Dichromats detect colour-camouflaged objects that are not detected by trichromats

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SUMMARY

To explain the surprisingly high frequency of congenital red–green colour blindness, the suggestion has been made that dichromats might be at an advantage in breaking certain kinds of colour camouflage. We have compared the performance of dichromats and normal observers in a task in which texture is camouflaged by colour. The texture elements in a target area differed in either orientation or size from the background elements. In one condition, the texture elements were all of the same colour; in the camouflage condition they were randomly coloured red or green. For trichromats, it proved to be more difficult to detect the target region in the camouflage condition, even though colour was completely irrelevant to the task. Dichromats \((n = 7)\) did not show this effect, and indeed performed better than trichromats in the camouflage condition. We conclude that colour can interfere with segregation based upon texture, and that dichromats are less susceptible to such interference.

1. INTRODUCTION

The advantages of colour vision are obvious to a normal observer who compares a colour photograph of a complex scene with an equivalent black and white photograph. In the achromatic picture, an object may be difficult to discern, either because its luminance is similar to that of the background or because the illumination is casting random shadows, but if such an object differs in chromaticity from its field it will be highly salient in the coloured photograph. The salience of colour is particularly obvious when identifying flowers and fruits, and this may be one factor leading to the evolution of trichromatic colour vision in primates (Mollon 1989). Given the obvious advantages of colour vision, it is surprising to find an incidence of dichromatic vision as high as 2% in the male population (Pokorny \textit{et al.} 1979); such men are completely unable to distinguish reds from greens in the range 550–700 nm, provided the stimulus is relatively small (say, 2° of visual angle). It has therefore been tempting to suppose that dichromats have some compensating advantage in the population.

During the Second World War it was suggested that colour-deficient observers could often penetrate camouflage that deceived the normal observer (Anon 1940; Judd 1943). The idea has been a recurrent one, both with respect to military camouflage (Reit 1979) and with respect to the camouflage of the natural world (Ford 1967; Kalmus 1965; Pickford 1965); indeed, it has been proposed that an advantage of this kind helps maintain the polymorphism of human colour vision (Ford 1967; Adam 1969). Yet the belief in this perceptual superiority seems to be maintained only by anecdotes. Judd's paper (1943) is limited to a masterly analysis of the theoretical possibilities. No experimental study seems to have been published, and one unpublished military study gave negative results (Whittenberg & Collins 1974).

In assessing the issue, a distinction must be made between the 6% of men who are anomalous trichromats and the more severely affected 2% who are dichromats (Judd 1943; Pokorny \textit{et al.} 1979; Nathans \textit{et al.} 1986). If target and background reflect physically different fluxes that match for the normal eye (i.e. are ‘metameric’) they may well look different to the anomalous trichromat, whose retina contains at least one type of receptor that is abnormal in its spectral sensitivity. But this means of penetrating camouflage is not open to the dichromat, whose vision is a reduced form of the normal and who therefore accepts normal matches. Nevertheless, we show experimentally that the dichromat can readily detect boundaries between textured regions under conditions where such boundaries are missed by the normal observer. By offering a rival perceptual organization to the normal eye, random colour variation can impede the pre-attentive segregation of textural boundaries, but dichromats are unaffected by this colour variegation, even when it represents for them a substantial random variation in luminance.

2. METHODS

(a) Apparatus and stimuli

The task set to the subjects was to detect, in a brief (200 ms) presentation, the position of a target area differing in texture from the remainder of the pattern (the back-


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Figure 1. The figure gives a schematic representation of the experimental conditions for investigating the effects of colour camouflage upon textural segregation. The observer's task is to detect the subregion of the pattern in which the elements differ in orientation from the background. In the cases shown, the subregion contains horizontally oriented rectangles, and the background contains vertically oriented rectangles. In the experiment, each element could be one of two different colours: red (open symbols) or green (filled symbols). (a) In the control condition all the elements were of the same colour, either red or green; (b) in the camouflage condition the elements were randomly coloured red or green. The actual stimuli used in the experiment contained $30 \times 30$ and the target area consisted of $7 \times 7$ elements in one quadrant of the stimulus. The observer's task was to detect the quadrant of the stimulus in which the target area lay.

(subject) A schematic representation of the texture segregation task is shown in figure 1. The target area could be in one of the four quadrants, and its position varied randomly over a series of 20 trials until it had occurred five times in each position. Subjects registered their decision by pressing the appropriate one of four buttons, and their overall success was measured by the number of correct responses in a block of 20 trials. All observers completed at least one block of 20 trials in each condition; the majority of subjects completed two blocks in each condition, and two of the authors (A.A. and M.M.) were tested repetitively. The data analysed were each subject's mean scores in each condition averaged over all blocks of trials.

The target subarea of the pattern differed from the rest of the pattern either in orientation or in both size and orientation of the texture elements. In the control condition, all the texture elements were the same colour (figure 1a). In the camouflage condition, the elements were randomly coloured to make a red-green mosaic (figure 1b). The textured subregion is much harder to detect in the colour camouflage condition. In the experiments, the spacing between texture elements was 20 arcmin. The target region contained $7 \times 7$ elements embedded in a $30 \times 30$ array of elements. In the size-orientation discrimination experiment, the target elements were 5 arcmin x 6 arcmin and the background elements 7 arcmin x 6 arcmin. In a third condition, the target elements were alphanumeric characters (upper case 'A's) in a background of 'B's.

Patterns were generated under computer control on a Barco (Model 33) colour monitor, which was viewed from a distance of 1.5 m. Photometric measures of the luminance of the actual pattern element used in the experiment were made with a photodiode and a filter with the transmission characteristics of the CIE photopic luminosity function ($V(\lambda)$) and these measurements were used to equate as nearly as possible the luminance of the red and green elements.

(b) Subjects

The subjects were 16 normal trichromats (ten males and six females), and seven male dichromats (two protanopes and five deuteranopes) screened initially by Ishihara Plates and subsequently by an anomaloscope. The dichromats were able to match yellow to either red or green by adjusting the radiance of the yellow, whereas trichromats required a unique mixture of red and green. The subjects experienced the various conditions of the experiment in a counterbalanced order.

3. RESULTS

The data from the various experiments are summarized in figure 2. All subjects were able to identify the position of the target area in the control condition, but trichromats were considerably impaired in the camouflage condition. Dichromats, however, were minimally affected by the colour camouflage.

Individual data (shown for the size-orientation condition in figure 3) made it quite clear that these effects were very similar in all the subjects tested. The differences between dichromats and trichromats were statistically highly significant according to both parametric and non-parametric tests. Separate analyses of variance of the orientation, letter and size data showed in each case the expected main effects of colour (control against camouflage), subject group (trichromat against dichromat), and a highly significant interaction between the two (orientation, $F(1, 17) = 24.4, p < 0.001$; letters, $F(1, 17) = 13.3, p < 0.002$; size, $F(1, 17) = 30.65, p < 0.0001$). There were no significant differences between males and females. Non-
Figure 2. The figure describes the observers' performance in detecting and reporting the position of the target area in patterns like those in figure 1. The measure of performance is the percentage correct identification of target position over a series of trials in which position varies randomly. The height of each bar represents the mean score over subjects in each condition of the experiment, and the error bar is the standard deviation of the individual scores. Results are shown separately for normal trichromats (obliquely hatched symbols) and dichromats (horizontally hatched symbols), and for three different kinds of discrimination (orientation, size-orientation, and letters). In the 'fixed' condition the texture elements all had the same colour; in the 'var' (variable/camouflaged) condition they were randomly coloured as in figure 1c. The results show that colour camouflage made the target harder to see for trichromats, but not dichromats.

Figure 3. The figure shows individual data from the size-orientation condition described in the previous two figures. Each bar represents the score of an individual subject in the fixed condition (filled black bars), or in the variable (camouflage) condition (unfilled bars). (a) Trichromats, (b) dichromats.

parametric Mann–Whitney U tests on the difference scores for each individual between the control and camouflage condition also revealed significant differences (size-orientation condition: $z = -3.766; p = 0.0002$; the effect was equally significant in the orientation and the letters conditions).

The insensitivity of the protanopes and deuteranopes to colour camouflage was specific to red–green variation between elements, as would be expected, and when the elements were red against blue, or green against blue, the dichromats and trichromats were not different (figure 4).

The absence of a colour-camouflage effect with red–green elements in dichromats rules out trivial
explanations of the effect in trichromats. Optical
defocus of one or other colour by chromatic aberration
in the camouflage condition would apply equally to
dichromats and trichromats. Unintended differences in
luminance would have been greater in dichromats, as
the stimuli were matched in luminance for the normal
observer. Moreover, we found in a further experiment
(figure 5) that luminance differences between elements
of the same colour had to be in the order of a log unit
before they produced comparable camouflage to the
colour case. Nor could the dichromats have simply
ignored the colour to which they were less sensitive.
This would be equivalent to deleting, randomly, half
the elements in the display, and a separate control
showed that this procedure had a highly detrimental
effect upon detection, approximately equal to the
colour-camouflage effect in trichromats.

4. DISCUSSION

Our finding that colour interferes with the detection
of texture agrees with previous reports (Callaghan et al.
1986; Callaghan 1989), and is also consistent with the
finding that chromatic gratings mask luminance
gratings in a detection task (Switkes et al. 1988). To
explain the camouflaging effects of colour, we may
assume that colour is an important stimulus for
dividing the image into meaningful regions and that
segmentation by colour can interfere with alternative
segmentations even when the colour variation is
spatially random.

The segmentation of the image into significant
regions is one of the main problems that has to be
solved by the early stages of vision. For example, to
detect a fruit on a branch we have to detect the region
of the image corresponding to the fruit against the
background, and against any partly occluding objects
such as twigs in the foreground. There are many
alternative attributes of images that can be used in
segmentation, including luminance, colour, texture
and depth. However, it is an interesting feature of our
visual system that we can entertain only one perceptual
organization at once, rather as we cannot simulta-
naneously instruct our limbs to flex and extend. To
explain the colour-camouflage effect, we propose that
when alternative methods of segmenting come into
competition, one of the potential organizations will be
selected at the expense of the others. Our first
impressions when viewing the randomly coloured
displays were that they appeared segmented into
differently coloured regions, even though in reality the
coloration was random. It is hard to penetrate this
perceptual organization to discover an alternative
textural segmentation. Our findings do not support
the strong statement that colour and shape are analysed
entirely independently and in parallel (Treisman &
Gelade 1980), although this may well be true of
processing before the level at which they compete.

It can be argued that there are sound computational
reasons for preferring colour to luminance as a method
of segmenting scenes. Non-specular objects lit by
dappled light will often be more spatially uniform in
the shape-of their reflectance spectrum than in their
luminance (Mollon 1989; Morgan 1991; Tresilian &
Morgan 1992). Even when lighting is uniform, the
luminance and texture of an object both depend
strongly upon surface orientation relative to the light
source. Luminance is a good guide to three-
dimensional shape (‘shape-from-shading’) but, for that
very reason, it can be a poor indication of what parts
of the image belong together. The same is true of the
texture of a three-dimensional object. Colour, con-
versely, is a reliable method of segmentation, provided
that there is not a strong specular component in the
reflectance spectrum, but is in general a poor guide to
three-dimensional shape. On functional grounds, we
might therefore expect colour to be a powerful
determination of early segmentation, and our results
suggest that this is the case.

We have confirmed anecdotal reports that dichro-
matcs can be at an advantage in penetrating colour
camouflage, but care must be exercised before pro-
posing this as the explanation of colour-vision poly-
morphism in human populations. If trichromatic
colour vision has an overall selective advantage, a
slight compensating advantage to dichromacy will
merely reduce the size of the advantage of trichromacy,
not eliminate it, and dichromacy will disappear from
the population. There are four ways in which a
polymorphism for colour vision could be maintained:
(i) heterozygous advantage; (ii) frequency-specific
selection for a minority form of perception; (iii) social
cooperation; and (iv) purely genetic effects, including
mutation pressure and unequal crossing-over. We
consider these in turn.

Heterozygous advantage would maintain dichro-
ancy if female carriers of the gene were at a selective
advantage. The advantage might be a pleiotropic
effect of the gene: Cruz-Coke & Varela (1966), for
example, suggested that carriers of colour blindness
had higher fecundity, but this claim has attracted little
support (Mollon 1987). Alternatively, the carriers
might enjoy a direct advantage in colour vision, but it
is not clear what this might be. We must distinguish
the case of dichromacy, considered here, from anomalous
trichromacy in which one of the normal pigments is
thought to be altered in its spectral sensitivity. In the
latter case, female carriers could express all four
photopigments (three normal and one anomalous)
and, owing to X-chromosome inactivation, the anom-
alous pigment would be segregated in a distinct subset
of retinal cones, so giving such women the potential
for tetrachromatic vision (Mollon & Jordan 1988).†
However X-chromosome inactivation does not explain
the maintenance of dichromacy; the carriers will be at
best no worse off than non-carriers, whereas the
dichromatic males will be at a disadvantage. We must
therefore look elsewhere for factors maintaining dichro-
macv in predominantly trichromatic populations.

† A heterozygous advantage of this kind appears to occur in New
World monkeys. Such primates are basically dichromatic, having
only a single X-chromosome locus for a photopigment in the
red–green range; but the locus is polymorphic and so the
heterozygous females have three types of retinal cone. They can
exploit this segregation of allelic products, in that they are
behaviourally trichromatic (Mollon et al. 1984; Jacobs & Neitz
1987).
Frequency-dependent selection occurs when the selective pressure acting upon alleles is dependent upon their frequency in the population (Clarke & Partridge 1988). Suppose, for example, that most classes of fruit were more easily detected by dichromats than by trichromats, but that a small class of fruits was more easily detected by dichromats. If the numbers of dichromats begins to be limited by the food supply, dichromats will be at a selective advantage because they compete more effectively in their niche. However, growth of their numbers is automatically limited by the scarcity of their specialized food supply. In principle, therefore, the ability of dichromats to penetrate camouflage, combined with a frequency-dependent selection, could account for the maintenance of dichromacy in natural populations.

Polymorphism could also be maintained by kin selection amongst genetically related groups. Where there is any degree of cooperation in foraging, it would be to the advantage of a group to have individuals covering a wide range of gathering skills. If dichromats are able to penetrate some kinds of camouflage more effectively than trichromats, their presence in the foraging group would be an advantage. This is actually just a version of frequency-dependent selection because the advantage depends crucially upon the relative frequencies of the different morphs in the group.

Finally, there may be no advantage to dichromacy at all, and the condition may be explained by purely genetic factors. Point mutation rates are typically much too small to explain a 2% gene frequency in the population. However, dichromacy appears to result not from point mutations but from unequal crossing-over at the red–green locus (Nathans et al. 1986). The frequency of such events cannot be directly estimated, but in at least one case it is known that rates of unequal crossing over are considerably higher than those of typical point mutations (Szostak & Wu 1980).

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