THE CHROMATIC ANTAGONISMS OF OPPONENT PROCESS THEORY ARE NOT THE SAME AS THOSE REVEALED IN STUDIES OF DETECTION AND DISCRIMINATION

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ABSTRACT

Wavelength discrimination for 1000-Td yellow lights was measured as a function of the wavelength of a 10-Td pre-adaptation field. Blue and red pre-adaptation fields impaired discrimination more than did violet or green fields. Our fields appear to act at a site that differences the long- and middle-wave cone signals, but this does not correspond to the 'red-green' process of Opponent Colours Theory.

INTRODUCTION

The concept of colour opponency has become commonplace in colour science; but it is prudent to distinguish at least three different types of 'opponent process':

1. *The opponent processes classically postulated by Hering.* The evidence for these processes lies in the phenomenological antagonism of red and green and of yellow and blue: we experience, for example, reddish blues and greenish blues but never yellowish blues (Hurvich and Jameson, 1957).

2. *The chromatically antagonistic processes identified in electrophysiological recordings from single units in the primate visual pathway* (De Valois, Abramov and Jacobs, 1966; Gouras, 1984; De Monasterio, 1984; Derrington, Krauskopf and Lennie, 1984). A chromatically opponent cell behaves as if it draws an input of one sign from one or more classes of cone and input of opposite sign from other types of cone. At early stages of the macaque visual system, there appear to be two common types of chromatically opponent cell — those that draw opposed inputs from the long- and middle-wave cones, and those that are excited by the short-wave cones and are inhibited by signals from some combination of the long- and middle-wave cones.

3. *The chromatic antagonisms revealed psychophysically in measurements of detection or discrimination.* Most of the evidence for these antagonisms has been published within the last two decades. It includes (a) the inhibitory interactions that occur between test flashes of different

wavelength (e.g. Boynton, Ikeda and Stiles, 1964; Guth, 1967; Krauskopf, 1974; Kranda and King-Smith, 1979; Thornton and Pugh, 1983; Stromeyer, Cole and Kronauer, 1985); (b) combinative euchromatopsia, the reduction of increment threshold that may occur when adapting fields of different wavelength are combined (e.g. Mollon and Polden, 1977a; Sternheim, Stromeyer and Spillmann, 1978; Polden and Mollon, 1980); (c) transient tritanopia and its analogues (the paradoxical losses of sensitivity to chromatic targets that occur when a coloured field is extinguished; see e.g. Hartridge, 1948; Mollon and Polden 1975; Augenstein and Pugh 1977; Pugh and Mollon, 1979; Reeves, 1981); and (d) selective losses of chromatic discrimination after adaptation to chromatic modulation (Krauskopf, Williams and Heeley, 1982).

Although textbooks commonly take Hering to have been vindicated by modern physiology, some electrophysiologists and some psychologists have cautioned us against equating opponent processes of types (1) and (2). First, the inhibitory input to a colour-opponent ganglion cell may serve to restrict the spectral range of the cell's excitatory response rather than to lend it two modes of response of the kind postulated by Hering (Gouras, 1971). Thus Livingstone and Hubel (1984) write: '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'. Secondly, the activity of a chromatically opponent cell in the primate retina does not consistently indicate the presence of light of a particular spectral band: a 'red-on centre, green-off surround' cell may respond only to long-wave light when the stimulus is photopic and of low spatial frequency, but will respond to all wavelengths (and to white light) when the stimulus is scotopic or of high spatial frequency (Hurvich and Jameson, 1970).

A central issue in contemporary psychophysics is the relationship between opponent processes of types (1) and (3). Pugh and his associates have explicitly identified the antagonisms seen in threshold experiments with the antagonisms of classical Opponent Process Theory (Pugh and Larimer, 1980; Thornton and Pugh, 1983). Others have doubted the identification (Polden and Mollon, 1980; Krauskopf et al., 1982). The present experiment is directed to this issue.

We measured the observer's ability to discriminate wavelength following pre-adaptation to coloured fields. Our experiment is descended from experiments on 'transient protanopia', but instead of measuring the threshold for detecting long-wave flashes (Mollon and Polden, 1977b; Reeves, 1981), or that for detecting chromatic flicker (Reeves, 1983), we have directly measured wavelength discrimination. Since theoretical interpretations of transient tritanopia (and the other 'dynamic dyschromatopsias') treat the loss of sensitivity as a property of chromatic channels, it seems appropriate to measure colour discrimination directly. Our experiments have thus come to resemble in some degree those of another tradition, in which wavelength discrimination is measured in the continuous presence of annular or superposed adapting fields (Hurvich and Jameson-Hurvich, 1961; Pokorny and Smith, 1970).

In the experiments reported here, we varied the wavelength of the pre-adaptation field but we always measured the observer's wavelength discrimination in the same spectral region, close to the wavelength that appeared unique yellow to him. According to Opponent Process Theory, wavelength discrimination in this region is mediated by the red-green opponent process (Jameson, Hurvich and Varner, 1979). We might suppose that this discrimination would be left undisturbed by pre-adaptation to two wavelengths, unique yellow and unique blue. For these two colours, being neither reddish nor greenish, are the ones, *ex hypothesi*, that leave in equilibrium the red-green process.

But consider a retinal channel that receives antagonistic input from the long- and middle-wave cones. Such a channel will be maximally polarised on the one hand by deep red light, and on the other by blue light of approximately 460 nm. It may seem counterintuitive that it is blue rather than green light that maximally polarises this channel; but very strong evidence for this proposition is given by the colour-matching functions of tritanopes, who are believed to retain the long- and middle-wave cones of the normal observer: in a matching experiment with two primary lights, the tritanope needs the greatest ratio of short- to long-wave primaries not in the green but in the blue spectral region near 460 nm (Wright, 1952; Fischer, Bouman and Ten Doesschate, 1952; Sperling, 1960). The same is true for normal observers under tritan conditions of viewing (Willmer and Wright, 1945). In the case of macaque monkeys (which have receptoral sensitivities similar to those of man), direct electrophysiological recording from isolated cones has shown that the maximum ratio of middle- to long-wave cone sensitivity occurs near 460 nm (Nunn, 1985).

Suppose then that wavelength discrimination in the yellow spectral region depends on a (tritanopic) channel that differences the signals of the middle- and long-wave cones and is unaffected by the short-wave cones — a channel in fact that resembles the most common type of colour-opponent cell found in the macaque retina (Gouras, 1984). We might expect that such a channel would be maximally disturbed by pre-adaptation to red light or to blue light.

In summary then, the effects of short-wave adapting fields are of particular interest for our present purpose, since very different predictions are made, on the one hand, by Opponent Process Theory, and, on the other, by a theory in which discrimination near 580 nm depends on a channel that differences the signals of the middle- and long-wave cones. Previous studies (Hurvich and Jameson-Hurvich, 1961; Pokorny and Smith, 1970; Loomis and Berger, 1979) have not investigated the effects of short-wave adapting fields in a way that would answer our question.

When bright coloured fields are used to produce 'chromatic adaptation', the effect of the field on post-receptoral, opponent sites is confounded with its effect upon the cones themselves. Selective adaptation of particular classes of cone could in itself disturb wavelength discrimination, either because it reduced the available dynamic range of the cones or because the ratio of the signals of two classes of cones became so large or so small that it lay outside the range of ratios that could be efficiently

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differentiated by post-receptoral channels. In the present experiments we wished to produce adaptation at a post-receptoral site while disturbing as little as possible the adaptive state of the receptors. We therefore used coloured adapting fields of only 10 Td, while using discriminanda of 1000 Td.

A second way in which the present experiments depart from custom is in the method used to measure wavelength discrimination: because we were concerned that our experimental results should not be distorted by changes in the observer's criterion, we used a two-alternative temporal forced-choice procedure. Conventionally, a method of adjustment is used in studies of wavelength discrimination, even though forced-choice procedures are almost invariably used for the analogous measurements in auditory psychophysics — and for measurements of colour discrimination by animals. There may be two reasons why the method of adjustment has continued to be used in the study of human wavelength discrimination: (a) whereas acoustic frequency can be rapidly manipulated under computer control, it has been less easy to arrange rapid manipulation of wavelength; and (b) in a forced-choice study of wavelength discrimination the experimenter has to find a way to prevent the observer from using variations in luminosity to solve the task. Difficulty (a) can today be solved by the used of monochromators with integral stepping motors. To deal with difficulty (b) we have imitated the solution devised by auditory psychophysicists (Henning, 1966) and introduced small random variations in radiance.

METHODS

Apparatus and stimuli

Stimuli were presented by a three-channel Maxwellian-view optical system under computer control. Two channels contained high-resolution monochromators (Bentham Instruments M300E) with integral stepping motors allowing steps of 0.05 nm. These channels provided the upper and lower halves of a 2° field (Fig. 1). In the present experiments the upper half-field was varied in wavelength while the lower remained fixed. The luminance of the upper field could be varied in steps of approximately 0.01 $\log_{10}$ unit by means of a neutral density wedge mounted on a stepping motor. The luminance of the fixed, lower field was 1000 Td throughout the experiment, and its wavelength was set to be unique yellow for the individual observer (see below). A third channel, containing a Jobin-Yvon monochromator (model H-10), provided a 6° adapting field of 10 Td and of various wavelengths. Twelve adapting wavelengths were used, ranging from 405 to 650 nm. The adapting wavelengths included unique blue, unique green, and unique yellow, as determined independently for the two observers. We included another theoretically significant wavelength, 458 nm, which is close to the wavelength that should maximally polarise any post-receptoral channel that extracts the ratio of the signals of the

middle-and long-wave receptors; this wavelength was chosen on the basis of tritanopic colour-matching functions (see Introduction). Also of particular theoretical interest is the shortest wavelength used, 405 nm, which is close to the tritanope's short-wave neutral point and thus might be expected to resemble yellow light in its effects on a channel that differences the middle- and long-wave signals.

The bandwidth of the Bentham monochromators was 0.7 nm and that of the Jobin-Yvon monochromator was 8.0 nm. Blocking filters were used in all three channels of the optical system in order to suppress any residual stray light.

Procedure

As a preliminary to the main experiments we determined for each observer three wavelengths that are of theoretical significance in Opponent Colours Theory: unique blue (the blue that appears neither reddish nor greenish), unique green (the green that appears neither bluish nor yellowish), and unique yellow (the yellow that appears neither reddish or greenish). In establishing these wavelengths it is crucial not to selectively adapt the observer by the sequence of presentation of targets (Hurvich, Jameson and Cohen, 1968) or to bias his response set. We therefore used a randomised double-staircase procedure used earlier to measure dichromatic neutral points (Mollon, Bowmaker, Dartnall and Bird, 1984). Isolated flashes subtending 2° and lasting 1 s were presented to the observer's dark-adapted eye by means of the apparatus to be used for the main experiment. The troland value of the flashes was 10. After each flash the observer indicated by means of pushbuttons whether the flash was, say, 'too red' or 'too green' (in, for example, determining unique blue) and the program made sequential adjustments of the wavelength so as to converge on the wavelength that attracted equal numbers of response of the two kinds. The step size of the staircase was 1 nm and the two staircases began 20 nm apart. The experiment was performed iteratively, the starting points being adjusted so as to lie equal distances above and below the previous estimate of the unique hue. The iteration was continued until no further change occurred in the estimate of the unique hue.

In the main experiment the 12 field wavelengths were tested in a random sequence. The experiment was repeated 8 times for each observer, a different sequence of the field wavelengths being used on each repetition. Before each individual threshold determination the observer adapted for 2 min to the steady adapting field. Thereafter a two-alternative forced-choice procedure was used to measure the wavelength-discriminaton threshold during brief occlusions of the adapting field. Fig. 1 illustrates the sequence of events on a given trial. The adapting field was twice occluded for 500 ms, with an interval of 1000 ms between the two occlusions. In each case, a 100-ms presentation of the bipartite target field occurred 200 ms after the offset of the adapting field. On one of the two presentations, chosen at random, the two halves of the field were identical in wavelength, and on the other the upper half-field had a wavelength that was greater
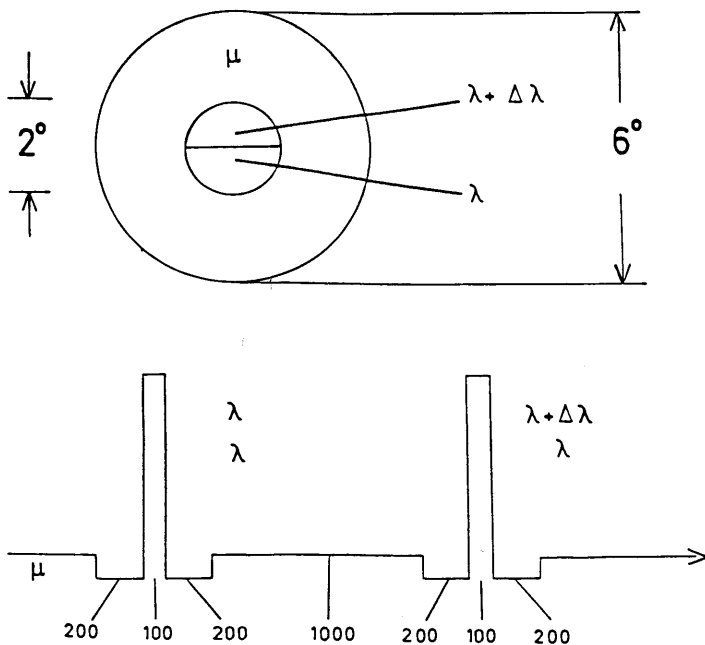
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Fig. 1. Above: The spatial arrangement of the stimuli for measurement of wavelength discrimination by a forced-choice method. The arrangement shown is for a positive presentation, when a difference in wavelength (λ) is present between the two half-fields. On the other presentation of each trial the wavelength is identical for the two half-fields. The wavelength (μ) of the larger, adapting field is varied between experimental runs. Below: The sequence of events on a single trial. Two presentations of the bipartite field occur, each during a brief occlusion of the dim adapting field. On the trial shown, the positive presentation occurred in the second interval. The numbers indicate time intervals in milliseconds.

than the standard by an amount $\Delta\lambda$. The observer was required to indicate by pushbuttons whether the half-fields differed on the first or second presentation. Acoustic signals indicated to the observer whether his response was correct. There was an interval of approximately 5 s between trials. The value of $\Delta\lambda$ was initially 3 nm and it was adjusted by the program so as to track the value that gave 71% correct responses (Moore, Glasberg and Shailer, 1984). As $\Delta\lambda$ became smaller the step-size of the staircase was reduced. The staircase continued for twelve reversals. Fig. 2 illustrates typical staircases for two different field wavelengths. Thresholds were taken as the mean of the last ten reversal points.

To prevent the use of luminosity cues, small mismatches of luminosity were introduced in the upper field. The size and direction of the mismatch was randomised before each presentation of each trial. The variations were centered on the true luminosity match (made at unique yellow by the observer before the experiment began) and the magnitude of the discrepancy was distributed uniformly in the range 0.0 to ± 0.1 log unit.
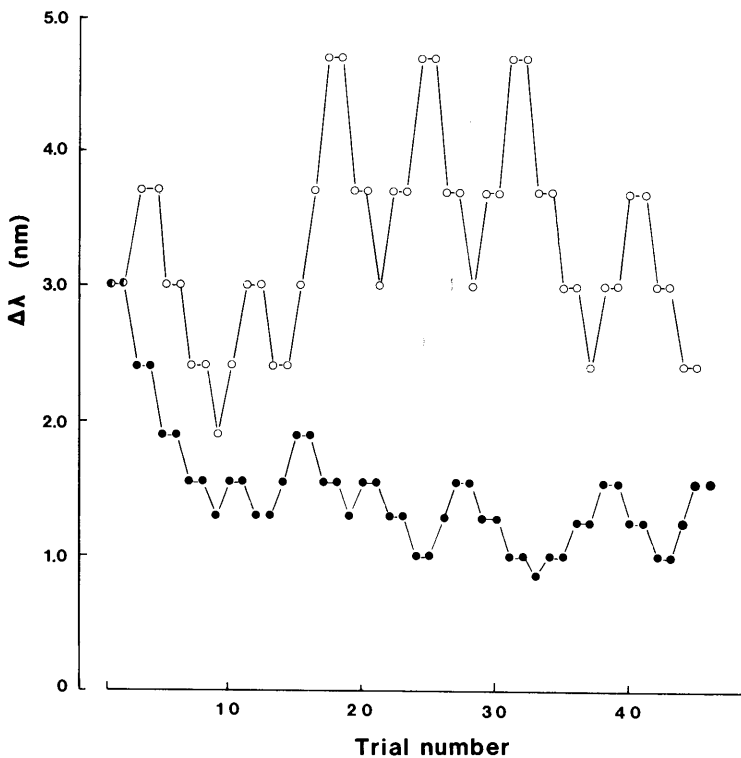
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Fig. 2. Illustrative examples of two staircases, showing how $\Delta\lambda$ is varied to estimate a threshold for wavelength discrimination. The ordinate represents the difference in wavelength between the upper and lower half-fields. The open circles represent data obtained with a 458-nm field; the filled circles represent data obtained with a 405-nm field. Observer: DC. Note the striking difference between these two short-wavelength fields.

The radiances of the fields were checked with a silicon photodiode (PIN 10, United Detector Technology) before each individual threshold determination. The diode had been recently calibrated absolutely and relatively by the National Physical Laboratory. Immediately before the experiment the wavelength scales of the monochromators were calibrated by means of a helium-neon laser. The measured backlash of the Bentham monochromators amounted to six steps of the stepping motor (equivalent to 0.3 nm). Therefore, in moving to any required wavelength our programs always made the final approach from the same direction; we were thus able to reset wavelength to within 0.05 nm.

Observers

The observers were the authors. Both are male and perform normally on the Nagel anomaloscope and the Farnsworth-Munsell 100-hue test.

For observer CR the values of unique yellow, green and blue were 578, 508 and 473 nm respectively; for JDM the values were 570, 504 and 473 nm.

Fig. 3 shows the results of the main experiment for the two observers. The abscissa represents the wavelength of the adapting field and the ordinate represents $\Delta\lambda$ at threshold, as defined above (see Methods).

For both observers discrimination is minimally disturbed by pre-adaptation to lights of a wavelength similar to that of the target. Discrimination is badly disturbed by adapting fields in the blue region of the spectrum. If our discrimination depended on a red-green process of the kind postulated by Opponent Colours Theory, then we should expect that pre-adaptation to unique blue would be not more disturbing than pre-adaptation to yellow. In fact, for both observers, unique blue is more
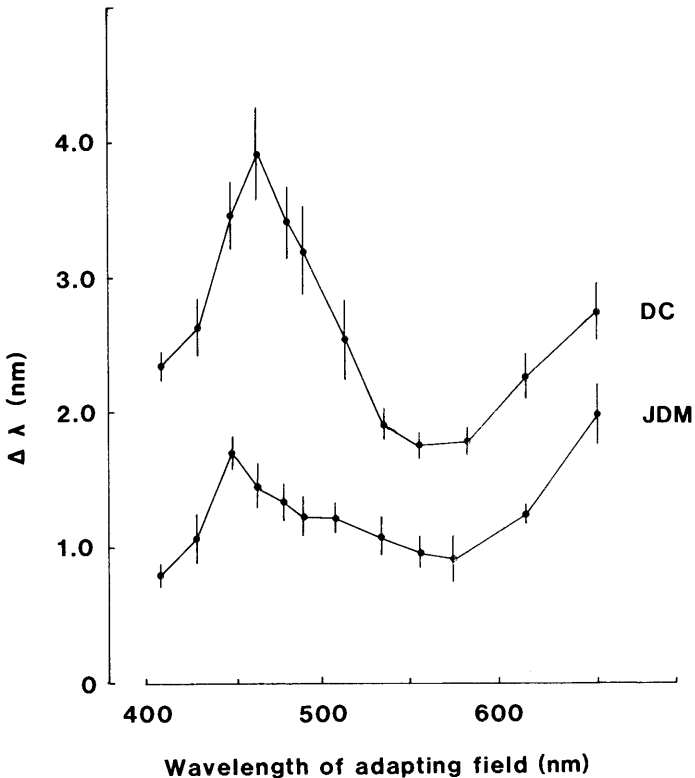

Fig. 3. Wavelength discrimination as a function of the wavelength of a pre-adapting field of 10 Td. The ordinate represents the threshold difference in wavelength. The data for JDM are correctly placed; those for DC have been shifted upwards by 1.0 nm. The error bars represent ± 1 S.E.M.

disturbing than is unique green, and for observer DC it is more disturbing than is a deep red. However, the short-wave maximum of the function does lie in the region we might expect if the observer's discrimination depended upon a (tritan) channel that simply drew opposed inputs from the middle- and long-wave receptors (see Introduction).

Of particular interest is the good discrimination found after adaptation to the 405-nm adapting field. This field appeared very reddish (and very bright) and yet it had much less effect than did a unique blue field. Since the 405-nm field would very strongly stimulate the short-wave cones, our results add to other evidence (Krauskopf et al., 1982) that modulation of the short-wave receptors has little or no effect on discriminations mediated by channels that extract the ratio of long- and middle-wave cone signals.

It is striking that dim blue and dim red fields of only 10 Td can disturb the discrimination of 1000 Td yellow lights. However, this finding is not mysterious in the context of theories that postulate adaptation at chromatically-opponent post-receptoral sites. The polarisation of a 'second-site' depends on the ratio of cone signals, not on their absolute magnitudes. A monochromatic field of only moderate brightness should be as effective as a much stronger one, and indeed may be more effective, since the signals of each cone class are probably compressed functions of radiance and therefore become more similar as the radiance of a monochromatic field is increased.

It begins to appear that the chromatically opponent channels revealed by recent psychophysics (particularly those revealed by studies of dynamic dyschromatopsia) are not the opponent processes of classical Opponent Process Theory. The present results complement those of Krauskopf, Williams and Heeley (1982), who suggested that the 'blue-yellow' process does not correspond to one of the cardinal directions of colour space that they were able to demonstrate by selective chromatic adaptation. Such results do not necessarily challenge Opponent Colours Theory, in so far as it postulates central antagonistic processes to account for phenomenological observations; but the domain of facts explained by that theory may be narrower than once supposed. The detection and discrimination of coloured lights may prove to be limited by processes that more nearly resemble the chromatically opponent interactions revealed in the retina by electrophysiological recording.

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