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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 *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 *et al.* 1979; Nathans *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-attentional 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-

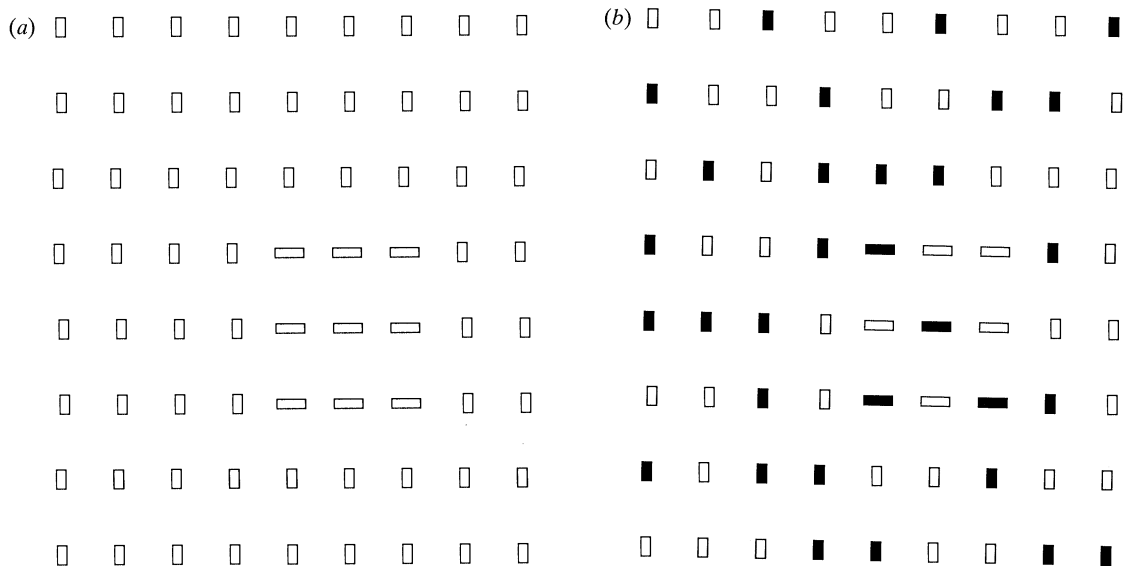


Figure 1. The figure gives a schematic representation of the experimental conditions for investigating the effects of colour camouflage upon textural segregation. The observer's task is to detect the subregion of the pattern in which the elements differ in orientation from the background. In the cases 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 30×30 elements and the target area consisted of 7×7 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.

ground). 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 7×7 elements embedded in a 30×30 array of elements. In the size-orientation discrimination experiment, the target elements were $5 \text{ arcmin} \times 6 \text{ arcmin}$ and the background elements $7 \text{ arcmin} \times 6 \text{ arcmin}$. 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-

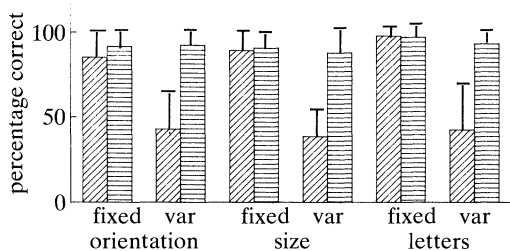


Figure 2. The figure describes the observers' performance in detecting and reporting the position of the target area in patterns like those in figure 1. The measure of performance is the percentage correct identification of target position over a series of trials in which position varies randomly. The 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.

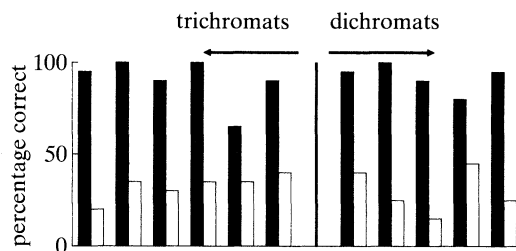


Figure 4. The figure shows results of an experiment similar to that described in the legends to figure 1 and 2, except that the texture elements were coloured red and blue instead of red and green. The dichromats are now as severely affected as the normals (trichromats) by the colour-camouflage conditions. A Mann-Whitney *U* test on the difference scores between control and camouflage conditions showed no significant difference between trichromats and dichromats ($z = -0.56$; $p = 0.58$). A similar result was found for green-blue mosaics.

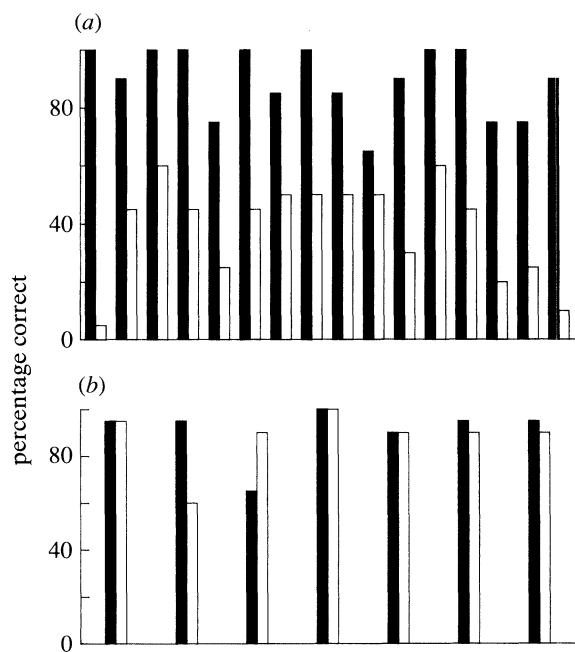


Figure 3. The figure shows individual data from the size-orientation condition described in the previous two figures. Each bar represents the score of an individual subject in the fixed condition (filled black bars), or in the variable (camouflage) condition (unfilled bars). (a) Trichromats, (b) dichromats.

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 vari-

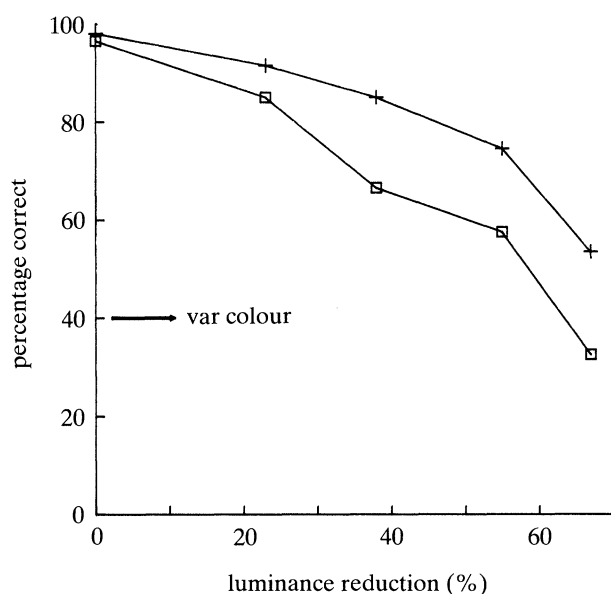


Figure 5. The figure shows the results of an experiment to determine the effects of luminance mosaics rather than colour variation in the texture elements. The stimuli were like those in figure 1b except that, instead of being different colours, the two classes of texture element were of different luminance. Half the targets had the same luminance as those in the colour experiments; the remainder were reduced by the amount shown on the horizontal axis (luminance reduction percentage). Each point represents the mean score over subjects (normal trichromats, crosses; dichromats, squares). The horizontal arrow on the vertical axis indicates the level of performance achieved by trichromats in the colour camouflage condition. Note that performance was better than this in the luminance condition even with a 70% reduction in luminance. Dichromats do somewhat worse in this condition than trichromats, possibly because they customarily pay more attention to segregations based on luminance.

ation 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 simultaneously 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, conversely, 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 dichromats can be at an advantage in penetrating colour camouflage, but care must be exercised before proposing this as the explanation of colour-vision polymorphism 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 dichromacy 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 anomalous 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 dichromacy 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 trichromats than by dichromats, but that a small class of fruits was more easily detected by dichromats. If the numbers of trichromats 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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