# The Contribution of Color to Visual Memory in X-chromosome-linked Dichromats

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We used a recognition memory paradigm to assess the visual memory of X-chromosome-linked dichromats for color images of natural scenes. The performance of 17 protanopes and 14 deuteranopes, who lack the second (red–green opponent) subsystem of color vision, but retain the primordial (yellow–blue opponent) subsystem, was compared with that of 36 color normal observers. During the presentation phase, 48 images of natural scenes were displayed on a CRT for durations between 50 and 1000 msec. Each image was followed by a random noise mask. Half of the images were presented in color and half in black and white. In the subsequent query phase, the same 48 images were intermixed with 48 new images and the subjects had to indicate which of the images they had already seen during the presentation phase. We find that the performance of the color normal observers increases with exposure duration. However, they perform 5–10% better for colored than for black and white images, even at exposure durations as short as 50 msec. Surprisingly, performance is not impaired for the dichromats, whose recognition performance is also better for colored than for black and white images. We conclude either that X-chromosome-linked dichromats may be able to compensate for their reduced chromatic information range when viewing complex natural scenes or that the chromatic information in most natural scenes, for the durations tested, is sufficiently represented by the surviving primordial color subsystem. © 1998 Elsevier Science Ltd. All rights reserved.

Visual memory    Color mechanisms    Color deficiency

## INTRODUCTION

Human color vision is believed to comprise two, largely independent subsystems, which evolved at different times (see Mollon, 1991): a primordial (yellow–blue opponent) subsystem and a phylogenetically more recent, second (red–green opponent) subsystem. The primordial subsystem compares the photon absorptions in the relatively sparse short (S)-wave cones with those in the more numerous long (L)- and middle (M)- wave cones. Ill-suited for analysing spatial detail, its evolutionary advantage was, presumably, to divide our light sensations into cool (short-wave), warm (long-wave) and neutral; and thus provide a new means of classifying objects (McDougall, 1901).

The second subsystem compares the photon absorptions in the L- and M-cones. The photopigments contained in these cones are now known to be encoded

by opsin genes that arose through gene duplication from a common forebear on the X-chromosome (Nathans, Thomas & Hogness, 1986; Nathans, Merbs, Sung, Weitz & Wang, 1992). The duplication event, which engendered trichromacy in Old World monkeys and man, may have coincided with the evolution of colored fruits in the African tropical rain forest (Allen, 1892; Polyak, 1957; see Mollon, 1991, for a recent discussion). Presumably its main evolutionary advantage was the better ability to detect ripe fruit amid the diverse foliage of the rain forest.

In this paper, we address the issue of the evolutionary significance of the second color subsystem and the benefit it brings to the analysis of complex visual scenes over and above that offered by the primordial subsystem. Our way of doing this is to look at the performance of observers who lack the second (red–green color opponent) subsystem, while retaining the primordial subsystem.

Such X-chromosome-linked dichromatic observers are relatively common, representing approx. 2% of the European male population and about 0.03% of the European female population. They are classified as either protanopic, missing the L-cone, or deuteranopic, missing the M-cone. Interestingly, although much quantitative information is available about the sorts of color confusions they make—and this information has been effectively applied to developing tests for diagnosing

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their color defects—little is known about how detrimental their color deficiency is for the perception of natural scenes, in which full three-dimensional color information is present.

On the one hand, anecdotal accounts emphasize the difficulties that the X-chromosome-linked color deficient experience in finding red fruit and berries amongst dense green foliage (Huddart, 1777; Nicholl, 1818; Colquhoun, 1829; see Mollon, 1991, for a review). On the other hand, many dichromats first become aware of their color deficiency when being screened for the armed forces or for driving licences. In fact, in most countries, color vision tests are not routinely applied during development and red–green color-blindness is not listed as a handicap.

To determine whether the lack of the second color subsystem can have repercussions for higher-level tasks such as the memory for natural scenes, we used natural images as stimuli in a recognition memory experiment, and asked what chromatic information adds to the already existing luminance information in performance. This question is particularly interesting because the second color subsystem is believed to have developed subsequent to and parasitic upon the system that carries information about spatial detail (Mollon, 1991).

In previous experiments, we have demonstrated that color normal observers are better at recalling color images than black and white images; and that the improvement has both a cognitive and a sensory component (Gegenfurtner, Wichmann & Sharpe, 1997). Do X-chromosome-linked dichromats, who lack the red–green opponent subsystem, also perform better for color images, despite their severely reduced color discrimination? Or are they disadvantaged compared with color normals?



FIGURE 1. Recognition rate (d′) as a function of exposure duration of the images during the presentation phase. Filled squares indicate images presented in color, filled circles indicate images presented in black and white. (A) Color normal observers. (B) Dichromats.

## METHODS

### Procedure

The experiment consisted of two phases: a presentation phase, in which subjects were sequentially presented a set of 48 images of natural scenes, and a query phase in which subject's memory for the images was tested. First, each image was presented for 50–1000 msec, with a 7-sec interval between successive images. In the subsequent query phase, the same 48 images were randomly intermixed with 48 new images (distractors), and the observers' task was to indicate whether they had already seen an image during the presentation phase. The query phase was self-paced; each image was presented until the subject reached a decision and gave a yes or no response.

### Stimuli

Both the test and distractor images were randomly chosen from a database of 96 images of natural scenes. The images were classified into four different categories: green landscapes with fields and trees, flowers, rock formations, and scenes containing man-made objects. Images were not formally screened for category membership, but when subjects were asked they were able to
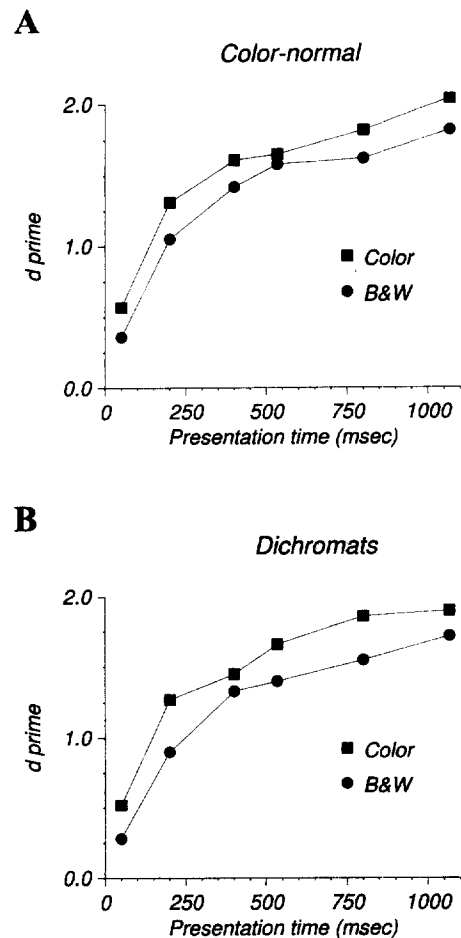
assign the images to the different categories without difficulty. Pilot studies ensured that, overall, the chosen images were recognized at approximately 75% correct, on average, by normal subjects (to avoid either floor or ceiling effects).

For each subject in all the experiments half of the 48 images were randomly chosen to be presented in color, the other half in black and white. The photometric luminance component of the image was identical under both conditions,* and the space averaged mean luminance was approx. $35 \text{ cd/m}^2$. Every image was immediately followed by a mask consisting of pixel blocks randomly chosen from color space, with the restriction that for the black & white images the mask was made up of black & white instead of colored blocks. Images that were presented in color during the presentation phase were always presented in color during the query phase, and likewise for black and white.

*Since the colored and black and white images were equated for luminance according to the standard luminosity function of the color normal observer, it is possible that there were differences in luminance between the two types of images for the protanopes and, to a lesser extent, for the deuteranopes.

Experiments were run on a Silicon Graphics Indigo II workstation with a 24-bit framebuffer. There were 60 refresh cycles per second. Images were presented for 3, 12, 24, 32, 48 and 64 frames, resulting in presentation durations of 50, 200, 400, 533, 800 and 1067 msec. The image presentation was ended by switching the hardware lookup table to a gray of mean luminance, while the mask was drawn into the frame buffer. The interval between the termination of the stimulus and the onset of the mask was 16.7 msec. The mask was presented for 200 msec, followed by another uniform field of gray at mean luminance.

## Subjects

Thirty-six normal trichromats and 31 X-chromosome-linked dichromats served as observers in the memory recognition experiment. They were paid for their participation. The color normal subjects (mean age 20–25 years) were students at the University of Tübingen. Sixteen were male and 20 were female. The X-chromosome-linked dichromats were recruited from a large database at the University of Freiburg i. Br., established for a project correlating red–green color-blind genotypes with phenotypes. They ranged in age from 15 to 55 years (mean age 26 years). All were diagnosed as protanopic or deuteranopic by standard color vision tests, which included the Ishihara pseudois-chromatic plates and the Nagel I anomaloscope. Dichro-macy was confirmed by foveal (2 deg) heterochromatic brightness curves measured as a function of wavelength by the minimal-flicker (25 Hz) method. Southern blotting analysis, performed by Dr J. Nathans (The Johns Hopkins University, Baltimore), indicated that six of the prota-nopes and eight of the deuteranopes had a single opsin gene in the red–green tandem array on the X-chromosome; the remaining 11 protanopes and six deuteranopes had two or more opsin genes. In the single-gene dichromats, exons 2–5 were PCR amplified and sequenced on both strands. This revealed that the eight single-gene deuteranopes had a single normal red (or long-wave sensitive) pigment gene with the senine polymorphic variant $R(Ser^{180})$ and that the six protanopes had a single 5′ red–3′ green-hybrid pigment gene: one with a R1G2 gene, one with a R2G3 gene, three with a $R3G4(Ser^{180})$ gene and one with a $R4G5(Ser^{180})$ gene (see Nathans et al., 1986). Only one of the dichromats was female (a multiple-gene deuteranope).

## RESULTS

Figure 1(A) shows the average results for the group of 36 color normal observers. Exposure duration of the images during the presentation phase is shown on the $x$-axis, and performance for correctly recognizing an image, d′, is plotted on the $y$-axis. Since there was no difference in the false alarm rate between luminance and color distractors, the proportion of correctly recognized images (hit rate) shows the same constant difference between color and black and white (as in Gegenfurtner et al., 1997). An analysis of variance revealed significant
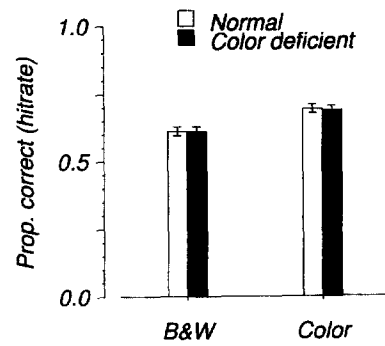


FIGURE 2. Comparison of the proportion of correctly recognized images (hit rate) for normal (open bars) and X-chromosome-linked dichromat (filled bars) observers. The left pair of bars indicates performance for images presented in black and white, the right pair performance for images presented in color.

main effects of presentation duration ($P < 0.001$), image category ($P < 0.001$) and for color vs black and white ($P < 0.001$). There was a weak interaction between category and presentation duration ($P < 0.05$).

These effects are discussed in detail in Gegenfurtner et al. (1997). In particular, it is interesting to note that performance for color images is significantly better at all exposure durations by a $z$-score of 0.25, which corresponds to a difference in recognition rate of approx. 5–10%. This difference is independent of exposure duration. The two curves are only vertically shifted. The performance difference is already present for 50 msec exposures and it remains constant up to exposure durations of 1 sec (the longest tested).

Interestingly, the curves for the X-chromosome-linked dichromats [Fig. 1(B)] are virtually identical to the ones obtained for the normal observers [Fig. 1(A)]. Again, there is an approximately 8% difference in performance in favor of the color images, and, again, this difference is fairly constant over different exposure durations. An analysis of variance showed the same main effects of image category ($P < 0.001$), presentation duration ($P < 0.001$) and color vs black and white ($P < 0.001$) that were observed for the color normal subjects. The interaction between exposure duration and image category was not significant for the dichromats. This indicates that processing of both types of images is quite similar in both groups of subjects.

Figure 2 compares overall performance of the dichromats with that of the normal observers. There is no difference whatsoever between the two groups, neither for color nor for black and white images. There was also no significant difference between protanopes and deuter-anopes in the task; nor between single-gene and multiple-gene dichromats.

## DISCUSSION

In a previous series of experiments in normal trichromats, we demonstrated that color plays an important role in recognition memory for natural scenes (Gegenfurtner et al., 1997). Recognition of color images

was 5–10% superior to recognition of black and white images at all the exposure durations tested between 50 and 1000 msec. In the present experiments, we find that there is absolutely no difference in recognition memory between trichromatic and dichromatic observers for the same natural scenes. On the one hand, this shows quite nicely that X-chromosome-linked dichromats, despite lacking the second subsystem of color vision and consequently color discrimination in the red to green spectral region, are far from being color-blind. They retain the primordial, blue–yellow opponent subsystem and this subsystem alone seems to be quite capable of supporting the enhanced performance for color images in our recognition memory task. On the other hand, this suggests that the practical purpose or evolutionary significance of the second subsystem, set out in the Introduction, is not to be sought in its beneficial effects on memory functions. Color does facilitate recognition memory, but it appears that dichromacy is perfectly capable of supporting the facilitation observed in color normals in our study. Does this mean that X-chromo-some-linked dichromats may be able to compensate for their reduced chromatic information range when viewing and analysing complex natural scenes? Or does it mean that the important information contained in most natural scenes is adequately represented by the spatial and the primordial color systems they retain? If so, then the evolutionary advantage of color vision provided by the red–green opponent subsystem may only be noted in more critical color-coded information than that used in our stimulus material.

One possible caveat has to be taken into consideration. Many X-chromosome-linked dichromats are only completely dichromatic for small viewing fields ( < 2 deg), such as those employed by the Nagel I anomaloscope. For larger fields, they become partially trichromatic and may be able to make coarse red–green discriminations. This is the so-called "large-field trichromacy", first observed by Nagel (1905) and documented since by many others (e.g., Smith & Pokorny, 1977; Nagy, 1980, 1982). The basis of this enhanced color discrimination is unclear, but some possible contributing factors such as rod intrusion can be eliminated under the conditions used in our experiments. Even under the most favorable conditions, however, dichromats would still have greatly reduced red–green color discrimination compared with normals (i.e., they would behave as extreme anomalous trichromats rather than as normal trichromats). Yet their performance on the recognition memory task was equal to that of normals.

When considering the role of the second color subsystem, it is interesting to speculate how complex color scenes, in particular our natural color images, appear to dichromats. Several researchers, most recently Usui and Nakauchi (1995) and Viénot, Brettel, Ott, Ben M'Barek and Mollon (1995), have considered this question by illustrating for the color normal observer, the reduced color gamut of the three types of dichromatic observer: protanopes, deuteranopes and tritanopes (the last lack S-cones and the primordial color subsystem).

Such simulations are based on colorimetric computations that are consistent with the known color confusions of dichromats. In addition, assumptions regarding the residual color sensations are largely based on reports by rare (and often highly suspect) unilateral dichromats. These simulations cannot allow for the ontogenetic changes that take place in a visual system that has developed in the complete absence of one of the three cone types. Visualizations based on these models show that the reduced (i.e., "dichromatic") images retain most of the structure contained in the original, even though certain details are completely lost; and this loss of detail might be expected to influence recognition memory.

If we consider, once again, the personal accounts of red–green color deficient individuals, it is perhaps less surprising that X-chromosome-linked dichromats do not show a performance deficit when viewing and recognizing our color images. Such accounts establish that they largely come to terms with the visual world; and are, under most circumstances able to orient and detect objects without impairment. It is only under certain, special circumstances, such as searching for fruit and berries against foliage, where lightness is varying randomly, that they have conspicuous difficulty. In man-made environments, they experience difficulties primarily with traffic and navigational signals (e.g., see Scholz, Andersen, Hofmann & Duncker, 1995), the predominant colors of which are red and green, and with complex visual displays, where color codes are used to delineate and mark out features in order to enhance efficiency or to reduce the risk of error.

Granted, color is indisputably an effective dimension for conveying information visually; and its full benefits are denied to X-chromosome-linked dichromats. However, the loss of the second subsystem of color vision seems to entail no important impairment on their coding and recognition of typical natural scenes, at least for the conditions tested in these experiments. Storage and retrieval of visual information may benefit from color vision, but, as far as these functions are concerned, the added value of trichromatic over dichromatic vision may well be negligible.

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