Colour illusion and evidence for interaction between cone mechanisms

IF one adapts the eye for several minutes to a yellow field of 700 cd m^{-2} and then looks at a small blue target, the latter appears green for 2 or 3 s. Target and field can be provided conveniently by Wratten 12 and Illford 622 filters respectively. But the effect fails not only if the adapting field is too dim, but also if it is too bright.

This illusion may be the suprathreshold counterpart of a remarkable, but neglected, observation made in 1949 by Stiles¹: when a long-wavelength adapting field was turned off, the detection threshold for the blue-sensitive mechanism of the eye increased. We have re-examined this paradoxical loss of sensitivity to determine whether there is evidence here for an inhibitory interaction between different classes of receptor.

The existence of the phenomenon is in doubt: Das' reported results similar to those of Stiles, but there is no evidence for the anomaly in the results given by Du Croz and Rushton³. We therefore began by measuring the threshold for violet target flashes in the first seconds after a long-wavelength field had been extinguished. A yellow (580 nm) adapting field, which subtended a visual angle of 6.5°, was presented in Maxwellian view. For 3 s every 18 s the field was interrupted by a dark interval. At a particular delay after each extinction of the field a 445-nm target flash was introduced. The latter lasted 15 ms, subtended a visual angle of 1° and was delivered to the centre of a fixation array consisting of four white points arranged in a diamond. The test flash and adapting field were concentric. The experiment was under computer control and the threshold for detecting the flash on 50% of trials was measured by a double staircase procedure⁴. No data were gathered until the field had been cycling for 4 min. A block of 50 trials was devoted to the measurement of each threshold and all stimuli within a block were presented at the same delay.



Fig. 1 Log threshold intensity for a violet test flash at various delays after the offset of a yellow field. The intensity of the field was $-1.4 \log \text{ erg s}^{-1} \deg^{-2}$. The broken line shows the threshold when the field is present. Observer, P.G.P.



Fig. 2 Solid circles show the threshold for a 445-nm target at various delays after the transition between 580-nm and 525-nm fields. The two fields were adjusted to raise the threshold by the same amount in the steady state: the two open circles, each based on ten determinations, show the empirical thresholds obtained in the steady state. Observer, J.D.M.

Typical results are shown in Fig. 1 where the log threshold for the 445-nm test flash is plotted at various delays after the yellow field has been turned off. The broken line shows the threshold for the same target when the field is present. Clearly the threshold does not follow a normal dark adaptation curve, but rises immediately after the field has been turned off and after 2.5 s has not yet regained the value it had when the adapting field was present. A target that is readily visible when the background is present becomes invisible when the field is extinguished.

The suppression of the blue-sensitive mechanism is even greater than at first appears, for we found that the mechanism responsible for detection of violet flashes after the field has been extinguished has the spectral sensitivity of π_4 , Stiles' green-sensitive mechanism. The threshold for the blue-sensitive mechanism must lie above the solid points in Fig. 1. Our results so far suggest that the suppression is confined to the blue-sensitive mechanism. Therefore we provisionally call the phenomenon transient tritanopia and suggest that the suprathreshold illusion arises from the change in the relative sensitivity of green and blue cones to short-wavelength light.

In a second experiment a 580-nm field was turned off as before but was replaced immediately by a dimmer green field of 525 nm that had been empirically adjusted to have the same adaptive effect on the blue mechanism in the steady state. The threshold for 445-nm flashes was then measured at various delays after the transition between the two fields. When considering this experiment it is useful to refer to the principle of univariance'. A single retinal cone, or a single class of cones, is colour blind. The input to a particular cone can vary in both wavelength and intensity, but once a quantum has been absorbed all information about its wavelength is lost. In principle, therefore, it is possible to adjust the intensities of two adapting fields until they are indistinguishable to the blue cones. According to the classical model of Stiles the adaptive states of the cone mechanisms are independent: that is, the sensitivity of an individual mechanism depends only on the number of quanta absorbed from an adapting field by that particular mechanism; and thus two adapting fields

that raise the threshold equally for the short-wavelength target must be producing an equal quantum catch in the blue cones. If the sensitivities of the mechanisms are indeed independent in the steady state and if they remain independent in transitional states then transient tritanopia must be a private matter among the blue cones and there should be no disturbance of sensitivity when we switch from the yellow to the green field. If, however, the threshold still rises after the transition, then there must be an interaction between mechanisms: the interaction may occur in the steady state, so that fields that raise the 445-nm threshold equally do not produce equal absorption in the blue cones (such a suggestion has been made, see for example, ref. 6); alternatively or in addition, a recovering long-wavelength mechanism may inhibit, or otherwise suppress, the blue cones during early dark adaptation, for the number of quanta absorbed by the long-wavelength mechanisms will fall as the transition is made between yellow and green fields that have the same adaptive effect on the blue cones.

The threshold for 445-nm flashes was measured on a steady yellow field of $-1.36 \log \text{erg s}^{-1} \text{degree}^{-2}$ and a steady green field was then adjusted until it raised the threshold for the violet flash to the same level. In a final check the thresholds on the two steady adapting fields were repeatedly measured in an alternating sequence. The two mean thresholds, each based on ten determinations, were within 0.01 log₁₀ units of each other and were approximately 0.5 log units above the value for the dark-adapted eye. Auxiliary measurements of increment threshold functions showed that detection was mediated by the blue-sensitive receptor mechanism that was termed π_1 by Stiles⁷. Figure 2 shows that transient tritanopia still occurs when the transition is made between two fields that have the same adaptive effect in the steady state: for several seconds after the substitution of the green field the threshold remains almost 1.0 \log_{10} units above its value on either of the steady fields.

We conclude that the blue-sensitive receptors are subject to inhibition from a mechanism with a different spectral sensitivity. Whether the interaction is confined to transitional conditions remains to be determined. Stiles distinguished three short-wavelength mechanisms, π_1 , π_2 , and π_3 : it is possible that we see in transient tritanopia an exaggeration of an inhibition that marks the difference between these mechanisms in the steady state.

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