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# Dichoptic difference thresholds for chromatic stimuli

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## ABSTRACT

We have investigated the properties of binocular color vision using a new measure: the Dichoptic Color Difference Threshold (DCDT). The DCDT is the smallest detectable difference in color between two dichoptically superimposed stimuli. DCDTs differ from conventional measures of binocular rivalry in that they are performance- not appearance-based. The dependency of DCDTs on (a) color direction and (b) color contrast was measured. The colors (chromaticities) of the stimuli were defined according to a scaled version of the MacLeod–Boynton color space, and the luminance and color contrasts of the stimulus pairs were equated using a matching procedure. DCDTs were measured using a forced-choice procedure in which subjects had to chose which of two stimuli had a between-eye-difference in color. DCDTs ranged from 9° to 22° of color angle depending on color direction. DCDTs were lower than binocular rivalry thresholds but higher than thresholds for discriminating the color pairs when placed side-by-side. There were no minima at either the cardinal color or unique hues directions, suggesting that DCDTs are not mediated by these mechanisms. DCDTs were however positively correlated with the measured perceived color difference between the color pairs when placed side-by-side.

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#### 1. Introduction

A range of phenomena implicate interactions between the signals from the two eyes – stereopsis, binocular summation, binocular fusion and binocular rivalry, to name just four. This communication deals with the last two of these in the context of between-eye differences in chromaticity, here simply referred to as color.

Binocular fusion is said to occur when a single perceptual state results from two images presented separately to the two eyes, irrespective of whether or not the images are identical (Hovis, 1989). In contrast, binocular rivalry is said to occur when conflicting perceptual states result from dissimilar images presented to corresponding retinal regions of the two eyes (see reviews by Blake (2001), and Alais and Blake (2005)). In the extreme of rivalry, only one of the two images is seen, usually by the dominant eye, while the other image is suppressed completely. By and large however, the two images alternate in perceptual dominance when rivalrous.

Binocular fusion and rivalry are often thought to be two sides of the same coin. However there exists a stage between fusion and rivalry; as one increases a between-eye difference in color from zero, a point is reached when the binocular image appears slightly lustrous, or 'shimmery'. At this point the between-eye difference is

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detectable, but there is no perceptual alternation. If subjects are required to discriminate between two dichoptic pairs, one with and one without a between-eye difference, a threshold for detecting the between-eye difference can be obtained (Formankiewicz & Mollon, 2009; Yoonessi & Kingdom, 2009). Unlike measures of binocular rivalry, dichoptic difference thresholds obtained in this way are Type 1 performance measures, in that there is a correct and an incorrect response on each trial (Kingdom & Prins, 2010). This is not to imply that dichoptic difference thresholds are superior to rivalry measures for understanding binocular function. Rather, they constitute an addition to the armory of binocular measures, and are useful for examining the relationship between monocular and binocular performance-based measures of visual function.

In a recent communication Yoonessi and Kingdom (2009) measured thresholds for detecting dichoptic differences in the average color and luminance of images of natural scenes. The results were used to determine whether the influence of natural-scene structure on an observer's sensitivity to color and luminance changes was mediated by mechanisms operating before or after the point of binocular combination. More recently Formankiewicz and Mollon (2009) measured dichoptic difference thresholds for the luminance and contrast of patches across a range of photometric and spatial parameters. In this communication we have measured dichoptic difference thresholds for uniform patches of color, and have termed these dichoptic difference color thresholds, or DCDTs. A DCDT is therefore the smallest detectable difference in color between two dichoptically superimposed stimuli.





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**Fig. 1.** The different phases of binocular interaction as applied to binocular differences in color (chromaticity). The Dichoptic Color Difference Threshold, or DCDT, is defined as the point in which a binocular color difference is just detectable. This point occurs at a much smaller binocular difference in color from that required to elicit an impression of rivalry – the Binocular Color Rivalry Threshold, or BCRT.

Fig. 1 summarizes the various percepts that an observer experiences, and the approximate position of a DCDT, as the between-eye difference in color is increased from zero. Fig. 2a shows three pairs of stimuli with different degrees of color difference. When freefused, the bottom pair in Fig. 2a should appear rivalrous while the top pair, which are identical, should appear perfectly fused. Readers may notice that the middle stimulus has a slight lustrous appearance, enabling it to be just discriminable from the top stimulus. The color difference in the middle pair is therefore close to the DCDT.

In this communication DCDTs have been measured across a range of color directions to gain a better understanding of how the visual system detects binocular differences in color. DCDTs have been related to measures of binocular rivalry (in the form of alternation), to thresholds for discriminating colors placed side-by-side, and to the perceived difference in colors placed side-by-side. In the next section we outline those aspects of color vision theory that are relevant to the present study, and review the relevant literature on dichoptic color interactions.

## 1.1. Cardinal colors and unique hues

In daylight vision the visual system detects light using three retinal photoreceptors, the S-, M-, and L-cones, which are maximally sensitive to short-, medium-, and long-wavelength lights respectively. The cone signals are then combined into three post-receptoral channels, one chromatic channel that differences L and M cone signals termed the 'L – M' channel, a second chromatic channel that differences the S cone signals with the sum of L and M cone signals termed the 'S - (L + M)' channel, and an achromatic channel that sums L and M cone signals, termed the 'L + M' channel. The existence of these channels has been revealed through psychophysical studies of adaptation (Krauskopf & Gegenfurtner, 1992; Krauskopf, Williams, & Heeley, 1982; Webster & Mollon, 1991; Webster & Mollon, 1994) masking (Li & Lennie, 1997; Mullen & Losada, 1994; Mullen & Losada, 1999; Sankeralli & Mullen, 1997), summation (Mullen, Cropper, & Losada, 1997; Mullen & Sankeralli, 1999), visual search (Monnier & Nagy, 2001), and motion integration (Krauskopf, Wu, & Farell, 1996). This scheme has led researchers to propose a two-dimensional physiologically-based color space, best known as the Derrington, Krauskopf and Lennie (DKL) space, in which colors are represented as levels of excitation within the two chromatic post-receptoral mechanisms (Derrington, Krauskopf, & Lennie, 1984; MacLeod & Boynton, 1979), as illustrated in Fig. 2b. The  $0-180^{\circ}$  axis corresponds to L - M, and the  $90-270^{\circ}$  axis S – (L + M). These axes are orthogonal to each other,

meaning that a stimulus defined along one of the two axes will not stimulate the mechanism responsive to stimuli defined along the other axis. The cardinal axes are also known as cardinal directions, and the colors they define, cardinal colors. Although many of the results obtained from studies of threshold color vision are best explained in terms of cardinal mechanisms, results using suprathreshold chromatic stimuli have generally favored an interpretation in terms of mechanisms tuned to a variety of color directions (D'Zmura, 1991; Flanagan, Cavanagh, & Favreau, 1990; Krauskopf, 1999; Krauskopf et al., 1986; Krauskopf, Wu, & Farell, 1996; Webster & Mollon, 1991; Webster & Mollon, 1993; Webster & Mollon, 1994; Zaidi & Halevy, 1993).

Cardinal colors however are not the only colors credited with forming the basis of cortical color organization. The theory of color-opponency, originally formulated by Hering (1964), and receiving its strongest support in hue-cancelation studies (Hurvich & Jameson, 1955) and recent brain-imaging studies (Parkes et al., 2008) is for some the basis of cortical color coding (Hurvich & Jameson, 1957; De Valois & De Valois, 1993; Valberg, 2001; see review by Wuerger, Atkinson, and Cropper (2005)). The theory of color-opponency posits two channels, one receiving opponent inputs from red and green, the other from blue and yellow. The unique hues, termed unique because for many they do not appear to be mixtures of colors, are the colors observed whenever one or other of the two color-opponent channels is at neutral. Thus unique red and unique green are seen when the blue-yellow color-opponent channel is at neutral, and unique blue and unique yellow are seen when the red-green color-opponent channel is at neutral. The unique hues fall in between the cardinal colors in the DKL color space (De Valois & De Valois, 1993; Malkoc, Kay, & Webster, 2005; Webster et al., 2000a; Webster et al., 2000b; Wuerger, Atkinson, & Cropper, 2005), and when combined in more-or-less equal amounts produce the binary hues purple, blue-green, yellowgreen, and orange (Malkoc, Kay, & Webster, 2005). The general arrangement of unique and binary hues is shown in Fig. 2c. An individual's unique hue settings are however a poor predictor of his/her binary hue settings (Malkoc, Kay, & Webster, 2005; Webster et al., 2000a: Webster et al., 2000b), and this has been interpreted as evidence against a special status for unique hues (Malkoc, Kay, & Webster, 2005).

#### 1.2. Dichoptic color interactions

Studies of dichoptic color interactions fall into two categories: those concerned with the perceived colors of dichoptically fused color pairs, and those concerned with the conditions for fusion and rivalry with dichoptic color pairs (see Hovis, 1989 for historical review). Since the present study is concerned with the conditions for fusion and rivalry, we will confine our discussion to this issue.

In a series of studies using monochromatic lights, Ikeda and colleagues (Ikeda & Nakashima, 1980; Ikeda & Sagawa, 1979; Sagawa & Ikeda, 1978) used the method of adjustment to measure the between-eye difference in wavelength  $\Delta \lambda$  that was needed to elicit an impression of inhomogeneity, i.e. rivalry.  $\Delta \lambda s$  were measured at a range of baseline wavelengths  $\lambda$ , and were found to be between 10 and 100 nm depending on the spectral region. In the most comprehensive of these studies, Ikeda and Nakashima (1980) found that when the dichoptic wavelengths were  $\lambda$  and  $\lambda + \Delta \lambda$ ,  $\Delta \lambda$  reached distinct minima around  $\lambda$ s of 470 nm and 570 nm, which are close to unique blue and unique yellow. Ikeda and Nakashima (1980) offered two interpretations of their results, one in terms of perceptual color distance, the other in terms of color-opponent theory. The perceptual distance interpretation was supported by measurements of the distances between  $\Delta \lambda$  pairs when measured by the (ostensibly) equal-perceptual-distance CIS UCS diagram. The distances were found to be more-or-less



**Fig. 2.** (a) Example dichoptic pairs: the top pair has no color difference, the middle pair a small color difference, and the bottom pair a relatively large color difference. Observers who are able to free-fuse the stimulus pairs might just detect a lustrous appearance in the middle pair, enabling it to be just discriminated from the fused top pair. If so, the middle pair will be close to the Dichoptic Color Difference Threshold. Observers may experience full-rivalry in the fused bottom pair. (b) Isoluminant plane in a modified version of the MacLeod-Boynton color space. Colors are represented along two chromatic axes:  $L-M (0-180^\circ)$ , and  $S - (L + M) (90-270^\circ)$ . (c) Perceptual axes of color vision defined by color appearance. Blue, yellow, red, and green are unique hues and define the principal axes; purple, blue-green, yellow-green and orange are the binary hues formed by combining unique hues in equal amounts.

constant in spite of large variations in  $\Delta\lambda$ . The color-opponent interpretation was supported by a model in which rivalry occurred once threshold was reached for colors in each eye that stimulated opposite poles of one or other of the red–green or blue–yellow color-opponent channels. The  $\Delta\lambda$  minima found at unique blue and unique yellow occurred because at these points the two wavelengths of the  $\Delta\lambda$  pair fell on either side of the neutral point of the putative red–green channel. Thresholds for discriminating colors along a line orthogonal to the yellow–blue line in color space have recently been shown to follow a similar pattern (Danilova & Mollon, 2010). Unfortunately  $\Delta\lambda$ s were not collected at sufficiently closely-spaced  $\lambda$ s in the Ikeda and Nakashima (1980) study to determine whether minima also occurred at unique green and unique red, which if they did would also implicate the involvement of the blue–yellow color-opponent channel.

## 1.3. Aims and hypotheses

One purpose of the present study is to re-examine whether perceptual distance or color-opponency determines the conditions for binocular rivalry/fusion using DCDTs. Given the recent evidence that the first post-receptoral stages of color vision are the cardinal mechanisms, we also test whether the cardinal mechanisms mediate DCDTs. Following Ikeda and Nakashima (1980) (and see also Danilova & Mollon, 2010), we might expect DCDTs to be minimal at the unique hues and maximal at the points in between, i.e. at the binary hues. By the same token we might expect minima at the cardinal directions and maxima at the points in between. On the other hand, it is possible that neither the unique hues nor cardinal mechanisms determine DCDTs, but instead perceptual distance.

Three methodological features of the present study are noteworthy. First, instead of using monochromatic lights, we have employed the colors on a cathode-ray-tube monitor, defined according to the DKL color space. Second we have employed performance as well as appearance measures of dichoptic color difference. Third, rather than measuring perceptual distance by referral to a color space in which physically equidistant points are ostensibly perceptually equidistant, such as the CIS UCS color diagram, we have measured perceptual distance psychophysically.

## 2. Methods

## 2.1. Subjects

The two authors, plus a naïve adult male observer were employed as observers. All had normal or corrected-to-normal visual acuity, as well as normal binocular vision and color vision, the last of these assessed by the Ishihara's Test for Color Vision Deficiency.

#### 2.2. Equipment and calibration

The stimuli were displayed on a Sony model GDM-F 520 color monitor controlled by a Matrox Parhelia graphics card whose framestore allowed luminances to be specified with a resolution of 8 bits per gun. This provided a resolution of approximately 1° of color angle in the color space employed, which for the smallest thresholds measured, the Monocular Color Difference Thresholds (MCDTs) provided three steps to threshold, and for the Dichoptic Color Difference Thresholds (DCDTs), the main topic of interest, 14 steps to threshold. Gun luminances and spectral emission functions were calibrated with a Photo Research SpectraScan PR 645 spectral radiometer, and luminances were linearized through look-up tables. The CIE 1931 chromaticities of the phosphors were red: x = 0.623, y = 0.340; green: x = 0.294, y = 0.608; blue: x = 0.149, y = 0.076.

Observers viewed the stimuli via a custom-built 8-mirror Wheatstone stereoscope, with an aperture of  $10 \times 10^{\circ}$ , and a viewing distance along the light path of 55 cm.

## 2.3. Stimuli

Each stimulus consisted of four, 4.57° diameter circular color patches presented on a  $10 \times 10^{\circ}$  gray background. Two of the patches (either upper or lower) were identical in color direction (the test pair), while the remaining two were different in color direction (comparison pair). When fused through the stereo-apparatus the subject saw two patches, one above the other, in which one patch was the test pair, the other the comparison pair. Example test-pairs are shown in Fig. 2c. The stimuli had a mean luminance of 25.7 cd/m<sup>2</sup> and varied around a mean chromaticity equivalent to Illuminant C (CIE 1931 x, y = 0.313, 0.334), which is mid-gray. The chromatic contrasts of the stimuli were defined relative to neutral gray background, according to their angle and contrast within a scaled version of the DKL color space. Contrasts were scaled so that the L - M contrast was ( $r_{mb} - 0.6568$ ) \* 1955 and the S - (L + M) contrast was  $(b_{mb} - 0.01825) * 5533$  where 0.6568 and 0.01825 are the r, b values of illuminant C, and 1955 and 5533 are the constants that scale contrasts along the L - M and S - (L + M)axes respectively. A contrast matching procedure was employed to scale the contrasts for each observer (see below), in which observers matched the perceived L - M and L + M contrasts relative to a fixed S - (L + M) contrast. Luminances were linearized using calibration tables and isoluminance was determined photometrically.

## 2.4. Procedures

#### 2.4.1. Unique and binary hue settings

The task was to set a "best example" of a given unique or binary hue using a two randomly-interleaved staircase procedure (Malkoc, Kay, & Webster, 2005; Webster et al., 2000a; Webster et al., 2000b). Subjects first adapted to a neutral gray background for 1 min. Each stimulus was a circular patch 6° in diameter presented in the middle of a  $28 \times 36^{\circ}$  gray field. Stimulus color contrast was the same as in the main part of the experiment (see below). The stimulus was presented repeatedly for 1 s with a 3 s inter-stimulus-interval, and was ramped on and off with a Gaussian envelope of 250 ms. Subjects were required to make a forced-choice judgment about its perceived color. For example, when observers were setting unique green, they responded by pressing a button indicating that the stimulus was either "too blue" or "too yellow", and when observers were setting binary blue–green, they responded



**Fig. 3.** Color angles employed in the experiment. Filled circles represent cardinal colors, open circles intermediate colors, filled triangles unique hues and empty triangles binary hues. Actual colors can be seen by inspection of Fig. 2a.

either "too green" or "too blue". There were 45 trials for each setting, and the hue angle was calculated as the mean angle of the last six reversals from two randomly interleaved staircases. Each observer made six settings for each unique and binary hue, and the values are shown in Fig. 3.

## 2.4.2. Dichoptic Color Difference Thresholds (DCDTs)

The method of constant stimuli was used. Each session began with 1 min of adaptation to a neutral gray background. On each trial, two stimuli were presented above and below fixation, one with and one without a between-eye difference in color. The stimuli were left on the screen until the subject responded, and subjects were encouraged to respond within 2 s. The unlimited exposure duration was a precaution to ensure that the stimuli were properly fused. The directions of the two colors in each dichoptic pair were always centered on the test color direction. There were 16 test color directions, and for each test direction 20 dichoptic pairs with angular differences ranging from 0° to 40°, i.e. at 2° intervals. There were 100 trials for each of the 20 angular differences, making a total of 2000 trials per psychometric function. The different dichoptic pairs were presented in random order in any one session. The task for the subject was to indicate with a mouse button the stimulus with the between-eye difference, which all subjects reported to be the more "lustrous". A beep was given for an incorrect response. A typical session involved between 200 and 400 trials.

## 2.4.3. Monocular Color Difference Thresholds (MCDTs)

The task for measuring MCDTs was the same as that for measuring DCDTs, except that the stimuli were presented side-by-side rather than dichoptically superimposed, such that the observer saw all four patches, two above and two below fixation. We used two methods of 4-patch monocular presentation, one termed "conventional" the other "haploscopic". In the conventional method, the stereoscope was removed and the four patches were viewed by one eye, the other eye being patched. In the haploscopic method, the stereoscope was used to present to the right eye the two patches to the right of fixation (with the left eye viewing the gray background), and to the left eye the two patches to the left of fixation (with the right eye viewing the gray background). The haploscopic method was arguably more directly comparable to the method for measuring DCDTs, where each eye only saw one of each dichoptic pair. For both conventional and haploscopic presentations, subjects were required to indicate whether the top or bottom pair contained the color difference.

#### 2.4.4. Binocular Color Rivalry Thresholds (BCRTs)

Since we were interested in the relationship between our DCDT measure and the more traditional measure of rivalry, we also measured Binocular Color Rivalry Thresholds, or BCRTs. A single dichoptic color patch was repeatedly presented in the middle of the stereoscope aperture with a stimulus exposure duration of 2 s and an inter-stimulus interval of 0.5 s. The difference in color direction of the dichoptic pair was increased or decreased on each trial by 2°. Observers responded either "fused" or "rivalrous" after each stimulus presentation. Subjects were encouraged to respond "rivalrous" when the stimulus appeared inhomogenous, either across space or time, and "fused" when perceptually uniform. Subjects performed 10 ascending and 10 descending runs, making a total of 20 runs. For each run the angular color difference at which subjects switched their decision from fused to rivalrous or vice versa was taken as the rivalry threshold, and the BCRT was determined as the mean rivalry threshold across the 20 runs. There was a significant amount of hysteresis; ascending runs produced rivalry thresholds around 60% higher than descending runs (calculated as the average difference between ascending and descending runs expressed as a percentage of the overall mean).

#### 2.4.5. Perceived color difference

The stimulus arrangement was the same as that for the haploscopic method for measuring MCDTs, i.e. there were four stimulus patches. The top pair was fixed with a mean color direction of 0° or 135°, and an angular color difference given by the subject's DCDT for that condition. The bottom pair was the comparison pair and on each trial had a fixed mean color direction, and an angular difference in color direction that was adjustable by the subject. The task for the subject was to adjust the angular difference in color in the bottom pair until it matched the perceived color contrast be-



**Fig. 4.** Example psychometric function for the measurement of a DCDT. The proportion correct detections of the pair with the dichoptic difference is plotted as a function of the between-eye difference in color difference circles. The continuous line is the best fitting Weibull function, with the threshold determined at the 82% level. Data from subject GI for the condition in which the test color was 90°.

tween the top pair. The procedure was the same as that used for the unique hue settings described above.

#### 2.4.6. Data analysis

The percent correct data were analyzed using the psychometric function tools in Palamedes (Prins & Kingdom, 2009). Each plot was fitted with the Weibull function,  $y = g + (1 - g)\exp(-(x/a)^b)$ , using a maximum-likelihood criterion, with the guessing parameter *g* fixed at 0.5, and the fitted parameters *a* defining the threshold at the 82% level and *b* the slope of the function. Standard errors of the threshold parameter were determined by bootstrap analysis and are shown on the graphs. Example percent correct data and fitted psychometric function are shown in Fig. 4.

## 3. Results

Dichoptic Color Difference Thresholds (DCDTs), Monocular Color Difference Thresholds (MCDTs) and Binocular Color Rivalry Thresholds (BCRTs) are shown in Fig. 5 for 16 test color directions: four cardinal colors (0°, 90°, 180°, and 270°), four intermediate colors (45°, 135°, 225°, and 315°), four unique hues and four binary hues. Stimulus contrast was fixed at 80%. The distance from the center of each plot gives the size of the threshold in degrees. The outermost line with filled circles shows the BCRTs, the middle line DCDTs, and the innermost line haploscopic MCDTs. Table 1 shows for each observer the mean and standard deviation for the three types of threshold across test color direction. We were unable to collect binocular rivalry thresholds for subject GI before he finished his participation.

The upper three graphs in Fig. 5 show each subject's data and reveal a clear ordering of thresholds: BCRTSs (rivalry) > DCDTs (dichoptic) > MCDTs (monocular). The mean and standard deviations (SDs) of the thresholds for each observer and across observers are shown in Table 1. Given that the DCDTs and MCDTs were measured using comparable psychophysical procedures, we calculated the ratio of DCDTs to MCDTs for each test color angle, then calculated the geometric mean and (upper) geometric standard deviations of the ratios across color angles for each observer as well as across observers. These are also shown in Table 1.

The three lower graphs in Fig. 5 show just the DCDT data on expanded axes, together with the points indicating the unique and binary hue settings for each subject. There is no suggestion of minima at either the unique hue or cardinal positions, or maxima in between. This was confirmed by a simple statistical test of correlation between the expected minima/maxima (given arbitrarily by values of value of 0 and 1) and each subject's data at these points. No value of Pearson *R*, whether positive or negative, was significant at the *p* = 0.05 level.

Fig. 6 shows the expanded MCDT data. The continuous lines show MCDTs obtained using the binocular method, dashed lines the haploscopic method. The results for the two methods are very similar.

## 3.1. Is hue a cue?

To measure DCDTs, subjects were required to discriminate between two stimuli, one a dichoptically superimposed pair of different colors, the other a dichoptically superimposed pair of the same color. It is possible that small differences in hue between the two stimuli served as a cue for discrimination. Therefore in a separate experiment we measured DCDTs with and without added mean color jitter. We did this by randomly selecting the test color directions for both members of each forced-choice pair within the range  $-1.5^{\circ}$  to  $+1.5^{\circ}$  of the nominal test color direction. Fig. 7 shows the results for four test color directions for one observer (GM). If



**Fig. 5.** Top row: polar plots of thresholds as function of color angle for three observers. Thresholds in degrees are plotted as distance from the origin. BCRTs (filled circles) are the Binocular Color Rivalry Thresholds. DCDTs (open circles) are the Dichoptic Color Difference Thresholds. MCDTs (filled triangles) are the Monocular Color Difference Thresholds. Error bars are not shown as they are all less than 1°, with the single exception of GI's DCDT 315° condition, which had an error bar of 1.1°. Bottom row: expanded polar plots for just the DCDTs (open circles). Also shown as small filled circles are the unique and binary hue positions for each observer.

#### Table 1

Means and standard deviations (SDs) of haploscopic MCDTs, DCDTs, BCRTs and DCDT/ MCDT ratios, calculated across all test color angles. The DCDT/MCDT ratios were calculated for each test color angle, and the means and SDs of the ratios were calculated as geometric means and upper geometric SDs.

Observer	MCDT		DCDT		BCRT		DCDT/MCDT ratio	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
FK	5.26	2.31	16.1	3.55	49.5	6.64	3.27	1.48
GM	3.41	1.12	14.7	3.61	48.4	9.94	4.67	1.72
GI	3.26	1.23	13.7	2.37			4.34	1.78
Overall	3.98	1.85	14.8	3.31	48.9	8.34	4.05	1.82

anything thresholds are on average slightly lower with the hue jitter, suggesting that hue is unlikely to be a cue for discrimination.

#### 3.2. Effect of stimulus duration

We used unlimited stimulus exposure duration in the experiments described above, in order to ensure the stimuli were fused. To understand more precisely the effect of stimulus duration on DCDTs, we ran an experiment in which we varied stimulus duration between 0 and 1500 ms. Fig. 8 shows the results. As the figure shows, DCDTs decrease as exposure duration increases up to about 250 ms, after which the function is more-or-less flat.

## 3.3. Effect of contrast

Since previous studies have suggested that color saturation is a factor determining binocular fusion and rivalry (reviewed by Hovis (1989)) we tested whether DCDTs were similarly dependent. We used a fixed color angle of 0°, and tested seven different contrast levels (7.93%, 11.66%, 17.15%, 25.2%, 37.04%, 54.43%, 80.00%). Fig. 9 shows the results from the three observers. DCDTs are plotted on a log scale as a function of color contrast, defined in one of two ways. Lines with filled circles are DCDTs measured in terms of angular difference, whereas lines with empty circles show DCDTs in terms of their physical distance on the color circle, measured by  $2k \sin(\theta/2)$ , where  $\theta$  is the DCDT expressed in terms of angular difference, and k is color contrast measured as the distance to the color from the origin. The figure shows that for subjects GM and GI, whereas DCDTs decline with color contrast when defined as angular color difference, they are near flat when measured in terms of color distance at all except very low color contrasts. FKs data however shows a slight upward slope of DCDTs as a function color distance. Overall however, color distance as opposed to color angle better accounts for the pattern of DCDTs as a function of color contrast.

## 3.4. Does perceived color difference correlate with DCDTs?

The previous experiment suggested that the distance between colors in color space accounted for much of the variance in DCDTs





Fig. 6. Comparison of Monocular Color Difference Thresholds (MCDTs) obtained by two methods. Dashed lines with empty triangles are thresholds obtained using the "conventional" method, in which the stimulus pair are shown side-by-side rather than dichoptically-superimposed, and viewed by the same eye. Straight lines with filled circles are thresholds obtained using the "haploscopic" method, in which the two stimuli are again viewed side-by-side, but by different eyes.







Fig. 8. DCDTs as a function of stimulus exposure duration for one subject and a baseline color angle of  $0^{\circ}$ .

when saturation was being manipulated. However, in our earlier main experiment in which contrast, and hence saturation was fixed, we nevertheless found significant variations in DCDTs dependent on color angle. Given that we did not appear to find any color directions with unique DCDT signatures, we decided to test the hypothesis that DCDTs were correlated with the perceptual distance between the dichoptic color pairs (see Section 2). The results are shown in Fig. 10 for the two authors. Significant positive correlations between DCDTs and perceived color difference are found for both observers and both conditions (Pearson *R* values for observer FK are 0.84 (p < 0.01) for reference color angle 0° and 0.69 (p < 0.01) for 135°; observer GM 0.89 (p < 0.01) for 0° and 0.97 (p < 0.01) for 135°). The data suggest that perceived color difference is a strong correlate of Dichoptic Color Difference Thresholds.

#### 4. Discussion

The following summarizes the key findings of our study:

- 1. We have defined a Dichoptic Color Difference Threshold, or DCDT, and found that DCDTs are around 10–20° for 80% contrast dichoptic color pairs defined within a modified version of the MacLeod–Boynton color space.
- 2. DCDTs are larger than Monocular Color Difference Thresholds (MCDTs) but smaller than Binocular Color Rivalry Thresholds (BCRTs).
- 3. DCDTs do not correlate with either the cardinal or unique hue positions in color space.
- 4. DCDTs measured in terms of angular color angular difference are inversely proportional to the degree of color saturation, consistent with the idea that the distance between colors in color space is an important factor in determining DCDTs.
- 5. DCDTs correlate well with the perceived color difference between dichoptic pairs.

Yoonessi and Kingdom (2009), in their study of the detection of between-eye differences in the mean color of images of natural scenes, found that the ratio of dichoptic to monocular thresholds was on average about 2.2. This is lower than the value of 4.05 found in the present study (Table 1), but suggests that the ordering of the thresholds is of general applicability. Why then are thresholds for detecting the difference between two dichoptically superimposed colors higher than when the discriminanda are placed side-by-side? Current models of binocular summation (e.g., Baker, Meese, & Georgeson, 2007; Meese, Georgeson, & Baker, 2006) do



Fig. 9. DCDTs as a function of color contrast. Straight lines with filled circles show thresholds in terms of angular distance, dashed lines with empty circles in terms of linear distance.



Fig. 10. DCDTs as a function of perceived color difference. The top two graphs are for observer GM, and the bottom two graphs for observer FK. Ref = reference color angle.

not explicitly deal with the detection of binocular differences, so it will be interesting to see if they can be made to do so. On the other hand Yoonessi and Kingdom (2009) suggested that the difference between dichoptic and monocular thresholds might lie in the fact that dichoptic differences are signaled via specialized channels for signaling binocular differences. Such channels are supported by both theory (Li & Atick, 1994) and evidence (Cohn & Lasley, 1976; Cohn, Leong, & Lasley, 1981; May, Zhaoping, & Hibbard, 2012). Yoonessi and Kingdom (2009) speculated that the gains of binocular-differencing channels might be reduced by activity in binocular-summation channels (which sum the two eye's signals), causing the higher thresholds for the dichoptic compared to monocular (side-by-side) stimuli.

The main finding of the present study is that dichoptic difference thresholds for chromatic stimuli are best predicted by perceived color difference, rather than by the cardinal or unique hue mechanisms.

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#### References

Alais, D., & Blake, R. (2005). Binocular rivalry. Cambridge, MA: MIT Press.

- Baker, D. H., Meese, T. S., & Georgeson, M. A. (2007). Binocular interaction: Contrast matching and contrast discrimination are predicted by the same model. *Spatial Vision*, 20, 397–413.
- Blake, R. (2001). Primer on binocular rivalry, including controversial issues. Brain and Mind, 2, 5–38.
- Cohn, T. E., & Lasley, D. J. (1976). Binocular vision: Two possible central interactions between signals from two eyes. *Science*, 192, 561–563.
- Cohn, T. E., Leong, H., & Lasley, D. J. (1981). Binocular luminance detection: Availability of more than one central interaction. *Vision Research*, 21, 1017–1023.

- Danilova, M. V., & Mollon, D. D. (2010). Parafoveal color discrimination: A chromaticity locus of enhanced discrimination. *Journal of Vision*, 10(1), 1–9 (article no. 4).
- De Valois, R. L., & De Valois, K. K. (1993). A multi-stage color model. Vision Research, 33, 1053–1065.
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, 357(1), 241–265.
- D'Zmura, M. (1991). Color in visual search. Vision Research, 31(6), 951–966. Flanagan, P., Cavanagh, P., & Favreau, O. E. (1990). Independent orientationselective mechanisms for the cardinal directions of color space. Vision Research, 30, 769–778.
- Formankiewicz, M. A., & Mollon, J. D. (2009). The psychophysics of detecting binocular discrepancies of luminance. Vision Research, 49, 1929–1938.
- Hering, E. (1964). Outlines of a theory of the light sense. Cambridge, Massachusetts: Harvard University Press.
- Hovis, J. K. (1989). Review of dichoptic color mixing. Optometry and Vision Science, 66, 181–190.
- Hurvich, L. M., & Jameson, D. (1955). Some quantitative aspects of an opponentcolors theory. II. Brightness, saturation, and hue in normal and dichromatic vision. Journal of the Optical Society of America, 45, 602–616.
- Hurvich, L. M., & Jameson, D. (1957). An opponent-process theory of color vision. Psychological Review, 64, 384–404.
- Ikeda, M., & Nakashima, Y. (1980). Wavelength difference limit for binocular color fusion. Vision Research, 20, 693–697.
- Ikeda, M., & Sagawa, K. (1979). Binocular color fusion limit. Journal of Optical Society of America, 69, 316–321.
- Kingdom, F. A. A., & Prins, N. (2010). Psychophysics: A practical introduction. Academic Press (an imprint of Elsevier).
- Krauskopf, J., & Gegenfurtner, K. (1992). Color discrimination and adaptation. Vision Research, 32(11), 2165–2175.
- Krauskopf, J. (1999). Higher order color mechanisms. In K. R. Gegenfurtner & L. T. Sharpe (Eds.), Color vision: From genes to perception (pp. 304–316). Cambridge: Cambridge University Press.
- Krauskopf, J., Williams, D. R., & Heeley, D. W. (1982). Cardinal directions of color space. Vision Research, 22, 1123–1131.
- Krauskopf, J., Williams, D. R., Mandler, M. B., & Brown, A. M. (1986). Higher order color mechanisms. Vision Research, 26(1), 23–32.
- Krauskopf, J., Wu, J., & Farell, B. (1996). Coherence, cardinal directions, and higherorder mechanisms. Vision Research, 36(9), 1235–1245.
- Li, Z., & Atick, J. J. (1994). Efficient stereo coding in the multiscale representation. Network, 5, 157–174.
- Li, A., & Lennie, P. (1997). Mechanisms underlying segmentation of colored textures. Vision Research, 37(1), 83–97.
- MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of Optical Society of America*, 69, 1183–1195.
- Malkoc, G., Kay, P., & Webster, M. A. (2005). Variations in normal color vision. IV. Binary hues and hue scaling. *Journal of the Optical Society of America A*, 22, 2154–2168.
- May, K. A., Zhaoping, L., & Hibbard, P. B. (2012). Perceived direction of motion determined by adaptation to static binocular images. *Current Biology*.
- Meese, T. S., Georgeson, M. A., & Baker, D. H. (2006). Binocular contrast vision at and above threshold. *Journal of Vision*, 6(11), 1224–1243 (article no. 7).
- Monnier, P., & Nagy, A. L. (2001). Uncertainty, attentional capacity and chromatic mechanisms in visual search. *Vision Research*, 41(3), 313–328.
- Mullen, K. T., Cropper, S. J., & Losada, M. A. (1997). Absence of linear subthreshold summation between red-green and luminance mechanisms over a wide range of spatio-temporal conditions. *Vision Research*, 37(9), 1157–1165.

- Mullen, K. T., & Losada, M. A. (1994). Evidence for separate pathways for color and luminance detection mechanisms. *Journal of the Optical Society of America A*, 11, 3136–3151.
- Mullen, K. T., & Losada, M. A. (1999). The spatial tuning of color and luminance peripheral vision measured with notch filtered noise masking. *Vision Research*, 39, 721–731.
- Mullen, K. T., & Sankeralli, M. J. (1999). Evidence for the stochastic independence of the blue-yellow, red-green and luminance detection mechanisms revealed by subthreshold summation. *Vision Research*, 39, 733–745.
- Parkes, L. M., Marsman, J.-B. C., Oxley, D. C., Goulermas, J. Y., & Wuerger, S. M. (2008). Multivoxel fMRI analysis of color tuning in human primary visual cortex. *Journal of Vision*, 9(1), 1–13 (article no. 1).
- Prins, N., & Kingdom, F. A. A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. <a href="http://www.palamedestoolbox.org">http://www.palamedestoolbox.org</a>>.
- Sagawa, K., & Ikeda, M. (1978). Color disparity threshold for stable binocular color fusion. Kogaku (Japanese Journal of Optics), 7, 103–113.
- Sankeralli, M. J., & Mullen, K. T. (1997). Postreceptoral chromatic detection mechanisms revealed by noise masking in three-dimensional cone contrast space. Journal of the Optical Society of America A, 14(10), 2633–2646.
- Valberg, A. (2001). Unique hues: An old problem for a new generation. Vision Research, 41, 1645–1657.
- Webster, M. A., Miyahara, E., Malkoc, G., & Raker, V. E. (2000a). Variations in normal color vision. I. Cone-opponent axes. *Journal of the Optical Society of America A*, 17(9), 1535–1544.
- Webster, M. A., Miyahara, E., Malkoc, G., & Raker, V. E. (2000b). Variations in normal color vision. II. Unique hues. *Journal of the Optical Society of America A*, 17(9), 1545–1555.
- Webster, M. A., & Mollon, J. D. (1991). Changes in color appearance following postreceptoral adaptation. *Nature*, 349, 235–238.
- Webster, M. A., & Mollon, J. D. (1993). Contrast adaptation dissociates different measures of luminous efficiency. *Journal of Optical Society of America A*, 10, 1332–1340.
- Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. Vision Research, 34(15), 1993–2020.
- Wuerger, S. M., Atkinson, P., & Cropper, S. (2005). The cone inputs to the unique-hue mechanisms. Vision Research, 45, 3210–3223.
- Yoonessi, A., & Kingdom, F. A. A. (2009). Dichoptic difference thresholds for uniform color changes applied to natural scenes. *Journal of Vision*, 9(2), 1–12 (article no. 3). Zaidi, Q., & Halevy, D. (1993). Visual mechanisms that signal the direction of color

changes. Vision Research, 33, 1037–1051.

## Further reading

- Dawson, S. (1915). The experimental study of binocular color mixture. British Journal of Psychology, 17, 510–551.
- Guth, S. L. (1991). Model for color vision and light adaptation. Journal of Optical Society of America A, 8, 976–993.
- Mattiello, M. L. F., Biondini, A., & Salinas, H. (1998). The dichoptic chromatic vision. Die Farbe, 44, 127–147.
- Mattiello, M. L. F., Salinas, H., & Benavente, C. (2000). Dichoptic discrimination of saturation. Color Research and Application (Supplement Volume), 26, 53–56.
- Pokorny, J., & Smith, V. C. (1977). Evaluation of single-pigment shift model of anomalous trichromacy. *Journal of Optical Society of America A*, 67, 1196–1209.
- Sagawa, K. (1982). Dichoptic color fusion studies with wavelength discrimination. Vision Research, 22, 945–952.
- Thomas, F. H., Dimmick, F. L., & Luria, S. M. (1961). A study of binocular color mixture. Vision Research, 1, 108–120.