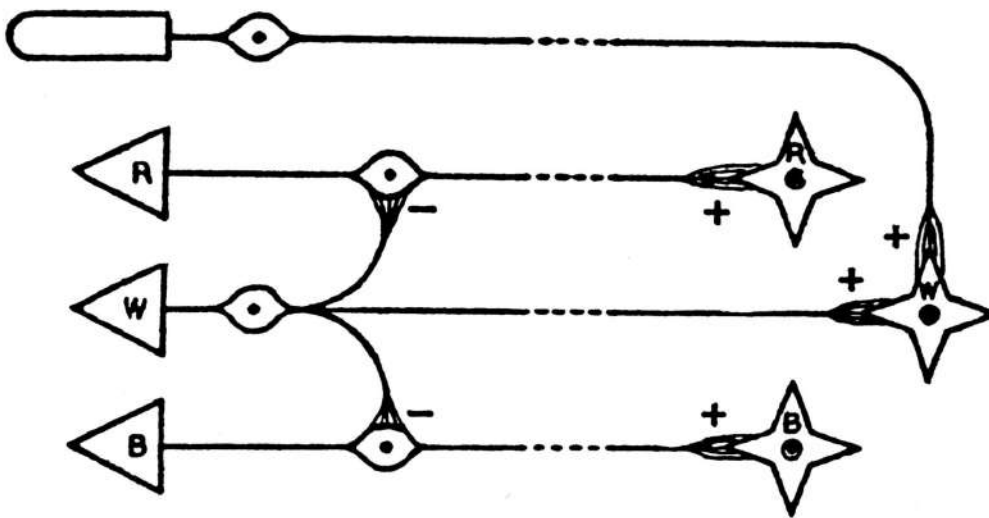
Fig. 2: ADAMS' model of colour vision

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

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

    (i)   *Specification of a set of receptors and other neural compo-nents*

  (ii) Specification of how the components are connected.

(iii) *Specification of the spectral sensitivities of the receptors and of the other transfer functions that relate the inputs of given components to their outputs.*

(iv) *Specification of how the transfer functions vary with adaptation.*

(v) *Specification of how particular human judgements or aspects of behaviour depend on particular output signals.*

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

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

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

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

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

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

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

R-G TERM

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

$$\beta = 0.015 \cdot \frac{R^2}{R^2+G^2} \quad \text{FOR} \quad R > G$$

$$\quad\quad\quad\quad \frac{G^2}{R^2+G^2} \quad , \quad R < G$$

$$F_{RG} = \text{Log}_e R - \text{Log}_e G : \quad T_{RG} = \beta$$

Y-B TERM

$$\left(\Delta C_{y-e}\right)^2 = \frac{1}{\gamma^2}\left(\frac{\Delta R}{2R} + \frac{\Delta G}{2G} - \frac{\Delta B}{\xi B}\right)^2$$

$$\gamma = 0.015 \cdot \quad \text{FOR} \quad G < 2.5B$$

$$\quad\quad = 0.015 \frac{G}{2.5B} \quad \text{FOR} \quad G > 2.5B \quad\quad \xi = \frac{5}{3}$$

$$F_{Y-B} = \frac{1}{2}\left(\text{Log}_e R + \text{Log}_e G\right) - \frac{1}{\xi}\text{Log}_e B$$

$$T_{Y-B} = \gamma$$

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

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

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

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

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

Now, it is often remarked that LAND's model contradicts what the electrophysiologists tell us. The accumulated physiology ostensibly suggests that there is a local extraction of the ratios of quantum catches in different cone types, and then some more global form of comparison of these ratios across the field [see, e. g. 4; 6] – whereas LAND's model places the spatially global comparison within a single cone system, preceding the comparison between cone systems.

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

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

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

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

1.5: The fifth requirement

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

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

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

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

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

2.1: *The similarity of existing models*

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

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

2.2.: *The modal model summarized*

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

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

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

2.3.: *Current developments*

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

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

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

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

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

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

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

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

2.4: A third zone?

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

a) the hypothesis that particular neurons secrete particular sensations, and

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

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

3.   The nature of luminance

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

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

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

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

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

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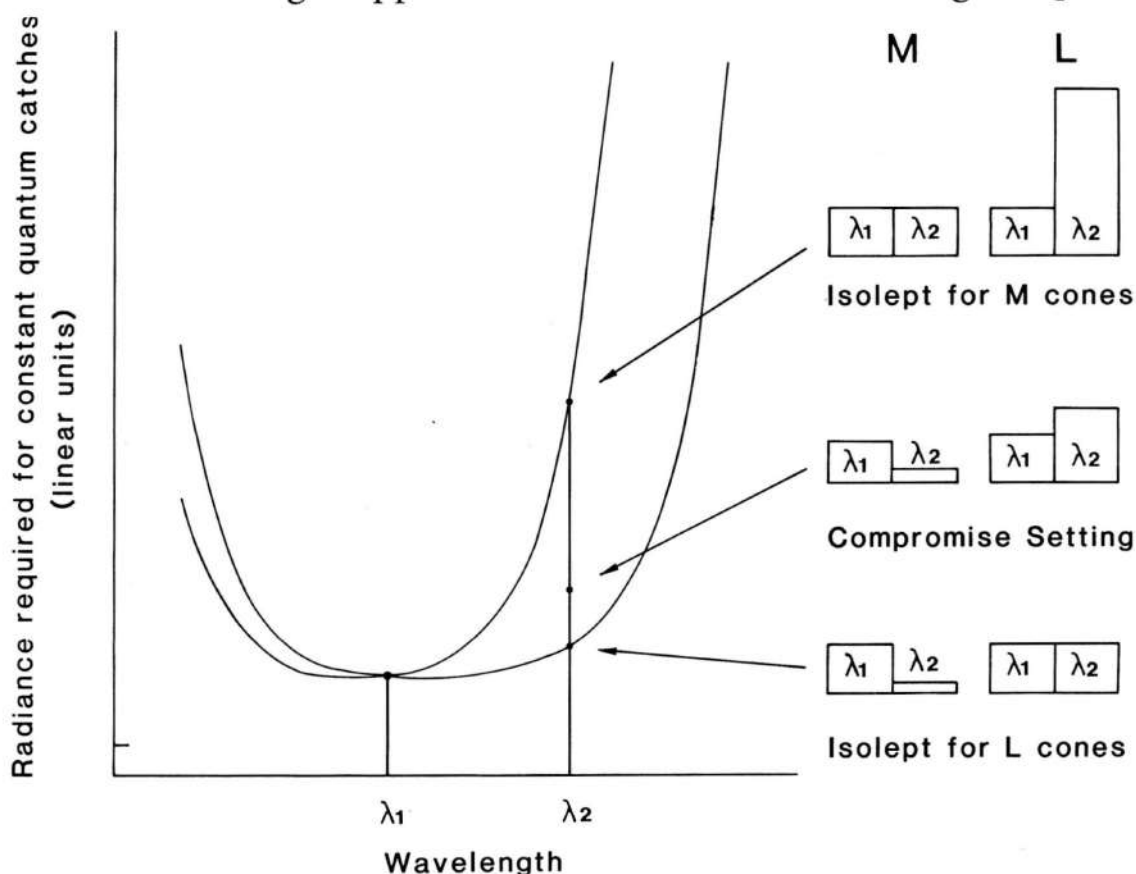

Fig. 5: An alternative interpretation of what the observer does when he or she is asked to make a minimum flicker or minimum-border setting in heterochromatic photometry. Two wavelengths, λ_1 and λ_2, are alternated in time or space. The observer adjusts the radiance of λ_2. To the right is shown schematically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

are alternated, and that the second of these is the variable. If the observer is a protanope, there is no ambiguity about how he should make a setting: he should set the radiance of λ_2 so that it lies at what RUSHTON, POWELL and WHITE [38] called the i s o l e p t, i. e. the radiance at which it gives the same quantum catch in the middle-wave cones as does the first light; he achieves a 'silent substitution' for the middle-wave cones. Similarly, if he is a deuteranope he must go for the isolept for the long-wave cones. But what is the normal to do? Let us suppose (this is the crucial assumption in this alternative interpretation of luminance) that he has both access to the a. c. components of the long- and of the middle-wave signals. He would like to achieve a silent substitution for both the long-wave and the middle-wave cones, but if he sets the variable radiance to the isolept for one of the two classes, there will be a marked modulation of the other class (Fig. 5, right-hand side). So, we may suppose that he compromises. He sets the variable at a position between the two isolepts, a position where both the residual signals are small. The exact position of his setting will depend on the relative weighting that his visual system gives to the a. c. signals from the two types of cone, and this may depend, say, on the relative numerosities of different cone types. He will, however, never venture outside the window between the two isolepts; for outside this window, both the residual signals can only increase. Since his settings are constrained in this way, they will come close to exhibiting additivity, even though there is no reified signal within his nervous system that represents luminance.

3.2: Equal luminance

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

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