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DETECTION OF LONG-DURATION, LONG-WAVELENGTH INCREMENTAL FLASHES BY A CHROMATICALLY CODED PATHWAY

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Abstract—This paper reports tests of the hypothesis that a 200 msec 667 nm, foveal test flash, presented upon a steady, 8° background, is detected by a pathway whose sensitivity is monotonically related to a linear functional of photoreceptor quantum catch. The measurement conditions used in this paper are the same as those used by Stiles in his π-mechanism analysis. The hypothesis is tested by measuring increment-threshold curves for various background wavelengths and for various mixtures of two backgrounds.

The results clearly reject the hypothesis. We propose two models that are consistent with the measurements reported here as well as measurements—using a 10 msec test flash—reported previously. We then discuss related empirical and theoretical work.

INTRODUCTION

The Stiles π-mechanisms are explicitly defined by observations made under a restricted set of experimental conditions. In particular, the standard duration of the test flash is 200 msec. Stiles found that seven distinct mechanisms, or branches, had to be postulated in order to account for the full range of increment-threshold data that he measured in his standard conditions. To account for the detection of long-wavelength test lights, Stiles required two mechanisms: π_5 and π'_5. This situation contrasts sharply, both empirically and theoretically, with that we found using a 10 msec, 667 nm flash. Empirically, we needed only one branch, not two. Theoretically, Stiles' results reject the hypothesis that the processes of adaptation probed by a 200 msec, long-wavelength test flash are controlled exclusively, over the full range of background intensities, by the quantum catch of a single class of photoreceptors. Our results with a 10 msec test flash do not reject that hypothesis.

In this paper we take up these empirical and theoretical questions respectively: (1) What are the differences between the increment-threshold measurements with 200 msec and 10 msec test flashes in the shape-invariance and field-mixture experiments, and (2) How can they be explained? Towards answering the first question we report a replication and extension of Stiles' increment-threshold measurements using a 200 msec test flash of wavelength 667 nm. The measurements were performed on the same observers and under the same adapting conditions as in the previous study (Wandell and Pugh, 1980).

Towards answering the second question we introduce two models, each of which is consistent with the increment-threshold results for 10 and 200 msec, 667 nm tests. We conclude with a discussion of the relationship between the ideas we introduce here and various closely related empirical and theoretical reports from other laboratories.

METHODS

The methods and procedures of this investigation are identical to those described in the previous paper (Wandell and Pugh, this issue, p. 613). The single difference is that the duration of the test flash was increased from 10 msec to 200 msec.

RESULTS

Increment-threshold curves

Figures 1 and 2 are graphs of increment-threshold data from the two observers, on various wavelength backgrounds. Each distinct set of symbols associated with a given field wavelength (the parameter above the curves) represents an increment-threshold curve obtained in a different session; each point on an increment-threshold curve is obtained from a two-alternative forced-choice staircase of 50–70 observations. For each experiment the data points within 1 log unit of absolute threshold were fit by computer to the Stiles (200 msec) template. This fitting procedure fixes the position of all the other points above the 1 log unit cutoff relative to the template.

With the curves slid by computer to coincide with the Stiles template for the region within 1 log unit of absolute threshold, it is evident that the increment-

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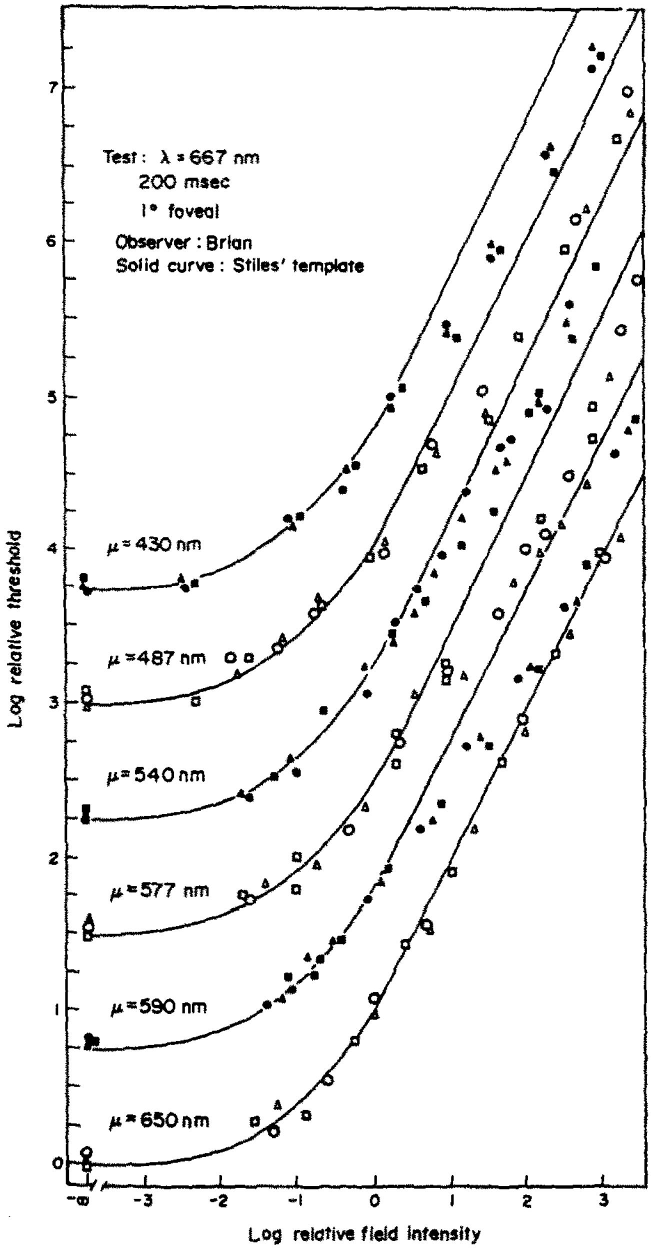

Fig. 1. Graph of threshold for 667 nm, 200 msec, 1°, foveal test flash versus normalized field intensity. Observer Brian. Data are grouped by field wavelength. Each plotted point is the threshold estimated from a staircase of 50–70 trials, as described in Methods. Different symbols refer to observations from experiments run on different days. Stiles' standard (200 msec) template was fit by a computerized least-squares procedure to the first log unit of each session's increment-threshold curve. This procedure fixed the position of each set of points with respect to the normalized field intensity axis. The 650 nm field data are well fit by Stiles' template across the entire range of field intensities; the data from other wavelength fields deviate downward from the template. The results for each field wavelength have been positioned vertically 0.75 log units above those below. Average absolute threshold +2 SEM: 5.88 + 0.06 log quanta deg^{-2} sec^{-1} (N = 18 experiments).

threshold curves for different wavelength adapting fields follow slightly different shapes. When the increment-thresholds on 650 nm fields are *shifted* to coincide with the template at low intensities, the high intensity thresholds also coincide with the template. However, when 430 nm fields are similarly *shifted*, the high intensity data points fall below the template by as much as half a log unit.

The conditions for these experiments are the same as those used by Stiles (1953) in his increment-threshold measurements. Stiles has not published many examples of full increment-threshold curves for 200 msec test flashes. However, our results are in good agreement with those he has published in two respects.

First, the increment-threshold curves on 650 nm

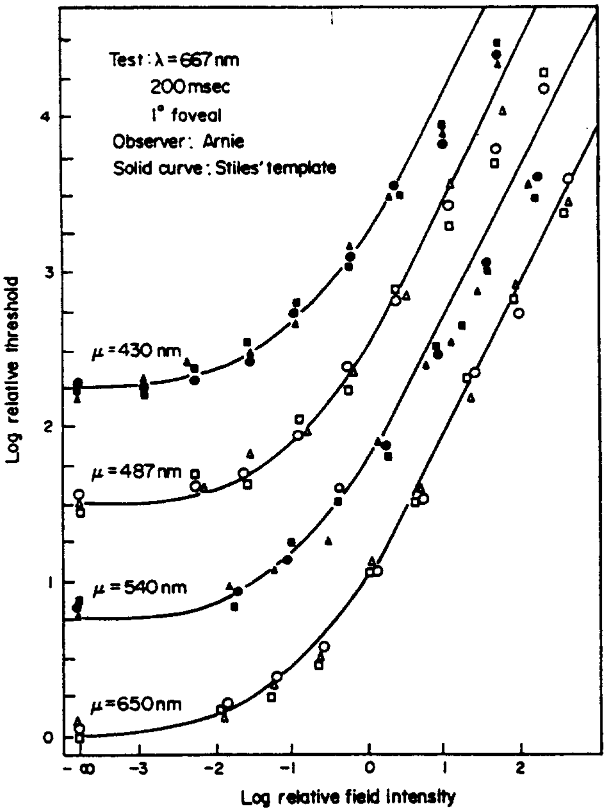

Fig. 2. Graph of threshold versus normalized field intensity for Arnie. See caption of Fig. 1 for details. Average absolute threshold +2 SEM: 6.40 + 0.06 log quanta deg^{-2} sec^{-1} ($N = 12$ experiments).

backgrounds, for both observers, are quite well fit over the full range of field intensities (here, 0 to 120,000 td) by the Stiles template (Wyzsecki and Stiles, 1967, p. 578). This template is drawn in Figs 1 and 2 as the smooth curve. See Fig. 16 in Stiles (1953) for comparable data.

Second, the deviations from the template for fields of other wavelengths are quite similar to those Stiles (1953, 1959) reports. They begin about 1.5 log units above threshold (approx. 100 td) and are very obvious on short- and middle-wavelength fields.

We note that these deviations from the template are not confined to short-wavelength adapting fields. For example, there is a significant deviation from the Stiles template for Brian's increment-threshold data taken upon a 577 nm field.

Intermediate discussion

Stiles, when confronted with failures of shape-invariance similar to those we report here, suggested that the pattern of results could be due to the effect of two mechanisms. One (π_5) mediated detection at low intensities. The second mechanism (π'_5) mediated detection on some high intensity fields—namely, those for which the high field intensity data fell below the template.

In Fig. 3 we diagram the account that would be given by the Stiles model for Brian's 430 nm results. To explain this figure fully, let us first reconsider the 650 nm field data. As can be seen in Figs 1 and 2, the 650 nm field data follow the shape of the template quite well. Therefore, in this instance, detection at the highest intensities could be mediated either by π_5 or by the second mechanism, π'_5. As is also shown in Figs 1 and 2, the 430 nm data deviate from the template

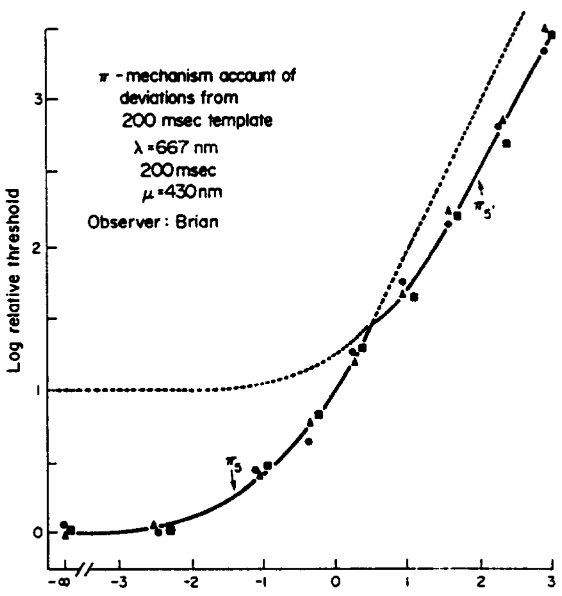

Fig. 3. π-mechanism account of the 430 nm increment-threshold data of Brian. Two distinct branches must be postulated. See text for details.

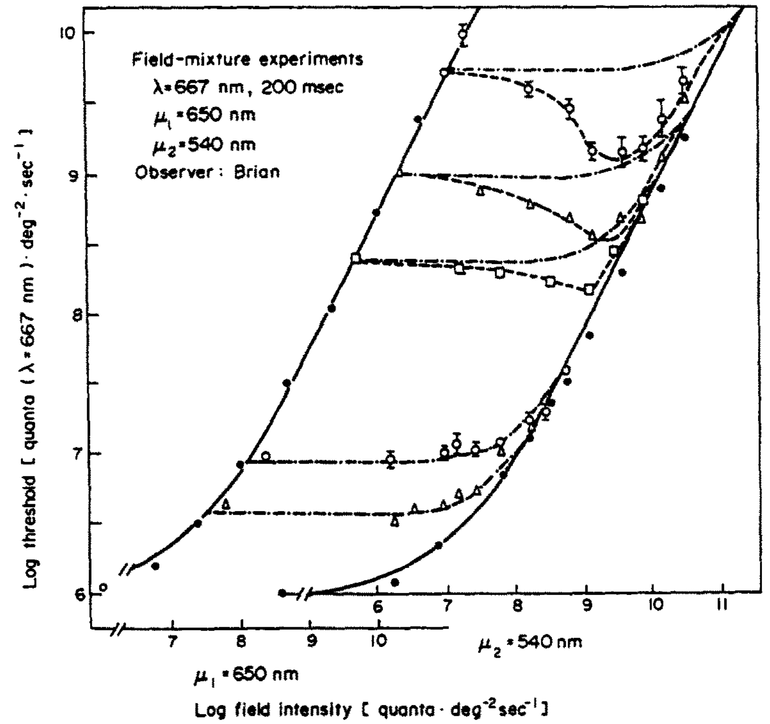

Fig. 4. Field-mixture experiments with 650 nm and 540 nm fields for Brian. The solid symbols represent increments upon the monochromatic fields; they are average curves obtained from the data of Fig. 1. The points intervening between the curves (open symbols) are the thresholds measured upon the field mixtures. The broken curves are the predictions of field-additivity.

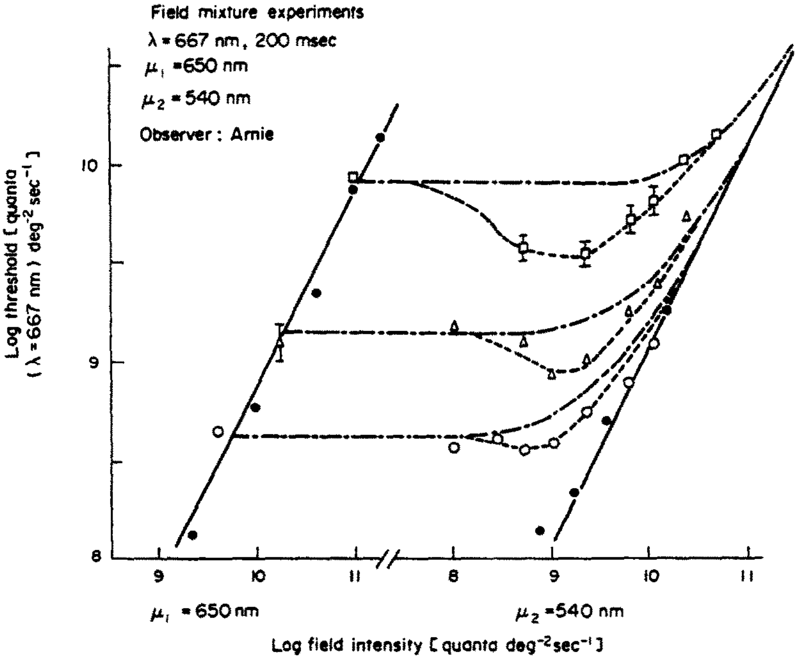

Fig. 5. Field-mixture experiments with 650 nm and 540 nm fields for Arnie. Solid symbols giving the increments upon the monochromatic fields, are averages from the results of Fig. 2. Broken lines are the predictions of field-additivity.

shape. Since the template shape for any single mechanism is by definition fixed, it is necessary to postulate a second mechanism to explain these deviations. The new mechanism must have a different field sensitivity: its template must be positioned in such a way as to pass through the data points that fall below the extrapolation of the π_5 mechanism's template. The theory thus accounts for any failures of shape-invariance that involve downward deviations from the standard template by invoking a new mechanism with a new field sensitivity. The procedure for defining the field sensitivity of the new mechanism allows that the present pattern of increment-thresholds be reasonably well fit.

In this discussion we have used the expression "deviations from the template" to emphasize that we have found no certain "breaks" (i.e. discontinuities in the first derivative) in the increment-threshold data.

Field mixture curves

Results from field mixture experiments with 650 nm and 540 nm fields are shown in Figs 4 and 5. The broken line associated with each mixture condition is the prediction of field-additivity. At lower field intensities the limited number of field-mixture experiments we have executed show no reliable deviations from the additivity prediction. We did not systematically investigate these intensities because Sigel and Pugh (1980) had already performed extensive field-mixture experiments at such intensities for a test flash of the same wavelength and duration. However, at the higher intensities we observe the striking result that mixing in additional quanta to the field improves threshold sensitivity for the 667 nm test flash. The admixture of the 540 nm fields causes threshold to drop by 0.25–0.6 log units from the level it had attained upon the 650 nm field alone. We have obtained this same result from three other normal observers (but failed to find it in one deuteranomalous subject). Similar results were reported by Sternheim *et al.* (1979) for detection of long-wavelength test lights flickering at low frequencies. An analogous result has been found for short-wavelength test flashes by Polden and Mollon (1977), and by Pugh and Larimer (1978).

Figures 6 and 7 show the results, for one observer, of several field-mixture experiments with various wavelength combination fields. Clearly, not all wavelength combinations generate the same dramatic effects as seen in Figs 4 and 5. One combination (430 nm and 487 nm) is approximately consistent with the additivity hypothesis while the other combination shows some deviations from additivity.

DISCUSSION

A puzzle now confronts us: how can we reconcile the observations of this and the previous paper with a single theory? We must resolve the apparent conflict between our results with a brief duration test, which are consistent with the field quantum-catch hypothesis, and the results with the long-duration test, which strongly reject that hypothesis. We will first describe two theoretical schemes. Each is consistent with our results and apparently with those of other workers. In the discussion that follows we limit our descriptions of the schemes to their qualitative properties.

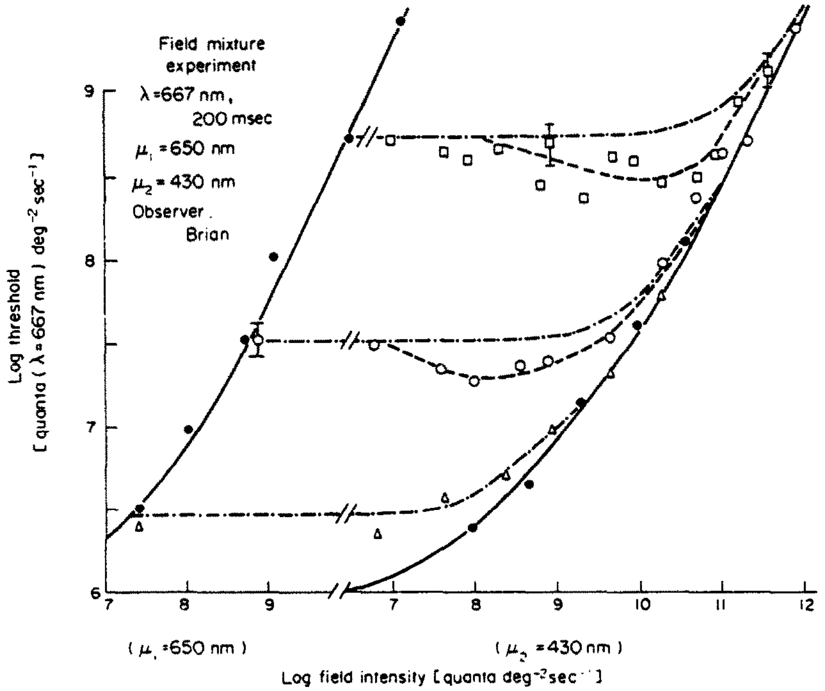

Fig. 6. Field-mixture experiments with 650 nm and 430 nm fields for Brian. Broken curves are additivity predictions.

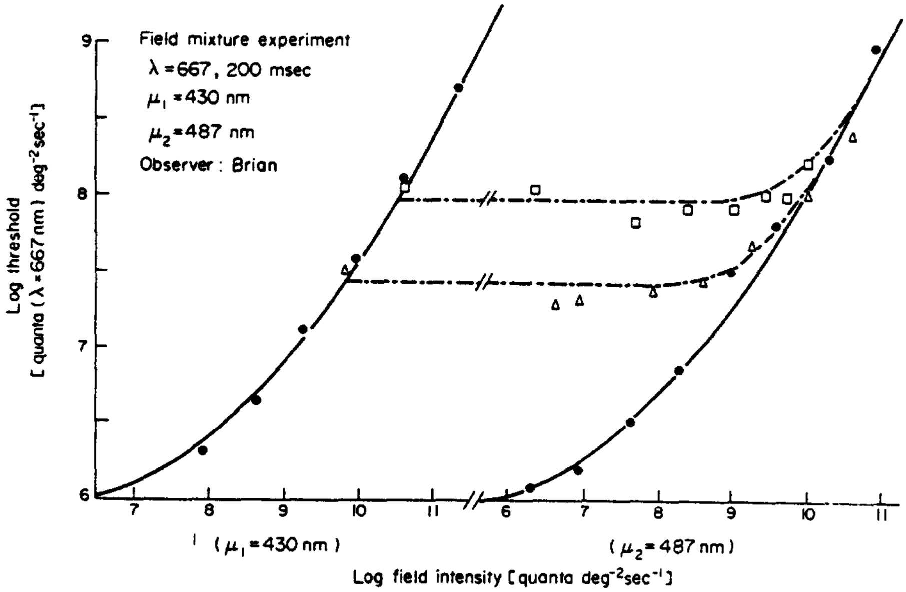

Fig. 7. Field-mixture experiments with 430 nm and 487 nm fields for Brian.

A model with only one detection-pathway

Figure 8 is a schematic of this model of threshold behavior under steady-state adaptation. There is only one route that the test signal may take to reach the detector. Our choice of 667 nm as the test wavelength makes it quite likely that the signal the subject detects originates in the long-wavelength photoreceptors. The field lights, in general, stimulate all classes of photoreceptors.

The central assumptions of the model are these:

1. The signals emerging from the first sites (indicated by the inverted triangles) are Univariant. That is, they signal only the rate of quantum catch of a single class of cones.

2. The second site receives signals of opposite polarity from the long-wavelength (γ) and middle-wavelength (β) photoreceptors. The short-wavelength (α) receptors contribute to the second site with the same polarity as the γ photoreceptors.

3. The first site elements adapt, but in a fashion consistent with Univariance.

4. In the steady state, beginning at about 100 td, the second site adapts only by shortening its integration time: that is, the time up to which time and intensity trade off to within measurement error. No sensitivity to brief test stimuli is lost. The shortening of the integration time at the second site becomes more extreme as the signal it receives (contributed by the three classes of cones, with varying polarities) drives it away, in either direction, from neutrality.*

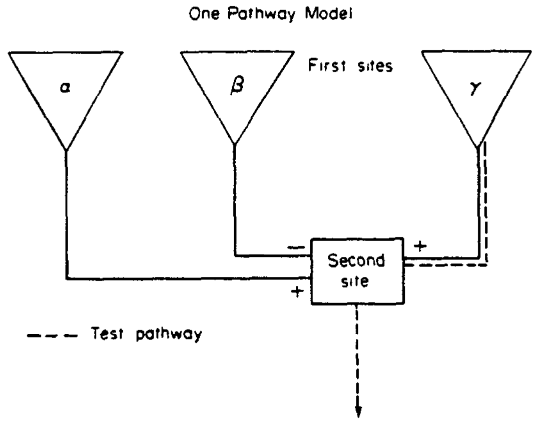

Fig. 8. Schematic of "one-pathway" model of adaptation and detection under present experimental conditions. See text for details.

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* An example of a simple system with these properties is the following: Suppose that for any adapted state, the second-site responds linearly in response to a threshold signal. Further, suppose that detection occurs when the peak output of the second site exceeds a fixed criterion. On this view, second-site adaptation is characterized by changes in the hypothetical impulse response function. Assumption (4) is equivalent to a constraint on the kinds of changes that the impulse response function may undergo as the adaptation state is varied. In the case of a box-car impulse response function, the width of the function, ζ_b, may change with the adaptation state, but the height of the box-car must stay fixed. In the case of an exponential impulse response, changes in the time constant, ζ_e, are allowed, but all external, multiplicative (e.g. gain) constants must remain fixed. For example, a simple calculation shows that a change in the time constant, ζ_e, from 100 msec to 50 msec will reduce sensitivity to a 200 msec test flash by 0.2464 log units while sensitivity to a 10 msec test flash is reduced by only 0.02 log units. Thus, if polarizing the second-site were to shorten ζ_e or ζ_b, only sensitivity to long duration signals would be materially reduced. Clearly, however, changes in an external, multiplicative constant would reduce sensitivity to 10 msec and 200 msec flashes equally. Therefore, both of these systems—a box-car impulse response with varying width or an exponential impulse response with varying time constant—are models of the second site that are consistent with assumption (4).

To explain how this model can account qualitatively for the data, we consider first the increment-threshold curves for a 10 msec test flash. The test signal stimulates the first site whose adaptation state obeys Univariance. Therefore, the reduction in detectability of the test due to adaptation of the first site will follow Univariance. When the test flash is very brief, the signal it generates will be within the integration period of the second site. Changes in the integration period of the second site will be immaterial to the observer's sensitivity as long as the value of the integration period greatly exceeds the duration of the signal generated by the test at the first site. Since sensitivity depends only on the first site, which is Univariant, brief-duration test thresholds will obey the field quantum-catch hypothesis.

Not so for tests whose duration exceeds the integration time of the second site. Sensitivity to these tests will depend upon the varying integrative capacity of the second site. Since the integration time at the second site is not consistent with Univariance, threshold measurements using long-duration test flashes will not obey the field quantum-catch hypothesis.

The nature of the predicted failure is that on backgrounds that strongly polarize the second site, the integration time will be brief. Therefore, thresholds will be raised relative to backgrounds with a neutral effect upon the second site.

By way of example, consider the 200 msec increment-threshold curves for 650 nm and 577 nm backgrounds in Brian's data (Fig. 1). The 650 nm field would polarize the second site while the 577 nm field would not. Therefore, as the intensity of the field grows, the integration period of the second site will shorten for the 650 nm background but not for the 577 nm background. This will be reflected in a growing separation of the two increment-threshold curves as the integration time shortens. Since the 577 nm field is approximately neutral with respect to the second site, adaptation on that field is proportional to the effect of the first site, alone. The 650 nm field thresholds rise more than this due to the polarization of the second site.

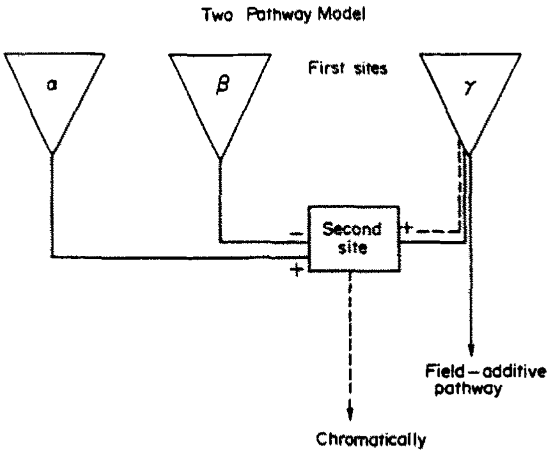

Fig. 9. Schematic of two detection-pathway model of adaptation and detection in present experimental conditions. See text for details.

Consider now the one detection-pathway model's explanation of field-additivity failures (Figs 4–6). When the test is measured against the 650 nm field alone, the second site is polarized and therefore the integration time is short. As we add in 540 nm light, the second site moves towards neutrality and the integration time lengthens. This change in integration time will not affect the 10 msec test threshold. But it will lower the 200 msec test threshold. Past the neutral point the second site re-polarizes and threshold begins to rise again. On the rising phase threshold grows for two reasons: the extra quanta at the first site and the shortening of the integration time at the second site.

A model with two detection-pathways

A schematic of this model is shown in Fig. 9. What differentiates this model from the one detection-pathway model is that the test flash—which again, initiates a response in the long wavelength photoreceptors—begins a signal along two neural routes. We suppose that the more sensitive of the two available paths mediates detection. We list the assumptions of the two detection-pathways model.

1. The first sites are Univariant. For one of the pathways (field-additive pathway) this is the only locus that adapts.
2. The second site in the chromatically-coded pathway, which is in series with the first site, receives signals of different polarity from the three classes of photoreceptors, as in the previous model. For the two detection-pathway model, however, we assume that the second site becomes less sensitive when moderate (roughly a few hundred td) or intense backgrounds provide it with a signal from the first sites that drives it away from neutrality.
3. The integration time of the second, opponent site is fixed and is longer than the integration time of the first site. This means that the pathway through the second site will have a longer integration time than the pathway that only passes through the first site.

Low intensity fields. An assumption of the two detection pathway model is that the second site does not adapt until moderate to high intensity fields are used. Therefore, the model predicts that increment-thresholds for both long and brief-duration flashes will be consistent with the field quantum-catch hypothesis on low field intensities. This prediction stands regardless of the pathway used by the test signal at low intensities. The prediction is consistent with the observations reported by Sigel and Pugh (1980), as well as those reported here.

High intensity fields. As the intensity of fields with a strong red or green valence growsn, the second site of the chromatically-coded pathway will polarize, and therefore attenuate the test signal. At some point this additional attenuation will offset any potential advantage due to the longer integration time of the chromatically-coded pathway. For these intense, chromatic adapting fields, both long and brief-duration flashes will be detected by the field-additive pathway.

The behavior of increment-thresholds of brief duration flashes will, therefore, always be simple. On both low and high field intensities the detecting pathway will be consistent with the field quantum-catch hypothesis. However, the increment-threshold results for long-duration flashes will be more complex, and will depend upon an opponent interaction.

The predictions of this model can be understood by returning to the example of Brian's 650 nm and 577 nm fields, and the long-duration (200 msec) test flash. At low field intensities the long-duration flash will be detected by the chromatically-coded pathway. This is true for both field wavelengths. Moreover, since the 577 nm background is neutral for the second site, the increment-thresholds on that background will depend only on adaptation at the first site throughout the entire range of field intensities.

On low intensity 650 nm fields the 200 msec flash will again be detected by the chromatically-coded pathway. However, at moderate field intensities the 650 nm field data will begin to rise faster than the 577 nm field data. This will be due to the increased attenuation at the second site. When this additional attenuation forces the threshold of the chromatically-coded pathway above that of the field-additive pathway, detection will switch over to the field-additive pathway. This hypothetical behavior is sketched in Fig. 10.

The two detection-pathway account of the additivity data is also shown in Fig. 10. The increment-threshold measurements on the intense, 650 nm field are mediated by the field-additive pathway. This is because the threshold of the chromatically-coded pathway is elevated by the polarization at the second site, as just discussed. As the 540 nm light is added-in, the brief-duration pathway obeys additivity (shown by the broken line). For the chromatically-coded pathway, however, the added light relaxes the polarization at the second site. Therefore threshold of this pathway drops until it becomes lower than the threshold of the field-additive pathway. At that point detection of the long-duration flash reverts to the chromatically-coded pathway. Finally, threshold begins to rise, again, as the polarization of the second site begins in the green direction. As this polarization continues, and the additional 540 nm field quanta have their effect at the first site, detection switches back to the field-additive pathway.

Before turning to other results and theories, we make a few brief remarks about the common structures of these two models. The common polarity of the γ- and α-cone input to the second site is not strictly necessary. From the increment-threshold and additivity results we see that short-wavelength fields act as though they were nearly neutral with respect to the second site. This means either (a) the relative spectral sensitivity of the γ- and β-cones reaches a maximum difference in the neighborhood of 540 nm and then decreases in the short-wavelength region, or (b) the sensitivity difference remains but the α-cones make a contribution that compensates for the difference between the γ- and β-cones. We think that (b) is probably correct, because the spectral sensitivities of the most likely candidate cone spectra do not show the behavior demanded by (a).

Both of these models predict that the increment-thresholds of 200 msec tests on second-site neutral (or

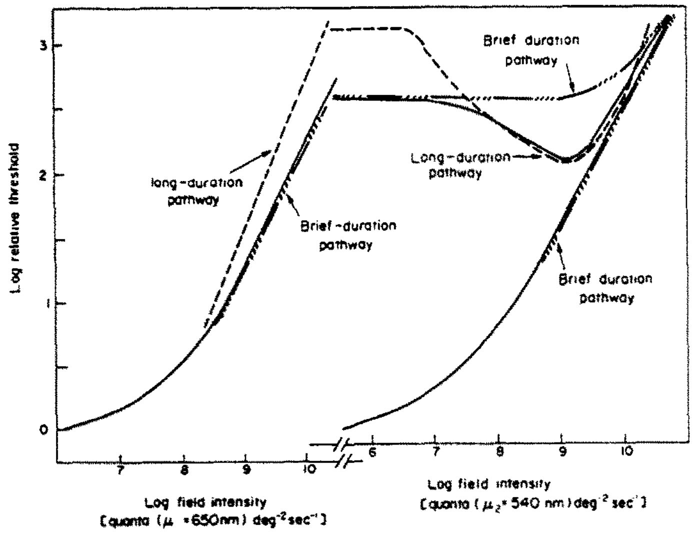

Fig. 10. Account by the two-pathway model of the 650 nm and 540 nm field-mixture data. The intermittently broken curve represents the threshold of the brief-duration pathway under the various monochromatic and bichromatic field conditions; the broken curve, the threshold of the long-duration pathway. The continuous curve is the observed resultant, assuming that the more sensitive pathway determines threshold.

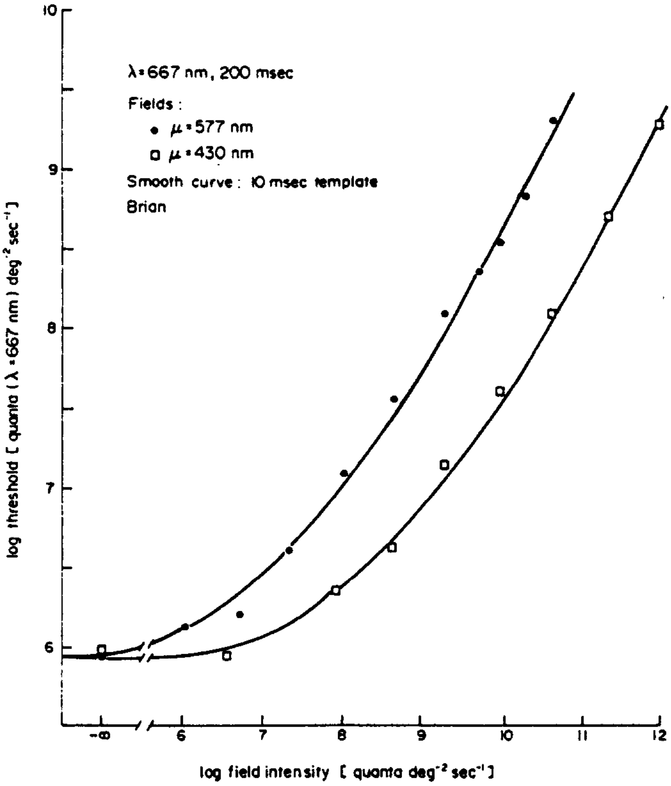

Fig. 11. Average increment-threshold curves of Brian (from the results of Fig. 1) for 200 msec, 667 nm test upon 577 nm and 430 nm fields. The smooth curve is the 10 msec template derived in the previous paper (Wandell and Pugh, 1980).

nearly neutral) fields will follow the 10 msec template. In Fig. 11 we plot the data from a 577 nm and 430 nm field against the 10 msec template derived in the previous paper. The agreement is good.

RELATED WORK

Our theoretical schemes are limited in scope. We have sought to explain only the effects of varying the wavelength and intensity of steady-state adapting fields upon test threshold. We have proceeded this way because of the theoretical simplicity of field mixture studies. This simplicity is due to our ability to specify, with some certainty, a single class of cones as the origin of the signal the observer detects at increment-threshold when the test flash is 667 nm.

By way of contrast, test-mixture experiments, *a priori*, pose more subtle theoretical problems. Test-mixture experiments are performed under conditions in which threshold signals originate in more than one class of cones. As the number of possible signal starting points increases, the number of potential pathways multiplies. Thus, theoretical reasoning must include hypotheses concerning the interactions between various detection pathways as well as hypotheses about the intrinsic properties of the pathways themselves (such as dynamic properties).

In the following discussion we review some of the results from field- and test-mixture experiments. In addition, we discuss Krauskopf and Mollon's (1971) paper on temporal integration. We conclude with comments on related theoretical treatments. The theories include those of Ikeda and Boynton (1962), Boynton *et al.* (1964), and Ingling and Tsou (1977) who comment specifically on the pathways for detecting signals from the long-wavelength cones.

Field-mixture experiments

There are only a few reports of field-mixture experiments using long-wavelength test stimuli. Boynton *et al.* (1966) were the first to perform field-mixture experiments. In the condition relevant to the present discussion, they used a 670 nm, 50 msec test flash (1° diameter, on a 10° background). Their results led them to reject field-additivity. In this pioneering investigation, they adjusted field intensities in order to bring fixed intensity test lights to threshold. As Boynton *et al.* (1966) themselves point out, this method is open to methodological criticisms. For additional discussion of this work, we refer the reader to Sigel and Pugh (1980).

Sternheim *et al.* (1979) have recently reported field-mixture studies using long-wavelength, flickering increments (4.5° tests on 4.5° backgrounds). They first measured threshold to sinusoidally modulated lights upon a 650 nm background. They then admixed 540 nm light to the background and re-determined threshold to these same flickering increments. They demonstrate that for low frequency flicker the admixture of the 540 nm field facilitates detection of low frequency flicker. No facilitation was observed when the test target was a rapidly flickering light. Sternheim *et al.*'s observations with flickering stimuli are consistent with our measurements using pulsed stimuli. Since the 200 msec flash has most of its energy in the low frequency part of the energy spectrum (about 85% of the energy is below 5 Hz) it is likely that such a flash is detected by the same pathway that detects low frequency flicker. The 10 msec flash has its energy distributed evenly across the range of frequencies to which the eye is sensitive. It is therefore not implausible that at moderate to high adaptation levels—when the cone impulse response is likely to be brief, and perhaps diphasic (Ikeda, 1965; Rashbass, 1970)—that a brief duration test is detected by the same pathway as a rapidly flickering test increment.

Sigel and Pugh (1980) report experimental tests of shape-invariance and field-additivity. They used the standard, Stiles experimental conditions 1°, 200 msec test; 10° background). They restricted the range of their measurements to field intensities that elevate threshold less than 1.2 log unit. They did so in order to avoid π'_5 intrusion. As we mentioned earlier, their measurements were consistent with both shape-invariance and field-additivity for these low intensity fields.

Test mixture experiments

The theoretical schemes given in Figs 7 and 8 can make no explicit, quantitative predictions about test mixture experiments without further elaboration. However, we can check for qualitative consistency between simple generalizations of these schemes and published test mixture data. The principal works we will discuss are those of Boynton *et al.* (1964), Stiles (1967), Krauskopf (1974) and Ingling and Tsou (1977). Guth (1965; see also, Guth *et al.*, 1969) has reported extensive experiments using the test mixture paradigm. Since neither the empirical nor theoretical content of those papers test hypotheses concerning the properties of the mechanisms which mediate adaptation, we do not discuss those papers.

Boynton *et al.* (1964) present and analyze their results in terms of the Stiles π-mechanism constructs. Taking the π-mechanism as an unanalyzable primitive, they test hypotheses about the types of interactions between mechanisms. In particular, they test the hypothesis that the mechanisms behave as independent pathways at increment threshold. Stiles (1967) emphasizes two general features of the rather complex pattern of results.

(1) When brief test flashes are used, independence is not contradicted.

(2) Independence is generally violated with long duration flashes. The largest violations are on high intensity fields. In these instances inhibitory interactions were found between tests formed by mixing long- and middle-wavelength light.

For the one pathway model, brief test flashes may not overlap in time at the second site, due to differential delays. Such delays could result from path differences, or from differential adaptation states. Flashes whose duration exceeds the differential delay will overlap at the second site, resulting in cancellative interactions.

One simple extension of the two detection-pathways model, that is consistent with the findings of Boynton *et al.* (1964), would postulate analogous one-site, "brief-duration" pathways from each class of cones. This extension, however, predicts independence (up to probability summation) for all brief flashes. Krauskopf's (1974) results unequivocally reject this extension. Krauskopf measured the threshold for 670 nm and 430 nm, 25 msec, test flashes, presented either simultaneously or separated by a 50 msec delay. Krauskopf found probability summation for simultaneous presentation, and found cancellative interactions for delayed presentations. These results show that there must be some convergence between test signals from the α- and γ-cones, even for brief-duration test signals. It is consistent with our results to suppose that the brief-duration pathway used by threshold signals from the γ-cones also receives signals from the other cone classes, but that these signals cause no steady-state adaptation of the pathway.

Temporal integration

Krauskopf and Mollon (1971) report increment-threshold curves measured with brief (10 msec) and long (200 msec) test flashes. Their report includes measurements with several test wavelengths. Of particular interest here are their observations with a 650 nm test flash. From increment-threshold curves they estimate the changes in integration time upon two background fields (500 nm and 600 nm). Their Fig. 4 summarizes their findings: the temporal integration period becomes shorter as background radiance grows. It does so in the same way for both wavelengths.

Our results do not contradict those measurements. They add the information, however, that the temporal integration for long-wavelength test lights does not change in the same fashion for all field wavelengths. This contradicts their conclusion that temporal integration is principally determined at a "stage in the visual system before interactions between chromatic mechanisms (Krauskopf and Mollon, 1971, p. 611)." For example, one can deduce from the increment-threshold measurements with the 10 msec flash in the previous paper, and the measurements with the 200 msec flash we report in this paper, that the critical duration on a 650 nm field becomes much shorter than the critical duration on a field near 580 nm or one near 430 nm, as the intensity of the field increases.

Related theoretical work

The outcome of the various test-mixture experiments called for a modification of Stiles' simple theory of independent mechanisms. Boynton *et al.* (1964) and Ikeda and Boynton (1962) presented various alternative conceptions. In Boynton *et al.* (1964) there is a tentative model put forth that rests upon four mechanisms and their interactions. This model was not offerred as a complete account, but only in a suggestive way.

Ikeda and Boynton (1962) suggested that the various mechanisms might have different integration times. Were this true, detection of brief- and long-duration test flashes might be mediated by different pathways, even though the test wavelength and the adapting conditions remained unchanged. Interactions for long-duration tests, and the absence of such interactions for short-duration tests, were explained by the different nature of these two pathways. The similarity of this notion and the present, two pathway model, is apparent. The present model also supposes the existence of two pathways with different integration times, thus paralleling Ikeda and Boynton's (1962) suggestion.

Finally, we add that Boynton *et al.* (1964) foresaw the possibility of models along the lines we are suggesting. In their concluding section they remark that as an alternative to the four-mechanism model they had described a few pages earlier, there might instead be "a sensitivity function mediated at a second stage in the visual system, reflecting an interaction between the outputs of the R- and G-receptors (Boynton *et al.*, 1964, p. 117)." This is the direction we have taken.

Ingling and Tsou (1977) propose an explanation for the spectral sensitivity of the π_5 mechanism. Their suggestion is based upon a model intended to provide "a simple, quantitative representation of those discrimination functions which include wavelength as a significant variable (Ingling and Tsou, 1977, p. 1075)." The Ingling–Tsou model proposes that the three cone classes initiate signals that are recombined in a general opponent fashion. All signals emerging from the second zone are then pooled at a single detection site. The signals from the second zone are pooled via a (non-linear) Minkowski metric summation, with exponent two. It is this non-linear combination of cone signals which they suggest controls the state of adaptation of the detection pathway. A similar function, but with slightly modified spectral sensitivity curve, would apply to detection of high frequency—and presumably 10 msec—increment-threshold data. Ingling and Tsou do not attempt to explain the empiricial properties of the relevant increment-threshold curves (e.g. integration time at increment threshold). Rather, their main goal seems to be to provide a fit to the π_5 spectral sensitivity function. However, we now know that π_5 can be fit with considerable precision by a linear combination of the Stiles and Burch (1955) small-field color matching functions (Pugh and Sigel, 1978). Therefore, the good fit they obtain with a non-linear combination rule cannot provide compelling support for their theory. Furthermore—as we point out in the previous paper (Wandell and Pugh, 1980)—no model postulating a nonlinear combination of cone quantum catches as the variable controlling adaptation can be consistent with the field-additivity we have reported for a 10 msec test flash.

Pugh and Mollon (1979) have proposed a comprehensive two-site, one-pathway model to explain the short-wavelength (π_1 and π_3) mechanisms. The first site (α-receptors) is Univariant while the second site is opponent (blue–yellow). Both sites adapt. The two detection pathway model we suggest contains "red/green" analogue to the Pugh/Mollon model in its two-site pathway. The 10 msec test flash results required that we modify that basic model by appending the one-site pathway, with its shorter integration time.

The present one detection-pathway model, unlike the Pugh–Mollon short-wavelength model, posits no sensitivity loss to brief duration test signals at the second site. Indeed, the differences between the 10 msec and 200 msec test flash data make such an assumption impossible for a one-pathway model. Were there such second-site attenuation of all test signals due to the field, both long- and short-duration test flashes would be subject to that change. Therefore, thresholds for neither could satisfy the field quantum-catch hypothesis. Here, we have replaced the Pugh–Mollon attenuation mechanism (which is analogous to the introduction of a neutral density filter) by a different mechanism that acts only by varying the temporal properties of the detection pathway. Thus, threshold elevation is effected by quite a different second-site mechanism in the one detection-pathway model presented here from the process which effects second-site threshold elevation in the Pugh–Mollon short-wavelength model.

CONCLUSIONS

Both in Stiles' work as well as the treatments by Boynton and Ikeda, the mechanism construct is given a special status: It is the primitive, undefined quantity. Their models of detection are founded upon the ability to empirically identify these mechanisms. The strength of that approach derived from the power of the Displacement Laws that served to define mechanisms. Failures of the Displacement Laws brought forth new mechanisms. The subsequent failures of test additivity created a need for positing interactions among the mechanisms.

In these papers we have attempted to directly analyze the mechanism construct. Special status is removed from the term mechanism and placed instead upon the term "class of cones." On this revised view it is natural to test the hypothesis that within a Stiles mechanism adaptation is controlled by a single class of cone; that is, the field quantum-catch hypothesis. Rejections of the hypothesis do not bring forth new primitives, but rather new relations among the fixed set of three primitives.

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Note added in proof—C. F. Stromeyer III has pointed out to us that in 1975 he carried out field-additivity experiments similar to those reported here in Figs 4 and 5.

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