Vision Research Vol. 19, pp. 435 to 440
Pergamon Press Ltd 1979. Printed in Great Britain

POST-RECEPTORAL ADAPTATION

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INTRODUCTION

In the dappled scenes of the real world, visual detection often depends upon hue, that is, upon the relative rates of isomerisation in different classes of cone. When this is the case, special rules govern our sensitivity. Thus King-Smith and Carden (1976) review evidence that space and time constants are larger when detection depends on chromatically opponent processes. In the present paper we concentrate on the blue-sensitive mechanism, but the phenomena discussed should not be seen merely as adaptational anomalies of that mechanism; rather it increasingly appears that the psychophysically-defined blue mechanism may reveal general properties of chromatically opponent channels, perhaps because signals originating in the short-wavelength receptors are transmitted only by such channels (Mollon and Krauskopf, 1973). We first assemble evidence that psychophysical sensitivity to signals originating in the short-wavelength receptors depends not only on photons absorbed by those receptors but also on an unidentified long-wavelength signal.

SUMMARY OF EVIDENCE THAT A LONG-WAVELENGTH SIGNAL CONTROLS THE SENSITIVITY OF THE BLUE MECHANISM

(1) *The long-wavelength lobe of π_1*

Fundamental to the question is the observation by Stiles (1953) that the increment threshold function for violet flashes on yellow, orange or red fields has two distinct branches (Fig. 1) which move relative to one another along the abscissa as the field wavelength, μ, increases above 560 nm. In his middle period, Stiles attributed the two branches to distinct cone mechanisms, which he called π_1 and π_3. (A further shallow branch, π_2, was seen for some observers at low field intensities.) To say the branches move independently along the abscissa is to say they differ in field sensitivity (this is represented graphically in Fig. 1): π_1 has a prominent long-wavelength lobe that is absent in the case of π_3.

De Vries (1948) suggested that the long-wavelength lobe of π_1 represented interference from red- and green-sensitive receptors. The proposal was recurrent (e.g. Stiles, 1959; Brindley, 1960; Mollon and Polden, 1975, 1976; Pugh, 1976). In support of the hypothesis it is sometimes said that the lobe is uncharacteristic of known visual pigments, but this is hardly a valid argument, since the field sensitivity of π_1 at 575 nm is ~ 2.7 log units below its sensitivity at 440 nm and no direct measurements have been published for any visual pigment at wavelengths at which its sensitivity is less than 1% of its sensitivity at λ_{max}. However, we may note that the long-wavelength lobe was absent in a blue cone monochromat whose test sensitivity at long wavelengths was measured against a $10^{3.3}$ td, 530 nm field by Daw and Enoch (1973) (their Fig. 3).

(2) *Variability in π_1 sensitivity*

In a population of 20 observers, Stiles (1946) found that the range of log field sensitivity of π_1 at long wavelengths was almost twice the range of test sensitivity at short wavelengths. Furthermore, there was no correlation at all between the sensitivities of π_1 at long and short wavelengths.

(3) *Non-additivity of fields*

Pugh (1976) has shown that short- and long-wavelength fields are super-additive in their adaptive effects on π_1.

(4) *Differences in time constants of adaptation*

When fields of varying μ are used to raise the threshold of π_1 by a fixed amount, the light adaptation time (time to reach equilibrium) increases from a low value of < 15 sec for $\mu < 500$ nm to a value of ~ 60 sec for $\mu > 600$ nm (Stiles, 1949b). Similarly, dark adaptation is more rapid after extinction of a short-wavelength adapting field than after adaptation to a long-wavelength field that produced the same change in sensitivity when present (Augenstein and Pugh, 1977).

These and other adaptational anomalies are discussed in detail by Pugh and Mollon (1979).

NATURE OF INTERACTION

Given this evidence that the sensitivity of the blue mechanism is in part controlled by a long-wavelength signal, what exactly is the nature of the interaction and what is the source of the long-wavelength signal? That the interaction is not merely inhibitory is demonstrated by the phenomenon of "negative masking" (Mollon and Polden, 1977b; Polden and Mollon, 1979): the threshold for a violet test flash may be substantially lower on a combination of blue and yellow fields than it is on the blue field alone. Pugh and Mollon (1979) propose a detailed model of the blue mechanism in which signals originating in the short-wavelength receptors are subject to attenuation at two successive sites: sensitivity at the distal site depends only on the rate of isomerisations in the blue cones themselves; sensitivity at the second, opponent, site depends on the balance of signals of opposite sign from long- and short-wavelength receptors. A crucial assumption is that the sensitivity of the

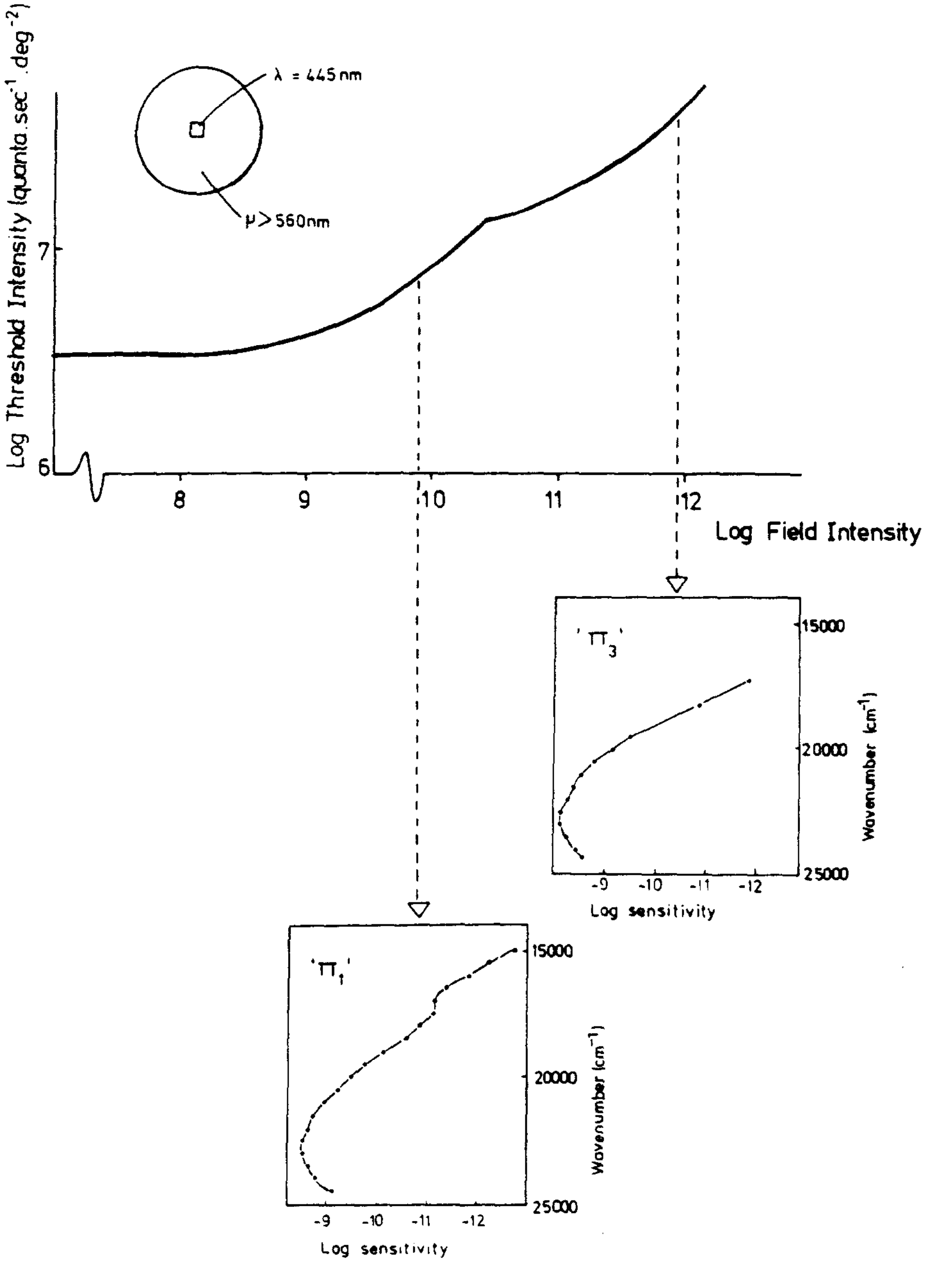

Fig. 1. A schematic diagram to illustrate the empirical grounds for distinguishing the π_1 and π_3 mechanisms of W. S. Stiles. The upper panel shows the increment-threshold function for violet flashes (of wavelength λ) on a steady long-wavelength field (of wavelength μ). The standard arrangement of Stiles' stimuli is shown (inset, top left). The positions of the two branches have been reconstructed from the sensitivities tabulated by Stiles (1978; Table B, p. 18). As μ is reduced towards 560 nm, the upper branch (π_3) shifts to the left more rapidly than does the lower branch (π_1) and thus at shorter wavelengths the inflexion is not apparent. The position of a given branch relative to the abscissa directly yields for any value of μ the field sensitivity at that wavelength. (Field sensitivity is defined as the reciprocal of the log field intensity required to produce a criterion change in threshold.) Thus the two spectral sensitivities plotted below represent (though not to scale) the lateral shifts of the two branches as μ varies. In the original experiments an auxiliary field was present when the primary field was of short wavelength (see Stiles, 1978, pp. 19–20).

opponent site is maximal when the channel is near the centre of its response range; sensitivity is reduced when the channel is polarized (by, say, a saturated yellow field or by a saturated blue field). Further evidence for such a position has been provided very recently by Stromeyer *et al.* (1978).

The origin of the long-wavelength signal remains to be established. Does it originate in a single class of cones? Or does it represent some combination of signals from the P535 and P565 cones? If so, what kind of combination?

We have made two experimental approaches to the question of the origin of the long-wavelength signal. One approach exploits the phenomenon of "negative masking" (described above) and results will be presented elsewhere (Polden and Mollon, 1979). The other, which we report here, exploits the remarkable loss of sensitivity of the blue mechanism that accompanies the offset of a long-wavelength field. This phenomenon, described by Stiles (1949a), was termed "transient tritanopia" by Mollon and Polden (1975).

Figure 2 shows previously unpublished measurements of transient tritanopia for three different td values of a yellow adapting field. The field (defined by an Ilford 626 spectral filter) had a peak wavelength of 575 nm and a bandwidth of 35 nm. The 445 nm test flash subtended 1° and was delivered to the centre of the fovea; its duration was 18 msec and it was presented at various delays after an interruption of the yellow field. Within a block of presentations the delay was fixed. Other experimental conditions were as described by Mollon and Polden (1977a). For each field value the horizontal broken line represents the threshold in the steady state, when the yellow field is actually present. In each case, the threshold rises as soon as the field is turned off and 2.5 sec later has not recovered the value that obtained when the field was present. The model of Pugh and Mollon (1979) accounts for transient tritanopia by supposing that a restoring force with a long time constant acts to reduce the polarisation of the opponent site. The restoring force, built up slowly during adaptation to the long-wavelength field, continues to act for some time after the field has been removed and thus produces a polarisation of the opponent site in the direction opposite to that produced by the adapting field.

TRANSIENT TRITANOPIA USED TO EXAMINE THE SOURCE OF LONG-WAVELENGTH SIGNAL

For our present purpose, a crucial property of transient tritanopia is that it can be obtained without

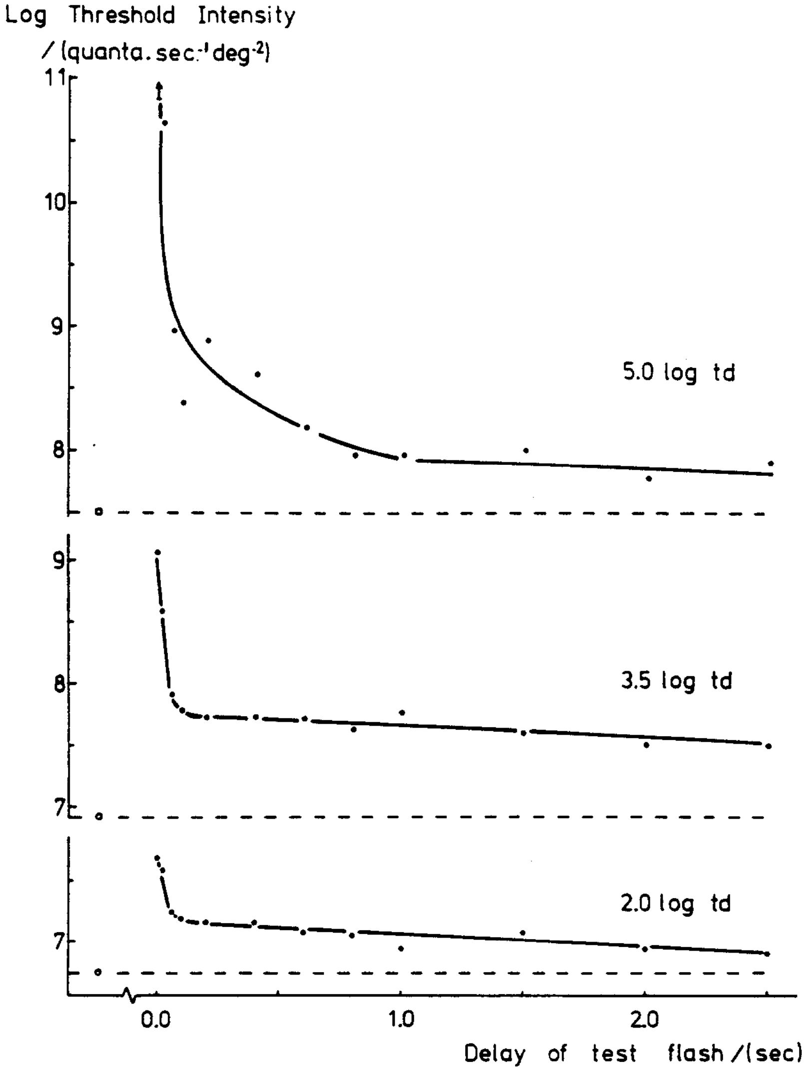

Fig. 2. Illustrative measurements of "transient tritanopia" following the offset of a yellow field. The td values of the fields were 10^2 (lower panel), $10^{3.5}$ (middle panel), 10^5 (upper panel). In each case the horizontal broken line represents the value of the threshold on the steady yellow field. Observer: PGP.

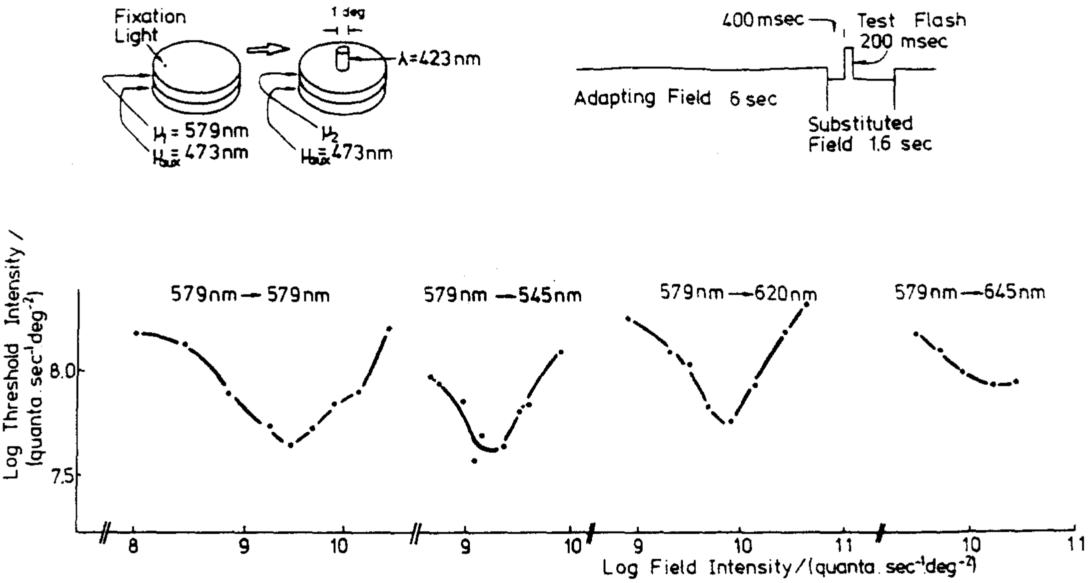

Fig. 3. Above: the spatial (left) and temporal (right) arrangements for the field-substitution experiments. Below: the threshold following the transition as a function of the intensity of the substituted field. Results are shown separately for 4 values of μ_2. Observer: PGP.

turning off the long-wavelength field: a small decrement in the field is enough to elevate the threshold of the blue mechanism (Mollon and Polden, 1977a, Experiment 5). In the present experiments, we presented violet test flashes 400 msec after the transition between a fixed yellow field and a second long-wavelength field of a different wavelength. If the long-wavelength signal originates in a single class of cones that obey what Rushton (1972) has called the Principle of Univariance, then there ought to be an intensity of the substituted field at which the transition is silent, at which, in other words, no change occurs in the long-wavelength signal. At this value of the field (the "isolept" in the terminology of Rushton, Powell and White, 1973) there should be no loss of sensitivity following the transition. If the isolept is established for substituted fields of several wavelengths, we obtain the action spectrum of the long-wavelength signal. (For an introductory exegesis of the silent-substitution method, see Mollon, 1979.)

The spatial and temporal arrangement of the stimuli is shown at the top of Fig. 3. A 579 nm field was present for 6 sec and was then interrupted for 1.5 sec by the substituted field (of wavelength μ_2). 400 msec after the transition, a 200 msec violet ($\lambda = 420$ nm) test flash was presented 2.5° from the fixation point. Between interruptions of the yellow field the intensity of the test flash was adjusted under computer control according to a random double-staircase procedure (Cornsweet, 1962). Each threshold estimate was based on 50 trials and measurements were completed at one intensity of the substituted field before we proceeded, in ascending order, to the next. Four minutes of light adaptation were allowed to each new field condition. The yellow (579 nm) field had a fixed intensity of $10^{9.62}$ quanta.sec^{-1}.deg^{-2}; its bandwidth at half-height, measured *in situ*, was 12 nm. Bandwidths of the substituted fields were in the range 12–15 nm.

Concerned that our long-wavelength fields should not directly affect the sensitivity of the blue cones, we introduced a steady blue auxiliary field ($\mu_{aux} = 473$ nm) of $10^{8.31}$ quanta.sec^{-1}.deg^{-2}, which remained present, and unchanged, throughout the experiment. The primary purpose of this auxiliary field was to maintain the blue-sensitive receptors in a moderate state of adaptation, so that we were confident that long-wavelength lights in the vicinity of the isolept could not directly affect the sensitivity of these receptors. If we assume that the blue-sensitive receptors have the spectral sensitivity of π_3, we can calculate that the addition of the 579 nm field of $10^{9.62}$ quanta.sec^{-1}.deg^{-2} would change by less than 1% the rate of absorptions in the blue receptors. Fields of similar intensity and longer wavelengths would have even less effect. A second purpose of the 473 nm auxiliary field was the more conventional one of suppressing other receptor mechanisms. Ancillary measurements of test sensitivity showed that our target and field parameters isolated the blue mechanism even when only the 473 nm field was present; the addition of the long-wavelength fields could only improve this isolation.

Other details of apparatus, experimental conditions and calibration procedures were as described by Mollon and Polden (1977a).

Results are given in Fig. 3 for a number of values of μ_2. The leftmost data are for a control condition in which we substituted one yellow field for another of the same peak wavelength and of similar bandwidth. The ordinate represents the log threshold intensity for the violet test flash; the abscissa represents the intensity of the substituted field. The function shows a well-defined minimum close to the abscissal value at which the substituted field has the same measured intensity as the first yellow field and at which the substitution should be silent. The elevated

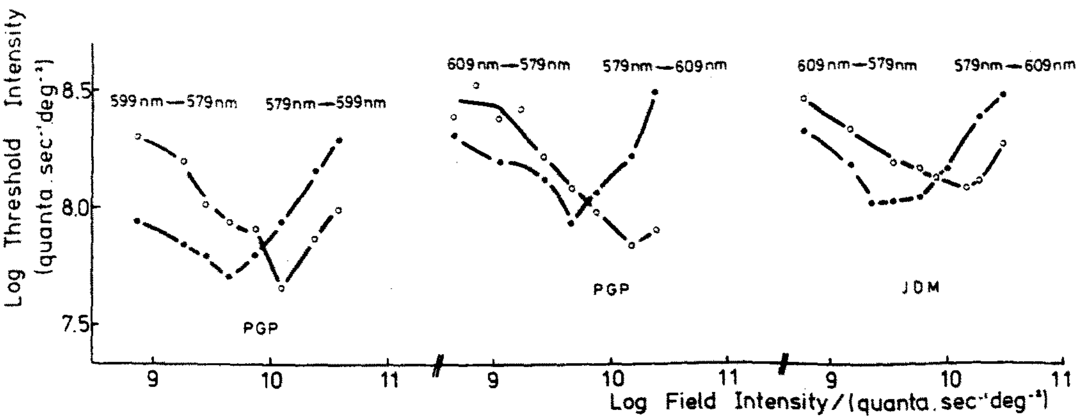

Fig. 4. Results for transitions from a fixed 579 nm field to a variable long-wavelength field (solid points) and from a variable field to the fixed 579 nm field (open points). In both cases it is the intensity of the variable field (of wavelength μ_2) that is plotted on the abscissa. Observers as indicated in figure.

data-points to the left represent transient tritanopia, since here the substituted field is weaker than the adapting field. The elevated points to the right demonstrate (perhaps for the first time) that relatively small *increments* of a long-wavelength field can significantly disturb the sensitivity of the psychophysically-defined blue mechanism under conditions where the change in the rate of isomerisations in the blue cones themselves is probably negligible.

The remaining data of Fig. 3 are for cases where the substituted field has a wavelength different from that of the primary yellow field. In each case there is an intensity of the substituted field at which the threshold is brought to a minimum. By plotting the reciprocal of this intensity against μ_2, we derived from preliminary measurements of this kind an action spectrum that was roughly similar to that of π_5 (Stiles, 1978; Table B, p. 18). Functions similar to those of Fig. 3 were also obtained when the transition was from 579 nm to shorter wavelengths (μ_2 = 521, 545, 560 nm), although in these cases we can be less certain that the substituted field does not disturb the adaptive state of the short-wavelength receptors themselves.

Thus far the method promises well. However, a further control recommends itself: would we derive the same value for the isolept when the transition is from the variable long-wavelength field to the fixed yellow field? In Fig. 4 the solid points correspond to thresholds measured (as before) 400 msec after transition from the 579 nm field to other fields of variable intensity. As before, the functions show clear minima. The open circles represent thresholds measured 400 msec after the transition *from* the variable field to the fixed 579 nm field. It is still the intensity of the variable field that is plotted on the abscissa. (So now the points to the right will represent transient tritanopia, since here the substituted field is the weaker; those to the left will represent the case where the substituted field is the stronger.) The function still passes through a minimum but the position of the minimum has shifted to the right: the variable field now has to be more intense if disturbance of the sensitivity of the blue mechanism is to be minimised. This proved to be the general rule: if substitution was from a longer wavelength to the fixed yellow field, then the variable field had to be more intense than when substitution was in the opposite direction. Such a result would be expected if more than one class of photoreceptor contributed to the putative long-wavelength signal. Even if two fields produced the same total signal in the steady state, at the moment of transition there would be increments and decrements in the rates of isomerisation in individual classes of receptor; the resulting transients would very probably lead to a change in the net total signal.

We conclude that the long-wavelength signal that controls the sensitivity of the psychophysically-defined blue mechanism does not originate in a single class of cones that obeys the Principle of Univariance. Our results are consistent with a signal that originates in both the P535 and the P565 cones.

Acknowledgement—This work was supported by MRC Grant No. G976/139/N.

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