Advantages and disadvantages of human dichromacy

Lindsay T. Sharpe Institute of Ophthalmology, University College London, London, United Kingdom

Emanuela de Luca Division of Experimental Ophthalmology, University Eye Hospital, Tübingen, Germany

Thorsten Hansen Abteilung Allgemeine Psychologie, Justus-Liebig-Universität Giessen, Giessen, Germany

Herbert Jägle Division of Experimental Ophthalmology, University Eye Hospital, Tübingen, Germany

Karl R. Gegenfurtner Abteilung Allgemeine Psychologie, Justus-Liebig-Universität Giessen, Giessen, Germany

We compared the visual detection thresholds for cone-isolating stimuli of trichromats (those with normal color vision) with those of X-linked dichromats, who lack either the long-wavelength-sensitive (L) cones (protanopes) or middle-wavelength-sensitive (M) cones (deuteranopes). At low (1 Hz) temporal frequencies, dichromats have significantly higher (twofold) thresholds for all colored stimuli than trichromats; whereas at high (16 Hz) temporal frequencies, they perform as well or better than trichromats. The advantages of dichromats in detecting high temporally modulated targets can be related to an increased number, through replacement, of the remaining L- or M-cone type. However, their disadvantages in detecting low temporally modulated targets, even in directions of color space where their increased number of cone photoreceptors might be expected to be beneficial, are best explained in terms of the loss of L–M cone opponency and the inability of the visual pathways to reorganize to allow the detection of low-frequency luminance modulation.

Keywords: cones, temporal modulation sensitivity, dichromacy, colorblindness, red–green color opponency

Introduction

X-linked (red–green) dichromats lack the function of either the long-wavelength-sensitive (L) cones (protanopes) or middle-wavelength-sensitive (M) cones (deuteranopes). As a result, their color vision is reduced from three (trichromacy) to two (dichromacy) dimensions, and they are unable to discriminate within the red–green dimension of color space. This loss not only implies colorblindness or color deficiency but also has consequences for the development of the cone photoreceptor mosaic as well as for the development and function of the postreceptoral cone pathways. Such changes must directly affect visual detection and discrimination, as well as color discrimination per se.

Any complete explanation of visual detection/discrimination in dichromacy must consider the consequences of X-linked cone photopigment/photoreceptor replacement. Are the missing L-cones in protanopes replaced by M-cones, and are the missing M-cones in deuteranopes replaced by L-cones? Or, are they absent and is the cone photoreceptor mosaic incomplete (interrupted)? How would the alternatives affect sensitivity at different temporal frequencies?

It must also consider the fate of the trichromatic L–M (sometimes known as red–green) opponent color neurons. Are they missing or are they replaced by L–L (red–red) or M–M (green–green) opponent ones in deuteranopes and protanopes, respectively? If so, how do the altered or reorganized inputs in the dichromat affect the development and function of the visual pathways?

Previously, other researchers have investigated the disadvantages of dichromats in visual detection (e.g., Dain & King-Smith, 1981; Loop, Shows, Mangel, & Kuyk, 2003; Schwartz, 1994; van Arsdel & Loop, 2004). However, they have not used cone-isolating stimuli to examine the influence of both slow and fast temporally modulated stimuli in the same group of observers or species. Rather, they have used monochromatic light as their stimuli, which did not allow them to directly relate the deficits in dichromat observers to the loss of individual cone types or to lack of reorganization of their postreceptoral connections.

We therefore decided to revisit this intriguing area by investigating contour detection thresholds in trichromats (those with normal color vision) and dichromats using cone-isolating stimuli flickering at different rates (see Gegenfurtner & Hawken, 1995; Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995). Based on both human psychophysical (Kelly & van Norren, 1977) and primate

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electrophysiological (Kremers, Lee, & Kaiser, 1992; Lee, Martin, Valberg, & Kremers, 1993) evidence, 1 Hz was chosen to favor the chromatically opponent L–M inputs (traditionally associated with the parvocellular or P-pathway). In addition, 16 Hz was chosen to favor the nonchromatically opponent or luminance L + M inputs (mainly associated with the magnocellular or M-pathway). By doing so, we obtain insight into what advantages red–green color discrimination can bring to object detection and analysis and, more important, what disadvantages its lack signifies.

We find that sensitivity for both slow- and fast-flickering cone-isolating stimuli is substantially altered in dichromacy.

Methods

Subjects

There were 13 trichromats (8 males, 5 females), 9 deuteranopes (all males), and 7 protanopes (all males) who served as observers in this study. All normal observers had normal (corrected) visual acuity and were classified as color normal based on their performance on standard color vision tests, including the Ishihara pseudoisochromatic plates and the Nagel type I anomaloscope.

The dichromats were classified as protanopes (missing L-cone function) or deuteranopes (missing M-cone function) according to their color matches (Rayleigh red–green equation) on the Nagel type I anomaloscope and performance on other basic color vision tests. They were further characterized by molecular genetic sequencing of their opsin gene arrays on the X chromosome (Table 1; for more details, see Jagla, Jägle, Hayashi, Sharpe, & Deeb, 2002; Sharpe et al., 1998). They otherwise had normal visual acuity and function and have served as subjects in other psychophysical experiments.

Phenotype	Genotype	Genes
D1	Single gene	L (S180)
D2	Single gene	L (S180)
D3	Single gene	L (S180)
D4	Single gene	L (S180)
D5	Multigene	L (A180) + M (A180)
D6	Multigene	L (A180) + M1L2 (A180)
D7	Single gene	L (S180)
D8	Single gene	L (S180)
D9	Multigene	L (S180) + M1L2 (A180)
P1	Multigene	L1M2 (A180) + M (A180)
P2	Single gene	L3M4 (S180)
P3	Single gene	L (S180)
P4	Multigene	L1M2 (A180) + M (A180)
P5	Multigene	L2M3 (A180) + M (A180)
P6	Single gene	L3M4 (A180)
P7	Multigene	L2M3 (A180) + M (A180)

Table 1. Phenotype and genotype of the deuteranope (D) and protanope (P) dichromat observers. Genotype is classified according to whether the subject carried a single or multiple visual pigment genes on their X chromosome. L- and M-normal gene types are characterized according to whether they contain the alanine (A) or serine (S) polymorphism at position 180 in the third exon. LM- and ML-hybrid gene types are further characterized according to where the crossover occurs between exons 1 and 5. For more information about gene arrays and mutations, see Sharpe, Stockman, Jägle, and Nathans (1999).

Contrast thresholds

Stimuli were displayed on a standard CRT monitor (Sony 21-in. GDM F500) that was driven by a Cambridge Research VSG 2/4 graphics board at a refresh rate of 120 Hz noninterlaced. The images were generated on the monitor by reading through the picture memory in a raster scan and then interpreting the numbers in each location as a color defined in a 256-element color lookup table. Two 8-bit digital-to-analog converters, which were combined to produce an intensity resolution of 12 bits, were used to control the intensity of each of the three monitor primaries. The luminances of each of the phosphors were measured at various output voltage levels using a Minolta CA-100 photometer. A smooth function was used to interpolate between the measured points, and lookup tables were generated to linearize the relationship between voltage output and luminance. We also made sure that additivity of the three phosphors held over the range of intensities used in these experiments (Brainard, 1989). The monitor was spectrally calibrated (CAS 140, Instrument Systems, München, Germany). The monitor spectra were multiplied with the Stockman and Sharpe (2000) cone fundamentals to calculate absorptions and contrasts in the L-, M-, and S-cones.

The contrast thresholds were measured with a four-alternative forced-choice staircase procedure for detecting either a low (1 Hz) temporally modulated (sinusoidally) target, chosen to favor the L − M chromatic (and presumably the P-cell) pathway, or a high (16 Hz) temporally modulated one, chosen to favor the L + M (and presumably the M-cell) pathway. Each observer's task was to detect the position of a 3-deg-diameter disk target, which was presented on a neutral gray background that was bright enough (10.2 cd/m^2 or 2.1 log scotopic trolands) to desensitize the rods. The disk target could assume one of four different positions (e.g., right up or left down), the center of which was displaced 4 deg eccentrically from the fixation point (see Figure 1). It appeared for 500 ms, starting from the neutral gray background and making an excursion in either the negative or positive color direction and returning to the neutral gray background. In the 16-Hz

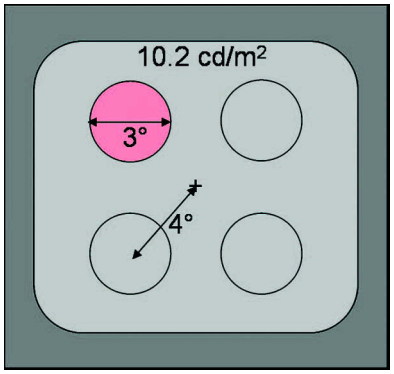

Figure 1. CRT stimulus conditions. The observer was required to fixate the central cross in the middle of a neutral gray background (10.2 cd/m^2 or 2.1 log scotopic trolands). A 3-deg-diameter disk target could appear at any one of four locations, centered 4 deg eccentrically from the fixation cross, for 500 ms, flickering at 1 or 16 Hz.

condition, eight complete cycles of full modulation were presented, but in the 1-Hz condition, only half a cycle of the full modulation was presented.

A silent substitution technique selectively modulated the target color contrast so that it stimulated only the L-cones, the M-cones, or preselected linear combinations of the L- and M-cones. The sensitivities were calculated according to the Stockman and Sharpe (2000) cone sensitivities. The modulation of cone excitation was quantified by the (Weber) cone contrast formula (Equation 1):

$$[100\% \times (E_{\text{stim}} - E_{\text{back}})/(E_{\text{back}})], \quad (1)$$

where E_{stim} and E_{back} are the cone excitations caused by the stimulus and the background, respectively. To verify cone isolation, we measured L- or M-cone contrast thresholds under both the 1- and 16-Hz conditions in protanopes (who lack L-cone function) and deuteranopes (who lack M-cone function), respectively, as well as in a blue cone monochromat (who lacks both L- and M-cone functions). In none of these experiments could any cone threshold for the missing cone type(s) below maximum contrast be measured. These control experiments also verified that the rods are not contributing significantly to the thresholds. As an additional control, S-cone contrast thresholds were measured in all observers. Those of the trichromats, dichromats, and the blue cone monochromat did not differ significantly, providing an internal reference point and indicating the independence of the developmental mechanisms that govern the relative numerosity of L-/M- and S-cones (see also Hofer, Carroll, Neitz, Neitz, & Williams, 2005).

Each observer's thresholds were measured at least six times for each of the six conditions and averaged.

Phenotype	Luminance	*SEM*	L-cone	*SEM*	M-cone	*SEM*
D1	1.90	0.12	1.70	0.12	–	–
D2	1.88	0.08	1.64	0.12	–	–
D4	1.55	0.11	1.38	0.10	–	–
D6	1.38	0.24	1.63	0.33	–	–
D7	2.48	0.37	2.41	0.46	–	–
D8	1.84	0.19	1.85	0.12	–	–
D9	1.50	0.12	1.28	0.08	–	–
P1	1.42	0.15	–	–	1.12	0.01
P2	2.20	0.14	–	–	1.77	0.12
P3	1.04	0.07	–	–	0.80	0.10
P5	1.71	0.20	–	–	1.43	0.10
P6	1.55	0.14	–	–	1.35	0.06
P7	2.39	0.09	–	–	1.73	0.12
T1	1.81	0.18	1.82	0.10	5.53	0.14
T6	1.76	0.12	2.34	0.05	3.55	0.09
T7	1.13	0.05	1.36	0.21	2.32	0.15
T8	1.68	0.17	1.75	0.18	4.78	0.32
T9	1.47	0.12	1.49	0.16	4.44	0.20
T10	1.20	0.04	1.63	0.17	3.10	0.16
T11	1.63	0.05	1.92	0.09	4.22	0.29
T12	1.34	0.10	2.17	0.10	2.65	0.10
T13	1.52	0.12	1.89	0.18	2.88	0.28

Table 2. Average percentage contrast thresholds measured with 16-Hz sinusoidally modulated targets for L + M cone (luminance) and L- and M-cone excitations in the individual deuteranope (D), protanope (P), and trichromat (T) observers. Standard errors of the mean (*SEM*s) are indicated for the six repetitions.

Results

Contrast thresholds were measured for detecting a low (1 Hz) temporally modulated target, chosen to favor the L − M chromatic opponent system and the P-cell pathway, or a high (16 Hz) temporally modulated one, chosen to favor the L + M luminance and M-cell pathway. The individual mean percentage contrast thresholds for L + M luminance and L- and M-cone excitations for each observer are listed in Tables 2 and 3 for the 16- and 1-Hz conditions, respectively. The mean percentage contrast thresholds for the trichromats, deuteranopes, and protanopes are shown in Figure 2.

Fast temporally modulated targets

For the 16-Hz modulated targets, the L + M (luminance) thresholds are similar for the trichromats (n = 9, 1.50 ± 0.08 *SEM*), deuteranopes (n = 7, 1.79 ± 0.14 *SEM*), and protanopes (n = 6, 1.72 ± 0.20 *SEM*). On average, the trichromats have significantly lower L-cone than M-cone contrast thresholds, by a ratio of 2.09 ± 0.23 *SEM* (t = −5.0430, df = 8, p < .001), which is consistent with approximately twice as many L-cone as M-cone numbers in the retina (Albrecht, Jägle, Hood, & Sharpe, 2002; Carroll, McMahon, Neitz, & Neitz, 2000; Cicerone & Nerger, 1989b; de Vries, 1948; Kremers et al., 2000; Kremers, Usui, Scholl, & Sharpe, 1999; Sharpe, Stockman, Jagla, & Jägle, 2005), on average, and correlates very well with average estimates derived from the relative contrast gains of their L- and M-cone-isolating multifocal electroretinograms (1.82 ± 0.29 *SEM*) (Albrecht et al., 2002) and from fitting the L- and M-cone spectral sensitivities to their 25-Hz heterochromatic flicker photometry (HFP) matches (1.94 ± 0.46 *SEM*) (Albrecht et al., 2002). Further, the M-cone contrast thresholds of the protanopes (1.36 ± 0.15 *SEM*) are significantly smaller than those of the trichromats (3.72 ± 0.36 *SEM*) by a factor of 2.74 (t = 25.72, df = 13, p < .001), whereas the L-cone contrast thresholds of the deuteranopes (1.70 ± 0.14 *SEM*) are only slightly smaller than those of the trichromats (1.82 ± 0.10 *SEM*). These results are consistent with cone pigment replacement (Berendschot, van de Kraats, & van Norren, 1996; Cicerone & Nerger, 1989a; Kremers, Usui, et al., 1999; Wald, 1966).

For eight of the nine normal observers, HFP data were available, from which we could estimate their L–M cone ratios. There is a highly significant inverse correlation between their 16-Hz L-cone modulation sensitivities and their L–M cone ratios estimated from 25-Hz HFP settings (Sharpe et al., 2005): r^2 = .686; F = 13.084, df = 1,6, p = .01 (Figure 3). Thus, at high temporal frequencies, a high L-cone modulation sensitivity (or low contrast threshold) is associated with a high estimated L–M cone ratio. This relationship would predict lower L-cone thresholds for the deuteranope observers. However, the absolute increase in L-cone numbers is relatively small, and the thresholds are already fairly low for the trichromatic observers. At these high levels of sensitivity, other factors might be limiting visual sensitivity.

Phenotype	Luminance	*SEM*	L-cone	*SEM*	M-cone	*SEM*
D1	2.51	0.06	2.17	0.09	–	–
D2	2.71	0.12	1.94	0.06	–	–
D3	2.50	0.08	1.96	0.09	–	–
D4	2.47	0.09	2.22	0.05	–	–
D5	2.65	0.13	2.84	0.01	–	–
D6	1.72	0.21	2.42	0.16	–	–
D7	2.75	0.20	2.86	0.23	–	–
P1	2.52	0.07	–	–	1.83	0.06
P2	2.88	0.09	–	–	2.14	0.08
P3	2.98	0.18	–	–	2.21	0.09
P4	3.15	0.13	–	–	2.29	0.05
P5	2.12	0.12	–	–	1.43	0.10
P6	2.40	0.05	–	–	1.77	0.12
T1	2.80	0.19	1.33	0.07	1.15	0.08
T2	2.35	0.09	0.93	0.02	0.87	0.06
T3	2.32	0.25	0.96	0.12	0.79	0.04
T4	2.06	0.10	0.97	0.12	0.89	0.06
T5	1.98	0.06	0.87	0.05	0.70	0.04

Table 3. Average percentage contrast thresholds measured with 1-Hz sinusoidally modulated targets for L + M cone (luminance) and L- and M-cone excitations in the individual deuteranope (D), protanope (P), and trichromat (T) observers. Standard errors of the mean (*SEM*s) are indicated for the six repetitions.

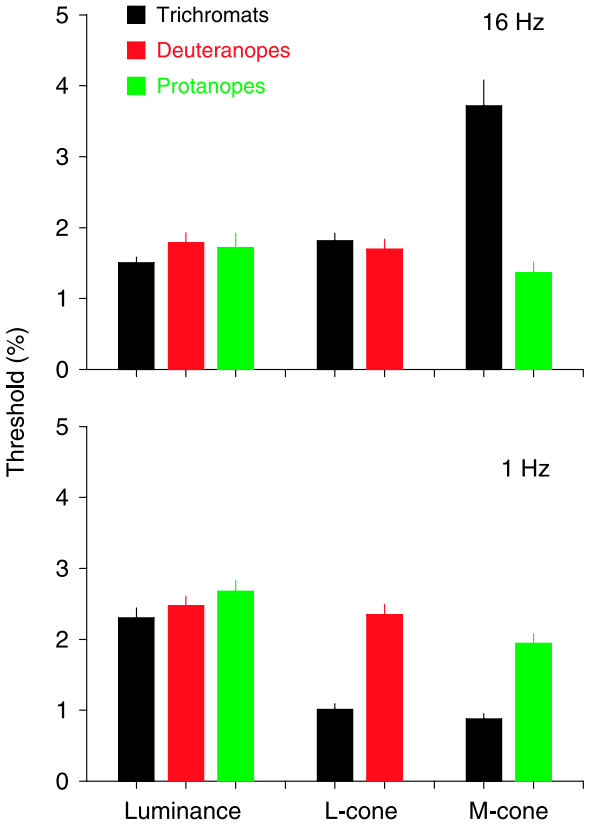

Figure 2. Bar histograms depicting the mean percentage contrast thresholds measured with 16 Hz (panel A) and 1 Hz (panel B) sinusoidally modulated targets, for L + M cone (luminance) and L- and M-cone excitations in trichromats (n = 9, black), deuteranopes (n = 7, red), and protanopes (n = 6, green). The L + M cone (luminance stimulus) was composed of equal amounts of L- and M-cone contrasts. Standard error of the mean (*SEM*) bars are shown.

Slow temporally modulated targets

In contrast to the 16-Hz results, at 1 Hz (Figure 2) the L-cone (1.01 ± 0.08) and M-cone (0.88 ± 0.08) contrast thresholds for the trichromats (n = 5) are about equal (ratio = 0.87 ± 0.03 *SEM*), indicating some balancing of the influence of disparate cone numbers in the L–M color subsystem (Brainard et al., 2000; Kremers et al., 2000). Moreover, the L + M cone thresholds at 1 Hz do not significantly differ among the trichromats (2.30 ± 0.14 *SEM*), deuteranopes (2.47 ± 0.13 *SEM*), and protanopes (2.68 ± 0.16 *SEM*). However, the L-cone contrast thresholds of the deuteranopes (2.35 ± 0.14 *SEM*) and the M-cone contrast thresholds of the protanopes (1.94 ± 0.13 *SEM*) are severely impaired, relative to those of the trichromats, by more than a twofold factor (t = 42.45, df = 10 and t = 63.38, df = 9; $p < .001$ in both cases). This occurs despite the fact that these observers have a significantly larger number of cones that are perfectly matched to the stimulus color. In principle, we would have expected the same sensitivity advantage of the dichromats for detecting M- or L-cone stimuli at the lower temporal frequency.

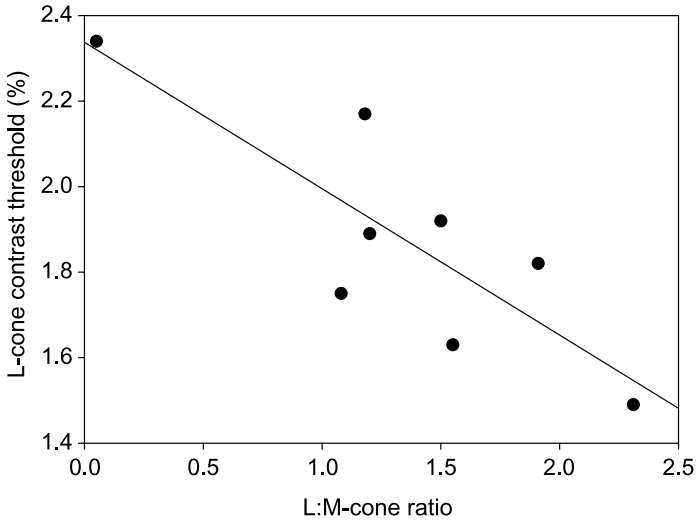

Figure 3. Correlation between each of eight trichromat observer's percentage L-cone modulation thresholds and their L–M cone ratios, as estimated from 25-Hz HFP measurements (Sharpe et al., 2005).

For the normal observers, there is no correlation between their L-cone modulation thresholds and their L–M ratios estimated from HFP measurements (r^2 = .006; F = 0.019, df = 1,3).

Additional directions in color space

To investigate this large discrepancy, we measured contrast thresholds in additional directions of color space. In Figure 4, complete threshold contours are traced out in the plane of color space spanned by the L- and M-cones for representative deuteranope (D2), protanope (P6), and normal (T5) observers. Similar results were obtained in two additional trichromat observers and in an additional deuteranope and protanope observer.

Thresholds for the dichromatic observers are completely determined by the amount of contrast in their remaining cone class, as indicated by the horizontal and vertical lines. At 16 Hz, thresholds for the normal observer mostly lie on a line parallel to the negative diagonal. This indicates that stimuli are detected by a "luminance" mechanism summing L- and M-cones at a ratio of about 2:1. Interestingly, the thresholds are much smaller near to the L − 2M cone excitation axis for the protanope, but not for the deuteranope, than for the normal observer. At 1 Hz, thresholds mostly lie on a line parallel to the positive diagonal, which indicates that the most sensitive mechanism takes the difference between L- and M-cone signals. These low temporally modulated colored stimuli are in fact what the human eye sees best (Chaparro, Stromeyer,

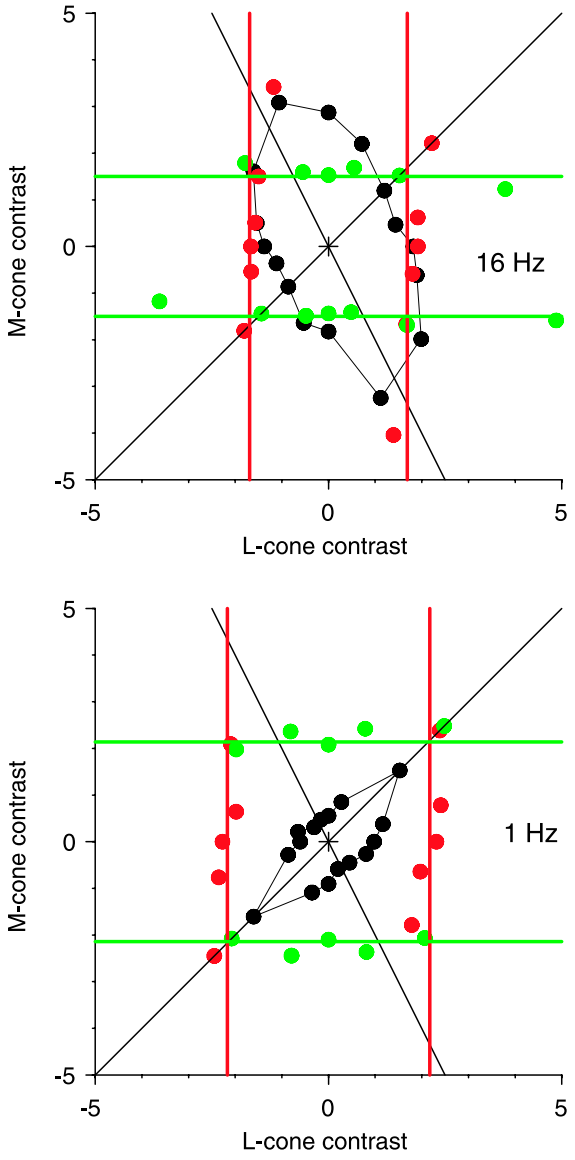

Figure 4. Sensitivity of a trichromat (T5, black), a deuteranope (D2, red), and a protanope (P6, green) for detecting high (16 Hz) and low (1 Hz) temporal frequency targets. M- versus L-cone percentage contrast thresholds are shown for various combinations of L- and M-cone modulations. The positive and negative diagonal lines represent the L + M (luminance) axis and the L − 2M (red–green) isoluminant axis, respectively. Thresholds are indicated by the distance from the origin. The vertical red lines are coplanar with the L-cone-isolating axis and indicate the sensitivity limits of the deuteranope; the horizontal green lines are coplanar with the M-cone-isolating axis and indicate the sensitivity limits of the protanope.

Huang, Kronauer, & Eskew, 1993). Its thresholds are smallest when the L- and M-cone signals are modulated with opponent signs rather than with the same sign. The dichromats do not have a functional red–green opponent mechanism, and therefore their increased cone numbers do not go along with higher sensitivity. On the contrary, their sensitivity is poor compared with trichromats (i.e., their thresholds are much larger along all excitation axes than for the normal observer).

Discussion

Trichromacy in Old World primates is associated with general advantages, such as finding reddish (ripe) fruit (Allen, 1879; Mollon, 1989; Nagle & Osorio, 1993; Osorio & Vorobyev, 1996; Polyak, 1957; Regan et al., 1998; Sumner & Mollon, 2000a, 2000b) or young (edible) leaves (Dominy & Lucas, 2001; Lucas et al., 2003) from a nearly equiluminant background of green foliage. As expected, then, natural selection should select against X-linked dichromacy (red–green color blindness) as an undesirable trait. Indeed, dichromacy is virtually nonexistent in all Old World primate species except man: The frequency of X-linked or red–green color blindness is estimated to be <0.1% in macaques (Onishi et al., 1999) as compared with >8% in Caucasians.

However, conversely, some psychophysical studies suggest compensatory advantages associated with X-linked color blindness, which may help to explain why the frequency of X-linked dichromacy is so curiously high in humans. For instance, protanopes and deuteranopes have been reported to be better than trichromats at breaking certain kinds of color camouflage that interfere with segregation based upon texture (Morgan, Adam, & Mollon, 1992). Further, it has been argued that color opponency diminishes spatial opponency by introducing chromatic noise and that the missing red–green color opponency of X-linked dichromacy leads to better spatial resolution (Abramov et al., 2000; Gordon, Delman, Abramov, Tannazzo, & Scuello, 2000) and visual acuity (Jägle, de Luca, Sérey, Bach, & Sharpe, 2005). In addition, surprisingly, dichromats seem to be able to compensate for their reduced chromatic information range when viewing complex natural scenes because their visual memory for colored scenes is not impaired, as compared with that of trichromats (Gegenfurtner, Wichman, & Sharpe, 1998).

Our results show that both compensatory advantages and disadvantages occur in dichromats in detecting a wide range of color and color + luminance contrasts and that the outcome depends critically upon the rate of temporal modulation. Although dichromats may be at least as good as or better, on average, than trichromats at detecting some chromatic contrasts that are rapidly modulated over time, they are significantly poorer at detecting contrasts that are slowly modulated over time.

Fast temporally modulated targets

The advantages that some dichromats show at detecting fast modulating (16 Hz) targets can be explained by the

following: (a) the tendency of such targets to favor cells in the M pathway, which are not chromatically opponent and therefore mainly unaffected by the lack of red–green color opponency (but see Stockman & Plummer, 2005); and (b) photopigment replacement, which would result in more cones of the same L- or M-type, feeding their signals into those (luminance-additive) cells. The combination of these factors would tend to increase sensitivity in certain directions of color space; that is, those that fall along or near the M-cone-isolating axis for protanopes and those that fall on or near the L-cone-isolating axis for deuteranopes.

Current models of gene expression in the X-linked photopigment gene array (for a review, see Sharpe et al., 1999; Smallwood, Wang, & Nathans, 2002) as well as evidence based on optical reflectance spectra of the fovea (Berendschot et al., 1996), psychophysical frequency of seeing curves (Cicerone & Nerger, 1989a, 1989b; Wesner, Pokorny, Shevell, & Smith, 1991), and contrast gains derived from the electroretinogram for dichromats favor the view in which the packing of foveal cones in dichromats is comparable with that in trichromats (Kremers, Usui, et al., 1999). In other words, the missing cone or photopigment type is assumed to be replaced in the photoreceptor mosaic of X-linked dichromats, with added M-cones replacing the lost L-cones in the case of protanopes and added L-cones replacing the lost M-cones in the case of deuteranopes.

Nevertheless, replacement may not always occur in dichromacy. In particular, a rare case of deuteranopia has been reported, in which a normal M-cone opsin gene is replaced by a gene containing mutations at nonspectral tuning sites that leads to the expression of a nonfunctional pigment (Carroll, Neitz, Hofer, Neitz, & Williams, 2004). Adaptive optics imaging revealed patchy loss of up to one third of the normal cones throughout the photoreceptor mosaic, which is consistent with a selective and complete loss of the subject's functioning M-cones. Although no measurements were made of cone modulation sensitivity, subjects would be expected to show normal (but not enhanced) L-cone contrast thresholds because they presumably have a full (and normal) complement of L-cones.

Accepting that photoreceptor replacement is the rule, the degree of replacement will vary considerably, among dichromatic observers compared with trichromats, because as has been well documented, there is a large variability in the L–M cone ratio in the trichromat eye, with estimates based on the various techniques ranging at least from 1:3 to 19:1 (Albrecht et al., 2002; Carroll et al., 2000; Carroll, Neitz, & Neitz, 2002; Cicerone & Nerger, 1989a, 1989b; de Vries, 1948; Hofer et al., 2005; Kremers et al. 2000; Kremers, Usui, et al., 1999). Thus, given a normal or typical *mean* L- to M-cone (L–M) ratio of 2:1 (Albrecht et al., 2002; Carroll et al., 2000; Cicerone & Nerger, 1989a, 1989b; de Vries, 1948; Kremers et al., 2000; Kremers, Usui, et al., 1999), deuteranopes, on average, with complete replacement, would have 1.5 times as many L-cones as trichromats, whereas protanopes would have 3 times as many M-cones. On the other hand, given an extreme L–M ratio of 19.0, a deuteranope, with complete replacement, would have only 1.05 times more L-cones as trichromats, but a protanope would have 20.0 times more M-cones. Thus, it may not be surprising that the L-cone modulation sensitivity of deuteranopes, on average, is similar or not significantly better than that of trichromats, whereas the M-cone modulation sensitivity of protanopes, on average, is highly significantly better than that of trichromats.

This speculation is supported by two additional observations. First, whereas there is more variability across trichromats than protanopes for the 16-Hz M-cone contrast thresholds, there appears to be no difference in variability between trichromats and deuteranopes for the 16-Hz L-cone contrast thresholds or among trichromats, deuteranopes, and protanopes for the 16-Hz luminance (L + M) contrast thresholds (see Table 2). Second, there is a highly significant correlation between the L-cone modulation contrast thresholds and the estimated L–M cone ratios of the individual normal observers (Figure 3). That is, a low L-cone modulation contrast threshold is associated with a high estimated L–M cone ratio, and a high L-cone modulation contrast threshold is associated with a low estimated L–M cone ratio.

Thus, leaving aside the problem of whether the increase in sensitivity with cone numbers is linear, large increases in number are much more likely to occur in the protanope than in the deuteranope, compared with the trichromat, and to be associated with significant increases in sensitivity at high temporal frequencies. However, it should not be forgotten that other factors will affect the relationship between cone numerosity and high temporally modulated L- and M-cone contrast thresholds. For instance, anatomical evidence indicates that peak foveal cone densities are highly variable, by more than a threefold factor, between individuals (Curcio, Sloan, Kalina, & Hendrickson, 1990).

Our results are consistent with the results of previous investigations using brief duration stimuli to measure incremental or absolute thresholds in dichromat and trichromat observers. In particular, Wald (1966) found that, for brief 40-ms flashes, the average peak sensitivity of the M-cones is 0.46 log unit higher in protanopes than in trichromats and that the average peak sensitivity of the L-cones is 0.25 log unit higher in deuteranopes than in trichromats.

Generally, other studies were not able to find such large or significant differences, using slow- or fast-flickering targets (Dain & King-Smith, 1981; Hsia & Graham, 1957; Schwartz, 1994), and none was able to assert that performance was poorer for dichromats than for trichromats. In addition, importantly, the interpretation of their data is confounded by the lack of cone-isolating procedures. For instance, Dain and King-Smith (1981) found that the difference in thresholds between deuteranopes and trichromats was greater for long-duration (e.g., 500 ms) than for

short-duration (e.g., 10 ms) flashes. Similarly, Schwartz (1994), using 10-ms incremental spectral flashes, found that deuteranopes have essentially the same sensitivity as trichromats for wavelengths >580 nm and that protanopes show no reduction in sensitivity for stimuli whose wavelength is <540 nm. Moreover, Hsia and Graham (1957) found that there was less than 0.1 log unit difference between absolute foveal thresholds for short-duration (10 ms), long-wavelength test flashes in trichromats and deuteranopes but that, on average, protanopes did better than trichromats in the short-wavelength part of the spectrum.

Slow temporally modulated targets

The disadvantages of dichromats compared with trichromats at detecting slow temporally modulated (1 Hz) targets in all color directions can most easily be understood in terms of the inability of postreceptoral reorganization to compensate for the loss of L–M opponency. Slow flicker rates or long incremental flashes tend to favor P-cells, which are often chromatically opponent in the normal observer and respond strongly to prolonged color flashes. In dichromats, they would be replaced by nonopponent cells with inputs of the same type, which respond weakly or do not respond at all to color contrast stimuli (see Dain & King-Smith, 1981): M center, M-surround cells in the protanope; L center, L-surround cells in the deuteranope.

As has been long known, sensitivity to low temporal frequencies is greater for red–green chromatic than achromatic stimuli, and cone-isolating stimuli appear to vary in chromaticity for a trichromat but in luminance for a dichromat. The high sensitivity of trichromats to cone-isolating stimuli at low temporal frequencies arises because they stimulate chromatic mechanisms. The fact that dichromats are relatively insensitive implies that the visual system is essentially set up as in trichromats and that it is not able to detect low temporal frequencies with achromatic mechanisms. It is debatable whether this limitation is due to the P-pathway system or higher level mechanisms.

Other researchers too have found that the sensitivity of dichromats to slow flicker rates or long incremental flashes is reduced compared with that of trichromats. For instance, Verriest and Uvijls (1977) found that deuteranope thresholds for 500-ms duration (656 nm) flashes were 0.33 log unit higher than those for trichromats. Likewise, Dain and King-Smith (1981) found that the difference in thresholds between deuteranopes and trichromats for long-wavelength (674 nm) 500-ms duration flashes is, on average, 0.53 log unit greater than for trichromats. In addition, Schwartz (1994) found that dichromats have a reduced sensitivity to 200-ms middle- and long-wavelength incremental flashes compared with trichromats. Our results are consistent with these earlier findings, but they also demonstrate that the increase in threshold even extends to stimuli that activate the remaining L- or M-cone type.

If the disadvantage in human dichromats is due to a possible defect or lack of reorganization in their postreceptoral color vision processing, it raises interesting questions about the evolutionary origins of the P-system and trichromacy. Did the P-system evolve before trichromacy, as has been suggested by Mollon (1989), among others? If so, what is its function, if not specialization of coding L–M signals?

Certain aspects of these issues have been investigated before (Loop et al., 2003; Schwartz, 1994; van Arsdel & Loop, 2004). Intriguingly, dichromatic humans require long-duration spectral increments to be as much as 0.4 log unit above detection intensity to see certain colors, whereas normally dichromatic animals such as chipmunks, 13-lined ground squirrels, and tree shrews are able to discriminate colors within 0.1 log unit of their detection thresholds (Loop et al., 2003; van Arsdel & Loop, 2004). This low color vision sensitivity in human dichromats may be an abnormal condition, indicating a possible defect in their postreceptoral color vision processing. Clearly, it would be worthwhile examining the difference between chromatic and achromatic sensitivities in dichromat New World monkeys (platyrrhines), in which the P-system, anatomically and physiologically, more closely resembles that in humans and other catarrhines. Intriguingly, the processing of chromatic information appears to be similar in the retinae of Old World trichromatic macaques and New World trichromatic marmosets (see Kremers, Silveira, Yamada, & Lee, 1999). Further, even in dichromatic marmosets, P- and M-cells have clearly different temporal response properties (Kremers, Weiss, & Silveira, 2004). Thus, the body of physiological and anatomical data seems to suggest that some of trichromacy had evolved before the divergence of the catarrhine and platyrrhine lines (Kremers, Silveira, et al., 1999), raising further questions about the evolution of postreceptoral "trichromatic" mechanisms.

Finally, the disadvantages that dichromats have in detecting slowly temporally modulated color contrasts have implications for testing the competency of the red–green color blind to perform navigational duties involving colored directional and warning lights. Lantern (detection) tests, especially applied under reduced visibility conditions, may be the most appropriate way to assess their actual capabilities, given that their signal detection, for the timing intervals used in navigational lights, as well as their signal recognition, may be impaired.

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Corresponding authors: Lindsay T. Sharpe or Karl. R. Gegenfurtner.
Email: lt.sharpe@cvrl.org or Karl.R.Gegenfurtner@psychol.uni-giessen.de.
Address: Institute of Ophthalmology, 11-43 Bath Street, London, EC1V 9EL, UK; or Abteilung Allgemeine Psychologie, Justus-Liebig-Universität Giessen, Otto-Behaghel-Strasse 10F, D-35394 Giessen, Germany.

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