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Visual Mechanisms that Signal the Direction of Color Changes

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Evidence is presented for a visual capacity specialized to sense the chromatic direction of change in colors over time. Discrimination thresholds were measured between pairs of suprathreshold color changes presented in consecutive intervals. In one interval, the color of a spatially uniform disk was changed at a constant speed along the circumference of a circle in an equiluminant color plane. In the other, an instantaneous change, which can be described as a vector in the equiluminant plane, was added to the circular color modulation. Averaging across conditions showed that the threshold for discriminating between a pair of purely temporal color changes was approximately proportional to the cosine of the color angle between them. The model that is presented to account for these results is based on parallel directional-color mechanisms that are tuned to different directions in color-space and are responsive to change in one color direction but not its opposite.

Color vision Higher-level color mechanisms Temporal processing

INTRODUCTION

The perceived colors of lights and objects sometimes change markedly in normal everyday conditions. The color of a light may change due to an alteration in the spectral emittance, passage through different filtering materials, or spectrally selective reflection. The color of an object may change due to changes in illuminant, inter-reflections or spectral reflectance (Nassau, 1983). Some of these perceived changes seem to have sufficient importance that words have evolved in ordinary language to describe them succinctly. For example, one meaning of the word "blush" is given in Webster's dictionary as "a reddening of the face". Austin (1962) showed that the analysis of different cases and constructions of appropriate ordinary language expressions is capable of providing reliable clues to sensory capacities. However, it is not clear from the manner that words like "blush" are used, nor from introspection, whether an observer has the capacity to perceive a continuous reddening or only a capacity to compare a rosier face (with respect to the surroundings) to the remembered color of the same face.

The issue of reminiscent of the argument about whether observers perceive "motion" *per se* of an object or only compare memories of positions over time (Dimmick & Karl, 1930; Kinchla & Allan, 1969). Some of the most convincing psychophysical evidence for a specialized capacity for motion perception comes from habituation experiments. After prolonged viewing of motion in one direction, stationary objects are seen as moving in the opposite direction (Wohlgemuth, 1911), the perceived null velocity corresponds to a non-zero velocity in the habituating direction (Sachtler & Zaidi, 1990), and contrast thresholds are elevated more for stimuli moving in the habituating than in the opposite direction (Sekuler & Ganz, 1963; Pantle, 1978).

In a similar fashion, habituation experiments have provided evidence for the existence of visual mechanisms specialized for responding to changes in color (Krauskopf, Williams & Heely, 1982; Krauskopf & Zaidi, 1986). The habituating stimulus in these experiments was a uniform disk whose color was modulated as a temporal sawtooth along a cardinal color line through mid-white, and the tests were step changes in the color of the disk from mid-white towards the two ends of the habituating color line. The results showed that thresholds for detecting step changes in opposite directions along a color line could be selectively elevated. For example, after a habituating modulation along a "blue–yellow" equiluminant line, when the ramp phase of the sawtooth was from "blue" to "yellow", thresholds for "yellow" steps were elevated more than thresholds for "blue" steps. When the sign of the habituating sawtooth was reversed, thresholds towards "blue" were elevated more than thresholds towards "yellow".

Krauskopf *et al.* (1982) noted that the ability to elevate threshold selectively in one direction relative to the complemenary direction must imply that stimuli in these directions are processed at least in part by different mechanisms. This rules out the standard type of opponent mechanisms which are simple linear combinations of cone signals and which respond with equal magnitude but opposite sign to two lights of complementary colors (e.g. Schrodinger, 1925; Boynton, 1979).

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The sawtooth habituation results, however, have even stronger implications. The results cannot be explained in terms of mechanisms formed through half-wave rectification of standard opponent mechanisms. For example, distinct "yellow" and "blue" mechanisms could be formed through half-wave rectification of a "blue–yellow" mechanism. When the ramp phase of the "blue–yellow" equiluminant habituating sawtooth is from "blue" to "yellow", the response of the "blue" mechanism starts at a maximum at the "blue" end, decreases linearly to zero at the mid-white, remains zero to the "yellow" end, and jumps to a maximum at the "blue" end. When the sign of the sawtooth is reversed, the response of the "blue" mechanism starts at zero at the "yellow" end, remains zero till the mid-white, increases linearly to a maximum at the "blue" end, and jumps to zero at the "yellow" end. This type of mechanism does not have the ability to sense whether its response is increasing or decreasing at any point in time. Consequently, the response of the "blue" mechanism is modulated equally by the two habituating stimuli. If equal stimulation leads to roughly equal desensitization, this type of mechanism predicts that threshold elevations for "blue" steps should be equal after both signs of habituating modulation. By similar reasoning, so should threshold elevations for "yellow" steps. Therefore, these types of mechanisms cannot be the substrate for the asymmetric empirical results.

The results for each color line require a pair of mechanisms whose response is a function of the sign of chromatic change, e.g. one of which is more sensitive to changes from "blue" toward "yellow" and one to changes from "yellow" toward "blue". Post-opponent mechanisms that detect whether the response of an opponent mechanism is increasing or decreasing over a period of time would have the required property. Zaidi and Halevy (1991) presented one scheme for deriving pairs of "directional-color" mechanisms each exclusively responsive to temporal change in one direction along a color line. The scheme takes the rectified derivative of the output of each opponent mechanism with respect to time. The differentiator is preceded by a temporal filter that attenuates high frequencies. This filter is used to keep the output of the differentiator within bounds, and to predict that the ramp phase of the 1 Hz sawtooth has the greater desensitizing effect. This class of "directional-color" mechanisms could also account for the perceptual effects of prolonged exposure to sawtooth brightness modulation described by Anstis (1967).

In the present study, our aim was to analyze visual responses to exclusively temporal changes in color. The main issue is whether discrimination between temporal chromatic changes is subserved by "directional-color" mechanisms. The second issue is how many such mechanisms there are and, in particular, whether there are "multiple" mechanisms tuned to chromatic directions other than just the four directions of color-opponent theory (Schrodinger, 1925) or the four chromatic directions along the cardinal axes (Krauskopf, Williams & Heely, 1986). The experimental procedure consisted of the measurement of discrimination thresholds between pairs of suprathreshold color changes that were presented in separate time intervals and could not be differentiated on the basis of spatial cues. One interval of every trial consisted of a "background" change in which the color of a spatially uniform disk was changed along the circumference of an equiluminant color circle. The other interval was a "probe" change in which an instantaneous change along an equiliminant color vector was added to the background modulation. Three parameters were varied across trials: the angular color direction of the probe vector, the phase angle of the background modulation at which the probe was added, and the manner (clockwise or counter-clockwise) of the background modulation. We used the direction-selective differences between thresholds to derive a model of a specialized visual capacity to sense the direction of temporal color changes.

EXPERIMENT

Background modulation

The chromaticities of the set of lights used in this study are depicted in Fig. 1 as an equiliminant color plane. The center of the diagram, *W*, is an achromatic light. The colors are specified in terms of the two equiluminant cardinal axes of Krauskopf *et al.* (1982) as represented in the chromaticity coordinates of the MacLeod and Boynton (1978) diagram. The triplets represent relative (L, M, S) cone excitations (Smith & Pokorny, 1975). Along the horizontal axis, L- and M-cone excitations change linearly in equal and opposite units so that their sum and S-cone excitations are kept constant. Along the vertical axis, S-cone excitation changes linearly whereas L- and M-cone excitations are constant. The dominant hues of lights around the circumference are approximately reddish at an angle of 0 deg, yellowish at 90 deg, greenish at 180 deg and violet at 270 deg. In this paper, the terms "angle" and "direction" will always be used in reference to the angles around the color plane.

The color of the "background" light was changed along the circumference of the circle in Fig. 1. A

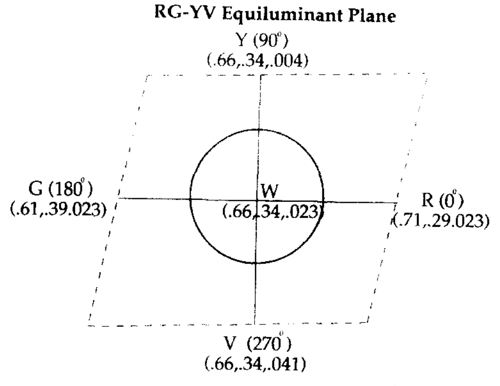

FIGURE 1. Equiluminant color plane representing range of lights used. L-, M- and S-cone excitations in MacLeod and Boynton (1978) chromaticity coordinates. The circle depicts the lights used as background modulation. The parallelogram depicts the equiluminant gamut available from the equipment at a luminance of 49.5 cd/m^2.

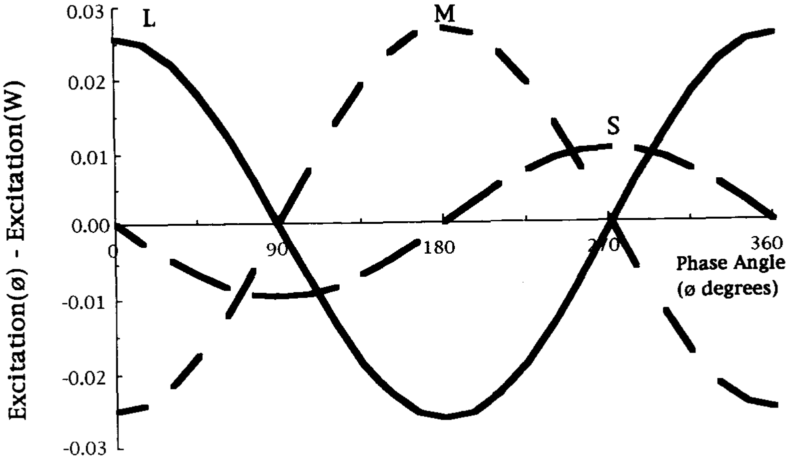

FIGURE 2. Excitation of L-, M-, and S-cones for each phase angle around the circle in Fig. 1, relative to excitation at W.

complete excursion around the color circle modulates the excitation of each of the three classes of cones through one complete sinusoidal cycle. The phase of the background modulation will be defined in terms of the color angles shown in the figure. For each phase angle around the circle, Fig. 2 shows the excitation of the L, M and S cones at the circumference, minus the excitation at the central white. The peak of the modulation occurs at 0 deg for L, at 180 deg for M and at 270 deg for S cones. For all colors on the circle, the response of any post-receptoral mechanism that linearly combines cone signals is given by the appropriate linear combination of the three sinusoidal curves in Fig. 2. As an illustration, the responses of two linear post-receptoral mechanisms at different phase angles along the circle are shown in Fig. 3. The responses of these two mechanisms are consistent with the two chromatic cardinal mechanisms of Krauskopf *et al.* (1982) and orthogonal to each other in the space defined by Fig. 1. As a consequence of a property of linear combinations, the response curves in Fig. 3 have the same frequency as the curves in Fig. 2.

Modulating the color of the background around an equiluminant circle has a number of advantages for exploring the properties of directional-color mechanisms. First, changing colors at a uniform angular velocity around the circle stimulates the early linear stages of the color system in a sinusoidal fashion, and thus provides a sinusoidal input to mechanisms at higher levels. Sinusoidal inputs to a system are useful not only as a basis for tests of linearity, but also as a means for characterizing linear operators and some classes of non-linear operators. Second, the phases of the peaks of the L-, M- and S-cone modulations are separated by multiples of 90 deg (Fig. 2), thus making it easier to define the spectral properties of directional-color mechanisms in terms of cone signals. In response to this modulation, L and M signals are perfectly negatively correlated, whereas in general these signals are highly positively correlated because of the similarity between L and M spectral absorption curves. Third, just as non-direction-selective spatial mechanisms can respond to stimuli moving across their receptive fields, signals from cones and linear opponent mechanisms will change in response to color changes. However, other than sluggish adaptation effects, the response will be a function of the instantaneous color, irrespective of the manner of the change (clockwise vs counter-clockwise). Therefore, the response of directional-color mechanisms can be isolated by comparing the effects of clockwise to counter-clockwise modulation. Fourth, by measuring thresholds for the incremental difference between two color changes, instead of between a change and a steady background, the differential response of each directional-color mechanism can be estimated over an extended range. This procedure is analogous to Craik's (1938) measurements of differential-sensitivity at brightness levels different from the brightness of the steady adapting background, and measurements of color

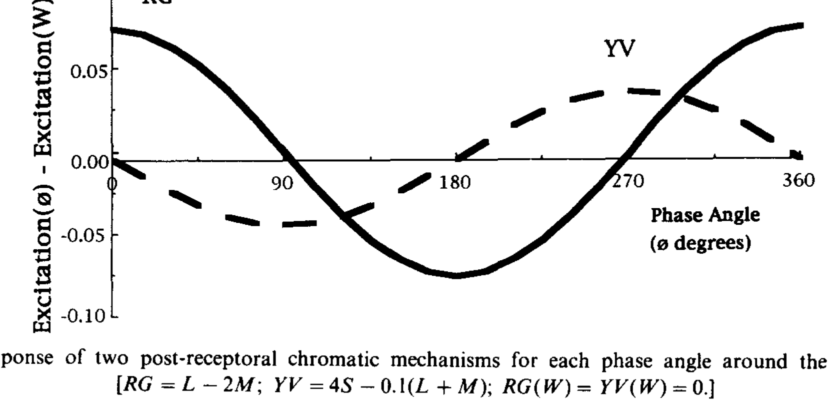

FIGURE 3. Response of two post-receptoral chromatic mechanisms for each phase angle around the circle in Fig. 1. [$RG = L - 2M$; $YV = 4S - 0.1(L + M)$; $RG(W) = YV(W) = 0$.]

discrimination around points in color-space that are different from the color of the adapting light (Zaidi, Shapiro & Hood, 1992).

Spatial configuration

The spatial configuration used in this study is shown in Fig. 4. A uniformly colored disk, subtending 8 deg of visual angle, was displayed in the center of a square white steady field of equal luminance (49.5 cd/m^2) subtending 10 deg of visual angle. A central dark fixation spot (1.5 min of arc) was continuously visible. The color of the disk was changed around the circumference of the color circle and probe color vectors were added to the background colors. There was thus a temporal cue when the probe was added, but no spatial cue.

Experimental procedure

After adapting to a steady light metameric to W in Fig. 1, the observer was presented with a number of trials each consisting of a background and a probe color change presented in separate time intervals in random order. In each trial, the color of the disk started from a random point on the circumference of the circle in Fig. 1 and was changed along the circumference in either the clockwise or counter-clockwise manner. In the background interval, the color of the disk was changed along the circle uninterrupted at a constant angular velocity. One example of a trial is depicted in Fig. 5. The background interval is shown in the left panel and the probe interval in the right panel. In this particular trial, the probe change was in the direction of a vector pointing towards 270 deg. In the probe interval, this vector was added to the color of the disk when the phase angle of the background modulation reached 270 deg. There was thus an abrupt change in the color of the disk. After the addition of the probe, the color of the disk was continuously changed in the counter-clockwise manner while the magnitude of the probe vector was linearly decreased to zero within a quarter of a cycle. Consequently, the appearance of the two intervals differed most at the instant that the probe was added, and the two intervals appeared identical except during the quarter-cycle following the increment. To help readers in visualizing the difference between the two intervals, a gray-level analog is presented in Fig. 6.

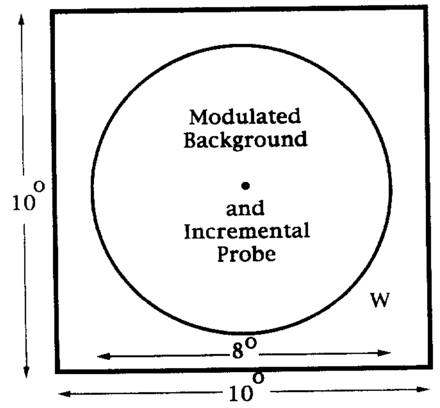

FIGURE 4. Spatial configuration of stimulus.

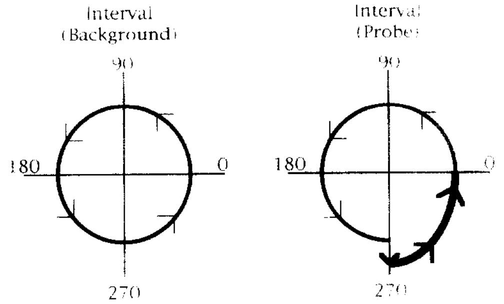

FIGURE 5. Chromatic sequences of a pair of color changes in a typical trial. The color of the background changes in the counter-clockwise direction.

In the background interval, the color of the disk is shown changing continuously from dark to light and back. In the probe interval, the addition of the probe created a discontinuous change. In each trial, observer DAH was required to identify which of the two intervals contained the abrupt change due to the probe increment. Observer QZ's task was to decide whether the changes in the two intervals were discriminably different. The two observers' results agreed with one another so that the difference in methods was of litte import.

The temporal sequence of a typical trial is described in Fig. 7. Prior to the commencement of the trial, the color of the disk was metameric to the steady white surround. At the onset of a trial the color of the disk was set to a random phase angle ϕ on the circumference of the color circle. The color was then modulated at 0.46 Hz through at least one complete circle before the first test interval which commenced at the predetermined background phase. In the trial that is illustrated, a probe

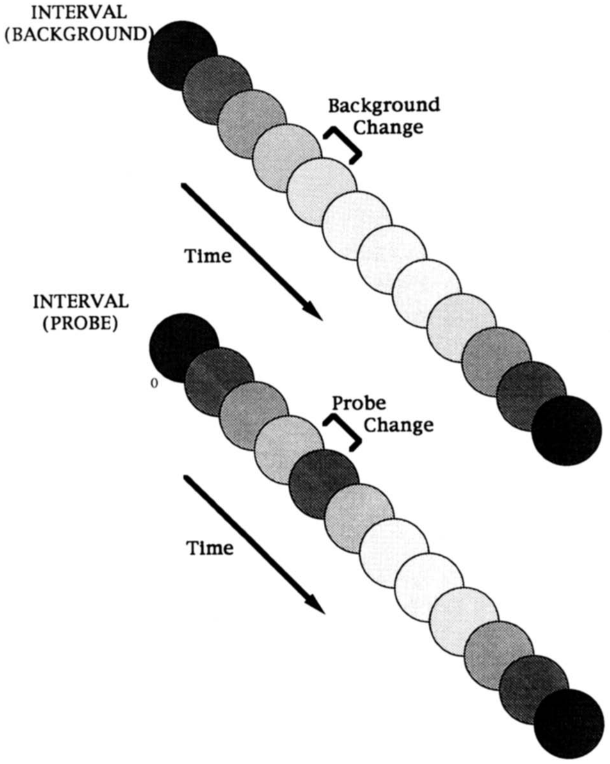

FIGURE 6. Gray-level analog of the observer's view of stimulus modulation in a typical trial.

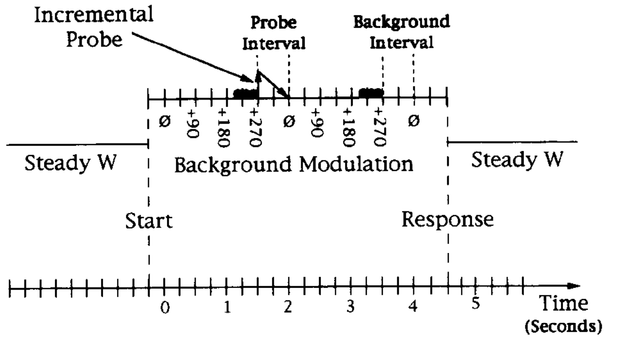

FIGURE 7. Temporal sequence for a two-interval trial. The background modulation was in the counter-clockwise direction, and the probe was added at a background phase of 270 deg. The dark dots represent the three beeps that signaled the onset of each interval.

vector was added at that instant. Each test interval lasted for a quarter of a cycle. After the first interval, the modulation continued until the second interval at the same phase was reached. Since the second interval was not a probe interval, a probe vector was not added. Subsequent to the second interval, the modulation continued until the observer responded. Three beeps, indicated by dots, signaled the onset of each interval. We chose this particular procedure after discarding a number of other spatial configurations and temporal sequences. Pilot experiments had revealed that observers responded exclusively to the temporal change only if there was no spatial cue as to which interval contained the incremental probe. In particular, if the probe and the modulated background were not spatially coincident, then the probe and background intervals could be differentiated on the basis of spatial configuration, and the results were quite different. In addition, reliable measurements were possible only if there were no abrupt temporal changes shortly before or after the test intervals.

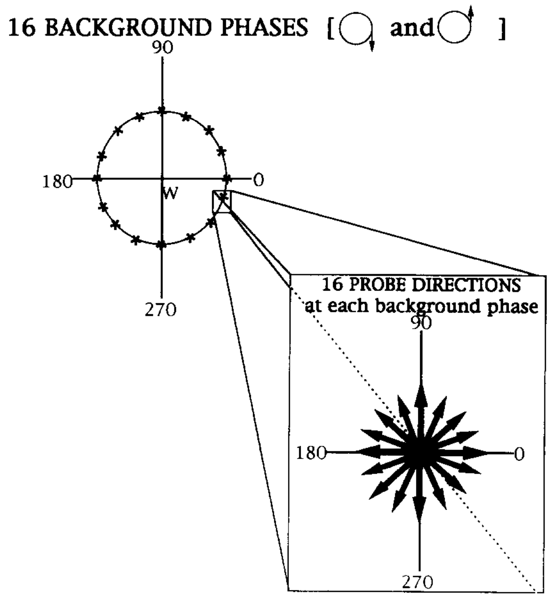

FIGURE 8. Complete set of experimental conditions. Two directions of background modulation (clockwise and counter-clockwise), 16 background phases (stars), and 16 probe directions (thick arrows).

Experimental parameters

Three parameters were varied in the experiment: the manner of the background modulation, the phase of the background modulation at which the probe was added, and the color direction of the probe vector. The complete set of conditions is depicted in Fig. 8. In a particular trial, the color of the background was changed in either the clockwise or counter-clockwise manner around the color circle. Thresholds for color changes were measured at sixteen background phases (0, 22.5, . . . , 337.5 deg). At each background phase, probe vectors were added in sixteen directions (0, 22.5, . . . , 337.5 deg). There were, thus, a total of 512 different conditions. A double-random staircase was run for each condition, varying the

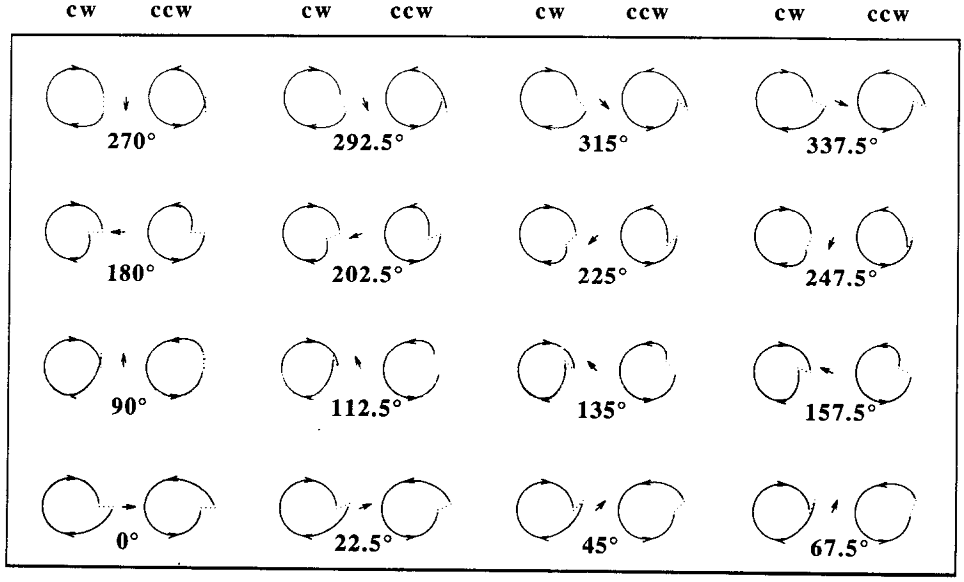

FIGURE 9. Complete set of chromatic sequences for probe changes at a background phase of 0 deg. Arrows on circles represent direction of background modulation (cw = clockwise; ccw = counter-clockwise). Arrows and numbers between circles represent the color angle of the probe vector. The dotted segments denote probes. The color of the disk changes instantaneously across the dotted segment.

length of the probe vector to estimate the 79% correct point on the psychometric curve. The 1024 staircases were run simultaneously (randomly interleaved) over a period of many months in short sets of 64 randomly chosen trials. Each data point was based on an average of 10 reversals of the staircases.

The complete set of chromatic sequences for probe intervals at a background phase of 0 deg are shown in Fig. 9. The background modulation is shown as segments of circles in solid lines. For every probe direction, the figure shows a clockwise and a counter-clockwise sequence around the color circle, indicated by the arrows on the circles. The instantaneous probe increment is shown in dotted lines. Between each pair, the figure shows a number and an arrow. These correspond to the color direction of the probe vector added to the background modulation. In a probe interval, the color of the disk could only be on the solid portion of a sequence, i.e. at the third beep the color jumped from one end of the dotted line to the other. Since the background phase was zero, the number of degrees also represent the angular difference between the background phase and the color angle of the probe direction. For any other background phase the chromatic sequences will have the same shape, except that each sequence shown in this figure will be rotated through an angle equal to the background phase.

Equipment and calibration

Stimuli were displayed on the screen of a Tektronix 690SR color television monitor. The observer viewed the screen binocularly through natural pupils. The screen was refreshed at 120 interlaced frames per sec. The distance between the screen and the observer was kept constant at 2 m by means of a fixed chin and forehead rest. The display consisted of 480 × 512 pixels, subtending 10 × 10.67 deg of visual angle. Images were generated using an Adage 3000 raster-based frame-buffer generator. The Adage allowed for 10-bit specification of the output of each TV gun leading to a palette of 2^{30} possible colors of which 256 could be displayed on any frame. All stimulus generation and data collection was done automatically under computer control.

As the first step in the calibration procedure, at the maximum output for all three guns (R, G, B), hardware controls on the Tektronix were manipulated to achieve an achromatic color of 99 cd/m^2 ($R = 24.2$, $G = 64.0$, $B = 10.8$ cd/m^2). The hardware controls were then locked. For each gun, the luminance of the screen was measured with a UDT photometer at each of the 1024 possible output values during 10,000 up and down series. For each gun the luminance of the screen was a non-linear function of voltage. The stored average values were used to compute back-transform tables to enable linear specification of the output of the guns. The calibration procedure also ascertained that the outputs of the three guns were independent.

For any light I, the fractional luminance of each of the three phosphors (B_I, G_I, R_I) was defined as the luminance of the phosphor at I divided by the luminance of the phosphor at the maximum output. The W point in Fig. 1 corresponds to the achromatic color of the screen when all three guns were set at the mid-point of their range, i.e. $R_W = G_W = B_W = 0.5$. The luminance at W was therefore equal to 49.5 cd/m^2.

The R, G, B values for lights on the axes were determined by first converting the manufacturer-supplied CIE chromaticity of the phosphors to cone excitations (Smith & Pokorny, 1975). In the units used in Fig. 1, the S, M, and L values at the maximum output of the three phosphors R, G and B are shown in equations (1), (2), and (3):

$$(S_B, M_B, L_B) = (0.039, 0.104, 0.114) \tag{1}$$

$$(S_G, M_G, L_G) = (0.0054, 0.498, 0.795) \tag{2}$$

$$(S_R, M_R, L_R) = (0.0007, 0.084, 0.405). \tag{3}$$

Cone excitations L_I, M_I, and S_I for any light I, were calculated by using the S, M and L values of the phosphors with their fractional luminances at I:

$$L_I = B_I L_B + G_I L_G + R_I L_R \tag{4}$$

$$M_I = B_I M_B + G_I M_G + R_I M_R \tag{5}$$

$$S_I = B_I S_B + G_I S_G + R_I S_R. \tag{6}$$

In Fig. 1, for every color H on the horizontal axis that is different from W, S_H is equal to S_W and $L_H + M_H$ is equal to $L_W + M_W$. Therefore:

$$B_H S_B + G_H S_G + R_H S_R = B_W S_B + G_W S_G + R_W S_R \tag{7}$$

and

$$\begin{aligned} &B_H(L_B + M_B) + G_H(L_G + M_G) + R_H(L_R + M_R) \\ &= B_W(L_B + M_B) + G_W(L_G + M_G) + R_W(L_R + M_R). \end{aligned} \tag{8}$$

The only unknowns in equations (7) and (8), are R_H, G_H and B_H. The gun values for the full gamut of displayable colors on the horizontal axis are found by solving these two equations for B_H and G_H as R_H is varied from 0 to 1.

For every color V on the vertical axis that is different from W, S_V is not equal to S_W but L_V is equal to L_W and M_V to M_W. Therefore:

$$B_V L_B + G_V L_G + R_V L_R = B_W L_B + G_W L_G + R_W L_R \tag{9}$$

and

$$B_V M_B + G_V M_G + R_V M_R = B_W M_B + G_W M_G + R_W M_R. \tag{10}$$

The gun values for colors on the vertical axis are found by simultaneously solving equations (9) and (10) for G_V and R_V, as B_V is varied from 0 to 1.

The dashed boundary shows the range of chromaticities that could be displayed at a luminance of 49.5 cd/m^2. To facilitate color calculations, the equiluminant plane was specified in polar coordinates with the two primary axes set orthogonal to each other, as shown in Fig. 1. The stability of the calibration was checked periodically by measuring the chromaticity and luminance of a number of standard points with a Minolta colorimeter. No adjustments were needed during the course of this study. The experiment was run in a darkened room without any significant ambient light reflected off the screen.

Observers

The two authors were the observers. QZ is a normal trichromat. DAH's Rayleigh match was on the protanomalous edge of the normal range and he passed D15. The initial equiluminant plane was based on the CIE 2 deg spectral luminosity function, V_λ. On the basis of HFP measurements for 16 pairs of complementary colors on the circumference of the circle, the plane had to be tilted 4 deg in elevation for DAH and < 1 deg for QZ.

Results

We have examined the results in a number of ways. A direct method to study the properties of direction-selective color-change mechanisms would be to consider each background change as a standard and to compare the lengths of vectors in different color directions required to discriminate probe changes from this standard. However, color-matching space is only invariant up to affine transformations (Schrodinger, 1920; Resnikoff, 1974; Zaidi, 1992), i.e. even though cone excitations change linearly along any color line in Fig. 1, the units of the two axes are entirely arbitrary relative to each other. Consequently, it is not possible to compare distances in different color directions without first defining comparable units in each direction. We use one such metric later in this section. However, any metric used for this purpose will have some arbitrary aspects and limitations (Snapper & Troyer, 1971).

As an alternate, we used an analysis that did not depend on arbitrary metric assumptions. For each probe vector, we compared the length of a probe vector at discrimination threshold at a particular phase of counter-clockwise background modulation to the threshold length for the same probe vector at the same phase of clockwise background modulation. For this purpose an index of direction selectivity (IDS) was computed for each probe direction and background phase combination:

$$\mathrm{IDS}(\delta, \phi) = \log \frac{\text{counter-clockwise}}{\text{clockwise}} = \log \frac{T_{\delta,\phi,\mathrm{ccw}}}{T_{\delta,\phi,\mathrm{cw}}} \quad (11)$$

where $T_{\delta,\phi,w}$ was the measured discrimination threshold, δ the probe direction, ϕ the background phase and w the manner of the background modulation. For any (δ, ϕ) combination, a positive value of the IDS indicates that the discrimination threshold when the background was modulated in a counter-clockwise manner was larger than when the background was modulated in a clockwise manner; a zero value indicates that the two thresholds were equal, and a negative value that the threshold was larger for the clockwise condition. Since the IDS is based on the ratio of threshold differences in the same color direction, its validity depends only on the property that cone excitations change linearly along every straight line in the color space. Moreover, because the IDS is a dimensionless quantity, it can be used to compare thresholds for discriminating probe changes in different color directions from a particular background change without imposing a metric on the affine space shown in Fig. 1.

We designed the IDS to isolate the response of directional-color mechanisms from that of standard static color mechanisms on the basis of the following reasoning: if the sensitivity of the observer, in the present task, depended solely on the instantaneous color of the background, then thresholds for a particular probe direction and background phase combination should be equal for counter-clockwise and clockwise modulation, i.e. the IDS would not be significantly different from zero for any (δ, ϕ) combination. Any significant departure from zero will indicate that the observer's sensitivity is affected by the direction of the background modulation.

The IDS results for the two observers are plotted in Figs 10 and 11. In Fig. 10, each panel consists of the results for a particular background phase. The background phase is shown in the top of each panel. Each data point is the IDS for the probe direction indicated on the abscissa. To make it easy to compare results for different background phases, the abscissa is expressed as the angular difference between the direction of the probe vector and the background phase-angle. So, for example, a value of 90 deg on every panel corresponds to a probe vector in the direction equal to the background phase angle plus 90 deg. Hence, values of 90 and 270 deg denote probe vectors tangent to the color-circle at that background phase, whereas 0 and 180 deg denote probe vectors orthogonal to the circle at that phase. Even though there is some random scatter in the data, there are also some similarities across the panels. There is a generated tendency for positive IDS values around 90 deg, negative around 270 deg, and close to zero around 0 and 180 deg. In Fig. 10, 0 and 180 deg refer to instantaneous changes in saturation only, while 90 and 270 deg to changes in both hue and saturation. For most background phases, increases and decreases in saturation without concommitant changes in hue are equally discriminable, but simultaneous changes in hue and saturation differ in discriminability depending on color change direction.

These systematic trends are clearer for both observers in Fig. 11, where the means of the IDS in the 16 panels for each observer in Fig. 10 are plotted against the angular difference between the probe direction and the background phase. The curves in Fig. 11 show that the IDS varies on average as a roughly sinusoidal function of the angular difference between the probe direction and the background phase-angle. At this point, it is worthwhile to refer the probe directions on the abscissa of Fig. 11 to the graphical representation of the probe intervals in Fig. 9. The left-most column of Fig. 9 shows pairs of probe intervals (counter-clockwise and clockwise) for angular differences of 0, 90, 180 and 270 deg between the probe vector and the background phase angle. At values of 0 and 180 deg, the probe vector is added in a direction orthogonal to the instantaneous

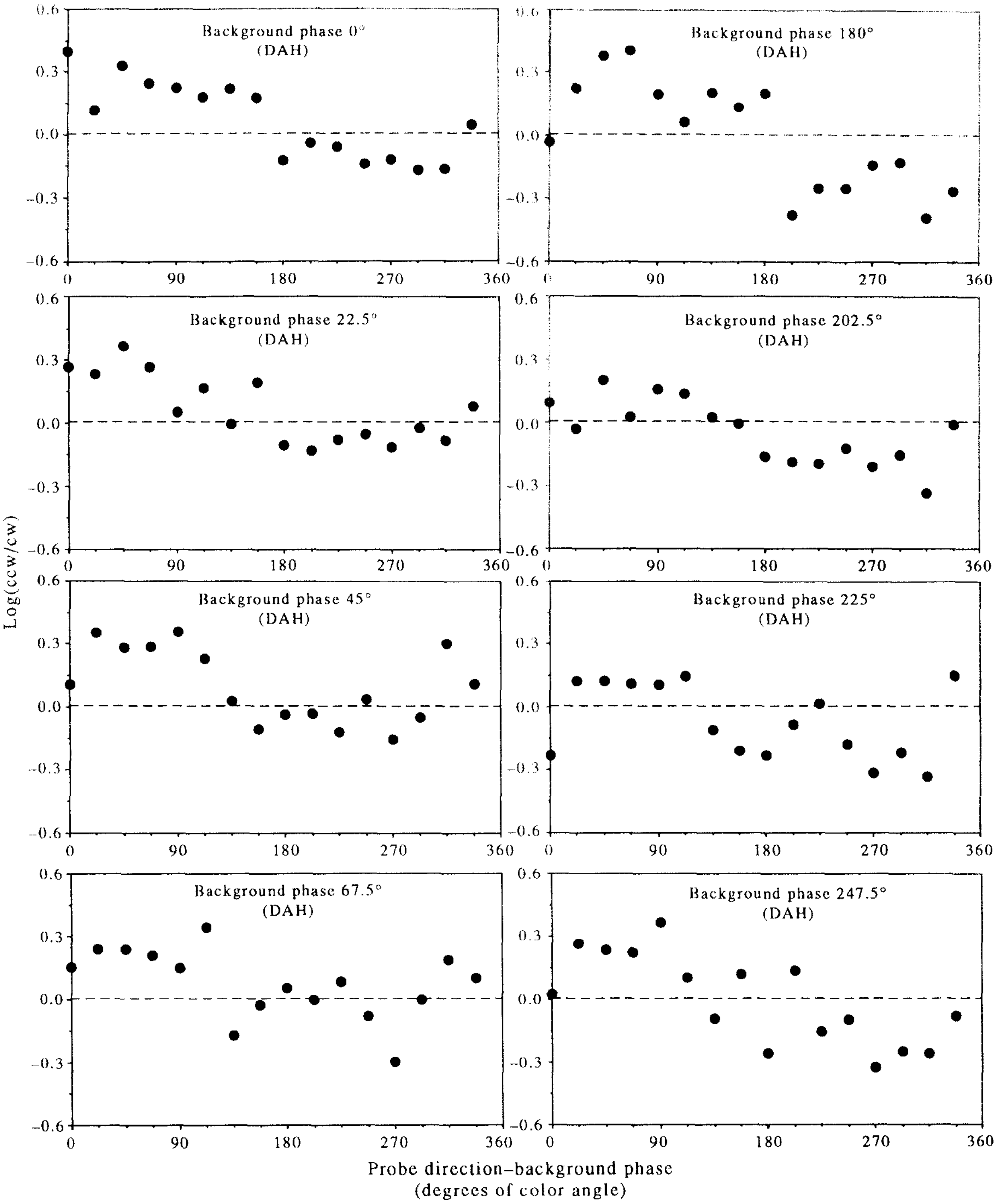

FIGURE 10(a, left). *Caption on p. 1047.*

direction of change of the color of the background for both counter-clockwise and clockwise background modulations. At a value of 90 deg, the probe vector is added in the same direction as the instantaneous direction of the change of the background modulation for counter-clockwise, but in the direction opposite to the background change for the clockwise condition. At a value of 270 deg the situation is the reverse of the situation of 90 deg. The average IDS curves in Fig. 11 show that discrimination thresholds for probe changes that were orthogonal to the background change were roughly equal for counter-clockwise and clockwise background changes. However, discrimination thresholds were larger when the probe vector was added in the same direction as the direction of instantaneous background change than for the same probe direction when the instantaneous background change was in the opposite direction. Hence, the observers' ability to discriminate between a pair of color changes depended on the angular difference between the directions of the color changes.

As discussed earlier, a comparison between thresholds for discriminating changes in different probe directions from the same background change is conceptually more straightforward, but relies on arbitrary metric assumption. In Fig. 12, normalized probe thresholds are plotted against the direction of the probe vector separately for the counter-clockwise and clockwise background conditions. The probe direction is expressed in terms of the

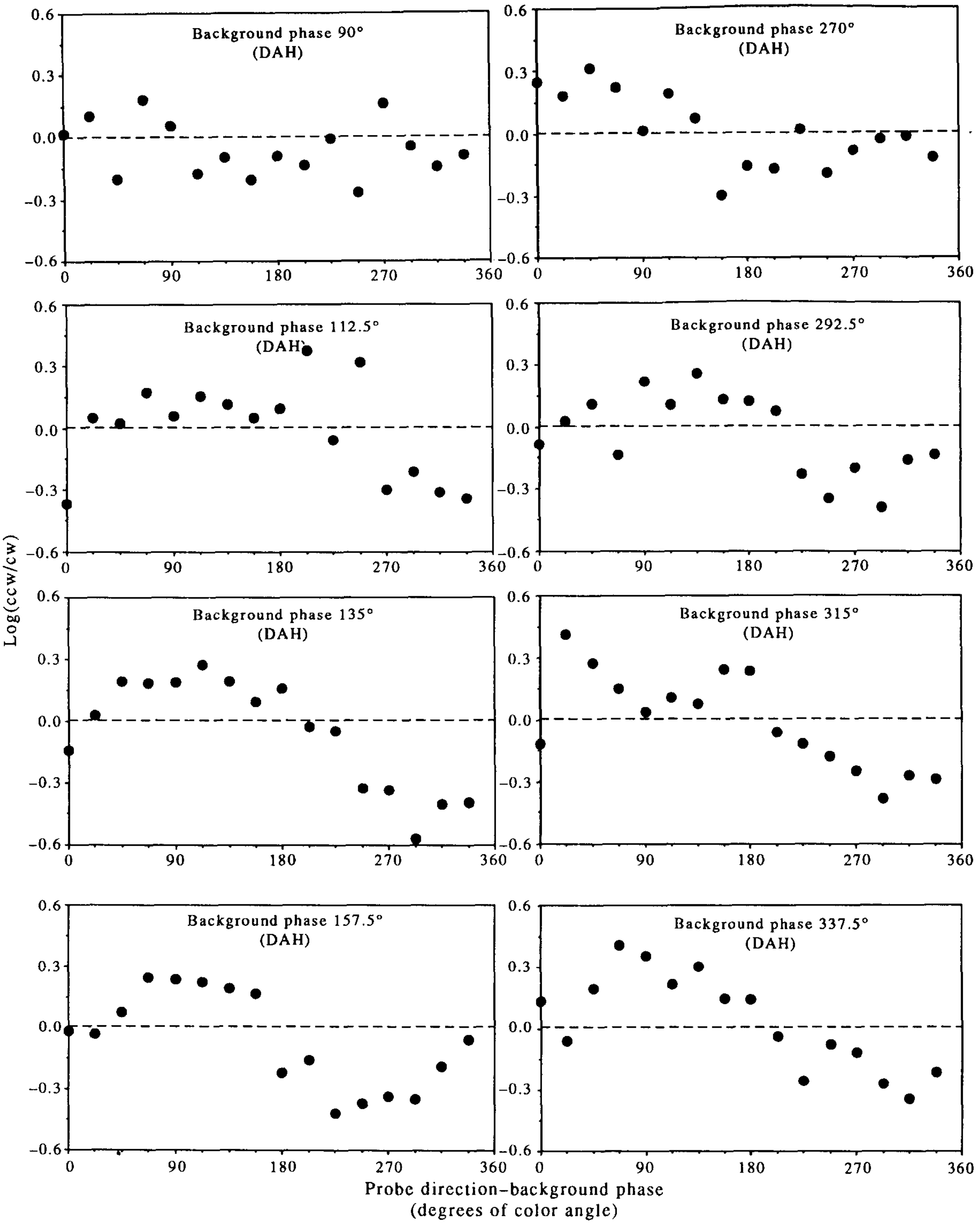

FIGURE 10(a, right). *Caption on p. 1047.*

angular difference from the background phase. For each observer, the data is the average of thresholds over the 16 background phases. Each discrimination threshold was normalized with respect to the mean threshold in that vector direction, i.e. each threshold was expressed as

$$\log \frac{T_{\delta,\phi,w}}{\bar{T}_{\delta}} \qquad (12)$$

where

$$\bar{T}_{\delta} = \frac{\sum_{\phi=0}^{337.5} (T_{\delta,\phi,\mathrm{ccw}} + T_{\delta,\phi,\mathrm{cw}})}{16+16}. \qquad (13)$$

Since the 16 directions of the instantaneous background changes were the same as the 16 directions of the probe vectors, we assume that these normalized units are roughly equivalent for different probe directions. For each observer, the curves of Fig. 12 are one possible decomposition of the curve in Fig. 11, i.e. the curve in Fig. 11 is equal to the counter-clockwise curve in Fig. 12 minus the clockwise curve. With this normalization, the counter-clockwise and clockwise curves are close to mirror images of each other. On the average, for both clockwise and counter-clockwise conditions, thresholds were close to the mean value for a probe direction when

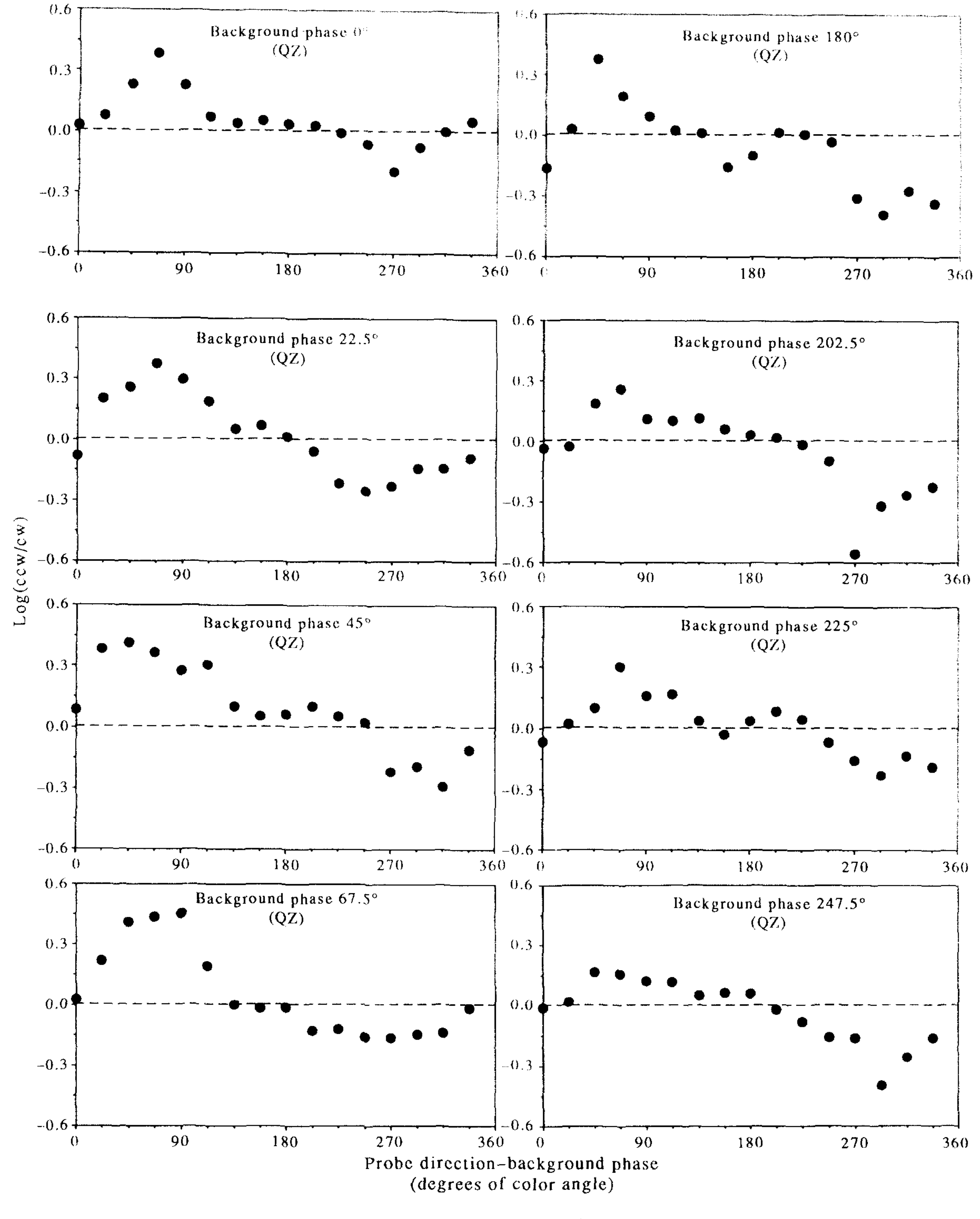

FIGURE 10(b, left). *Caption on facing page.*

the probe change was in a direction orthogonal to the background change, greater than the mean when the probe change was towards a similar direction to the background change and less than the mean when the probe change was towards the opposite direction.

Figure 13 makes the dependence of the magnitude of the discrimination thresholds on the relative direction of the two color changes even clearer. In Fig. 13, the data in Fig. 12 are replotted as a function of the difference in color angle between the *directions* of the probe vector and the instantaneous background change. The instantaneous direction of the background modulation at phase-angle ϕ is equal to $((\phi + 90) \bmod 360)$ deg for counter-clockwise modulation and to $((\phi + 270) \bmod 360)$ deg for clockwise modulation. In Fig. 13, an abscissa of 0 deg indicates that the instantaneous change due to the probe vector was in the same color direction as the instantaneous change due to the background modulation. Values of 90 and 270 deg indicate changes in orthogonal and 180 deg in opposite color directions. The discrimination thresholds vary approximately as a cosine function of the angle between the incremental change and the instantaneous background change. This graph shows that the

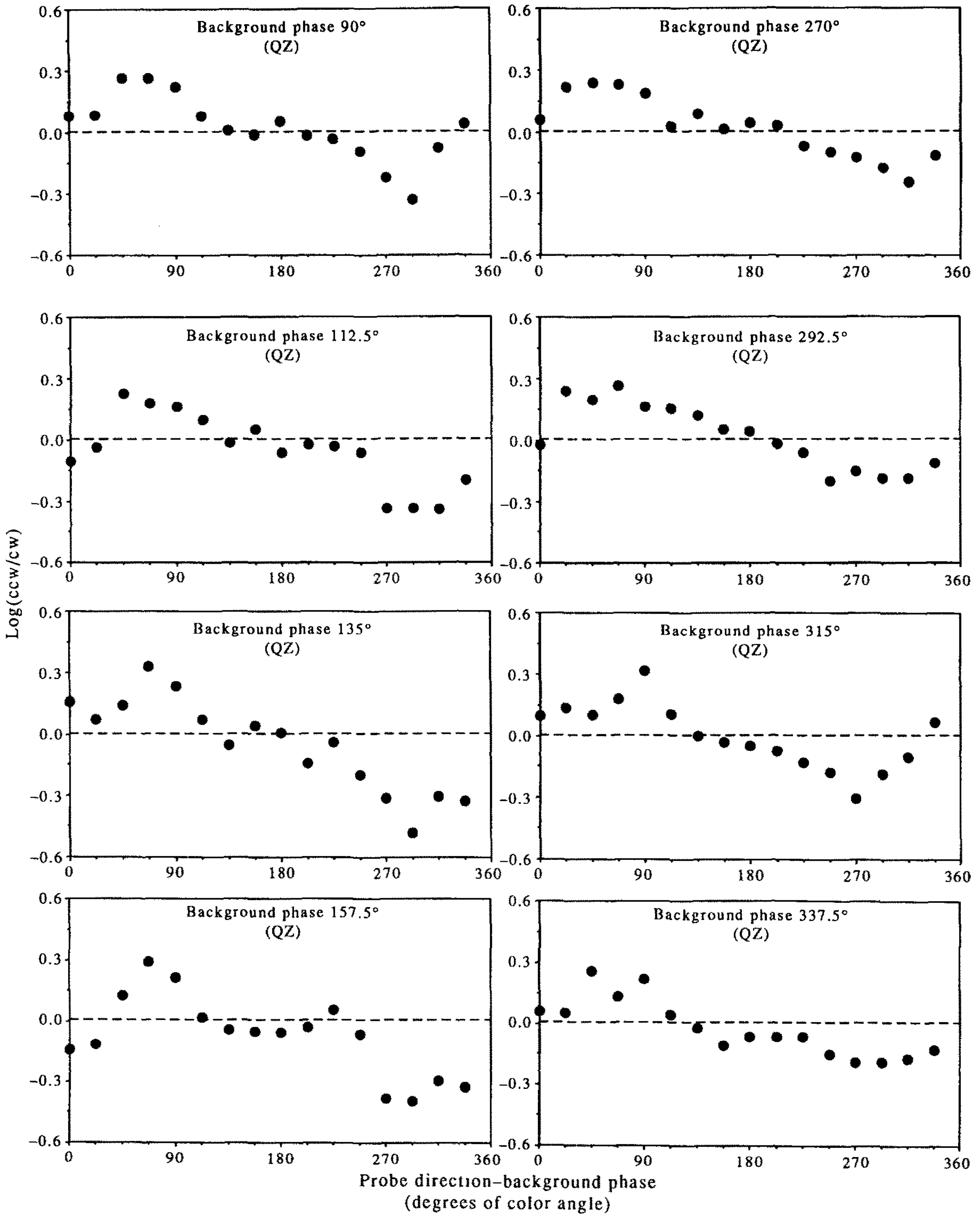

FIGURE 10(b, right).

FIGURE 10. In each of the 16 panels for observers DAH (a) and QZ (b), the index of direction selectivity (IDS) given in equation (12) is plotted for all probe vectors added at a particular background phase. The probe direction is expressed as the angular difference from the background phase angle.

clockwise and counter-clockwise results are very similar, which indicates that the main factor limiting discrimination between pairs of color changes was the relative color direction of the changes and that other factors like the adaptation state of first and second stage mechanisms had negligible effects.

DISCUSSION

In this paper we have analyzed a color discrimination task in terms of sensitivity to the direction of temporal *changes* in color. A more traditional analysis could postulate that probe thresholds vary solely as a function of the discriminability between the *appearances* of the stimuli. We designed the experimental procedure so that the greatest difference between the two intervals was the instantaneous color change at the start of each interval. Figure 9 shows pairs of chromatic sequences (clockwise and counter-clockwise) for each probe direction. The beginning and end points of each dotted line show the relative positions for the instantaneous colors at the start

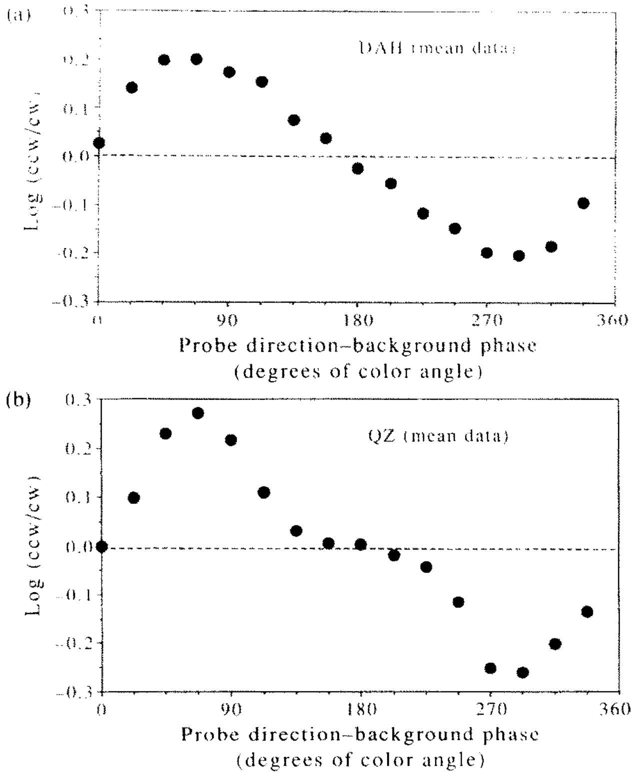

FIGURE 11. The mean of the data shown in Fig. 10 plotted in the same fashion, i.e. average IDS vs probe direction expressed as angular differences from the background phase angle. Panel (a) shows the data for observer DAH and panel (b) for QZ.

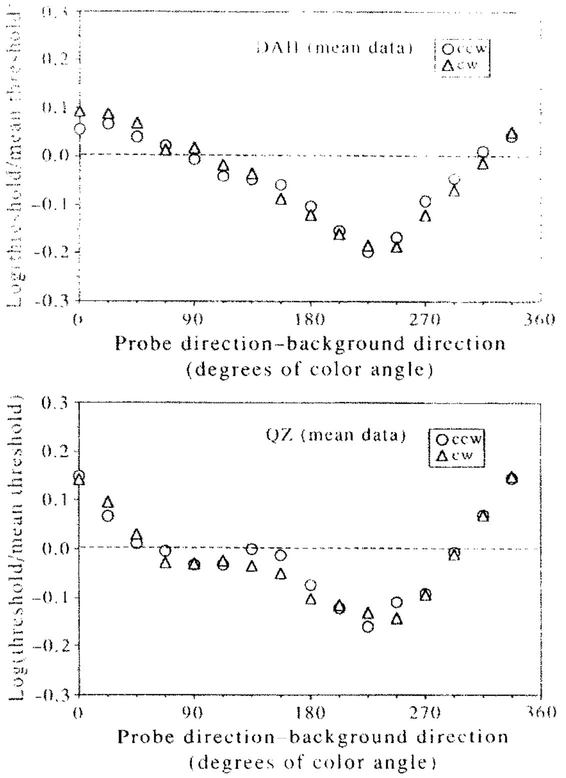

FIGURE 13. Normalized thresholds in Fig. 12 replotted vs the angular difference between the directions of the color changes in the background and probe intervals.

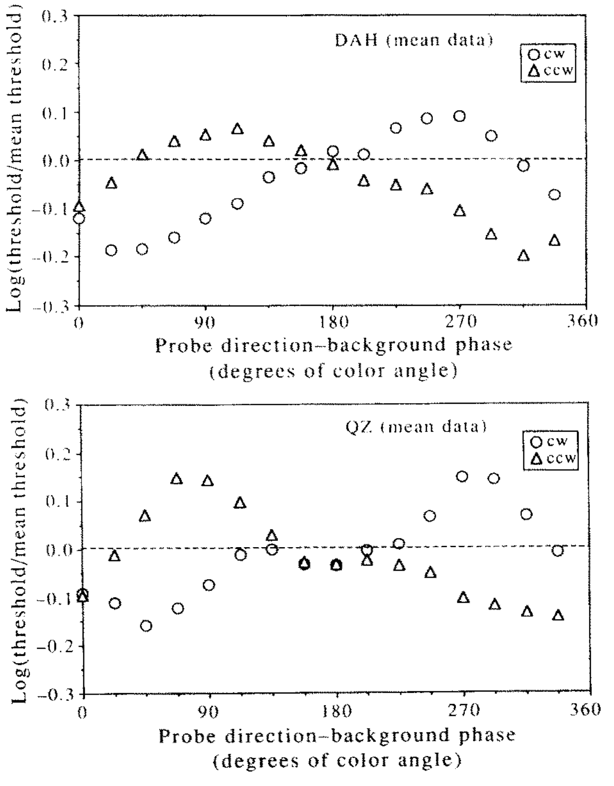

FIGURE 12. Normalized probe thresholds [equation (13)] plotted against relative probe direction, separately for counter-clockwise (circles) and clockwise (triangles) modulation. The results are the average for the 16 background phases.

of the background and probe intervals respectively. In each pair, the instantaneous colors at the start of the background interval were identical for the clockwise and counter-clockwise conditions. Figure 9 shows that if probe vectors of equal length were added to the two conditions, then the instantaneous colors at the start of the probe interval were also identical for the two conditions. In the color-change experiment, if an observer had relied entirely on memory for static color *appearance* to discriminate between the probe and background intervals, there should have been no significant difference between pairs of clockwise and counter-clockwise thresholds. That is, for all (δ, ϕ) combinations, $T_{\delta,\phi,\mathrm{cw}}$ should have been equal to $T_{\delta,\phi,\mathrm{ccw}}$, and the curves in Figs 10 and 11 should be flat and equal to zero (see also Sachtler & Zaidi, 1992). Consequently, any attention paid by an observer to color appearances rather than to color changes, could only have attenuated the direction-selective effect of discrimination by means of directional-color mechanisms.

In visual science there is a long tradition of explaining quantitative psychophysical results in terms of underlying physiological mechanisms, e.g. Maxwell (1860) on the substrate of color matches. When the pychophysical results address a complex visual capacity, like the discrimination between two perceived color changes, the explanation requires multiple stages of physiological mechanisms, and the psychophysical–physiological link is not straightforward. We have simulated a model that includes the components that are required for a specialized visual capacity for sensing the direction of color changes. In this model, we chose to use 16 directional-color mechanisms whose preferred directions of color change were evenly distributed, i.e. the directions $\Theta = 0, 22.5, \ldots, 337.5$ deg. The response of each mechanism was proportional to the rectified projection of the color change per unit time toward the preferred direction of that mechanism, followed by a logarithmic compression. The magnitude of the response of a mechanism tuned to a direction Θ to a color change in the direction Ψ was thus maximal when $\Psi = \Theta$, and zero for $|\Psi - \Theta| \geqslant 90$ deg. We assumed that when a probe was added to the background modulation, two instantaneous color changes occured simultaneously, so that each mechanism received two independent inputs. The rectified projections of the two color changes were taken separately before they were summed within a mechanism, and the log compression was taken on the sum of the projections. For any color change, the output of each independent directional-color mechanism was treated as a vector with length equal to the magnitude of the response, and with direction equal to the preferred direction of the mechanism. The response vectors were then summed to give a vector C whose length and direction characterized the color change. The probe and background conditions were represented by two different color-change vectors, C_B and C_P. The model assumed that the observer could discriminate the probe from the background change when the difference between C_P and the projection of C_B on C_P was greater than a criterion level.

Figure 14 shows normalized predictions from numerical simulations of the model, plotted on axes similar to Fig. 13. Each set of symbols represents predictions for a particular amplitude of background modulation. The curves in Fig. 14 represent predictions for each individual background phase and are valid for both clockwise and counter-clockwise modulations. The average of all the identical curves would, of course, be equal to the same curve. Each set of symbols follows a roughly cosine curve, maximum at probe direction equal to the instantaneous direction of background change, and minimum for probes in the opposite direction. The amplitude of the predicted curve increases as the amplitude of the background modulation was increased. The main deviation from the cosine rule is that the amplitude of 0 deg is not always predicted to be equal in absolute value to the amplitude at 180 deg. This deviation is also present in the empirical results. However, the averaged empirical results in Fig. 13 exhibit other noticeable deviations from the cosine function. These deviations may be due to a number of factors, such as distortions due to the metric used for the color space. The model only considers the instantaneous change in each interval, whereas an integrated change over a small time window may provide better predictions. In addition, the different temporal aspects of the background and probe changes were not explicitly considered in the model.

Despite the variability of the data for individual backgrounds, a number of alternate schemes can be ruled out on qualitative grounds.

(i) If standard or rectified versions of opponent mechanisms are used in the model instead of directional-color mechanisms, the predictions are quite different. Other than small adaptation effects, the response of opponent mechanisms is a function of the instantaneous color irrespective of the direction of color change. These mechanisms therefore cannot explain the systematic difference between the threshold pairs $(T_{\delta,\phi,\mathrm{cw}}, T_{\delta,\phi,\mathrm{ccw}})$. In addition, if the log compression is applied solely to the response of opponent mechanisms, thresholds are predicted to be maximal when the probe direction is equal to the instantaneous phase of the background. This is not borne out by the empirical results.

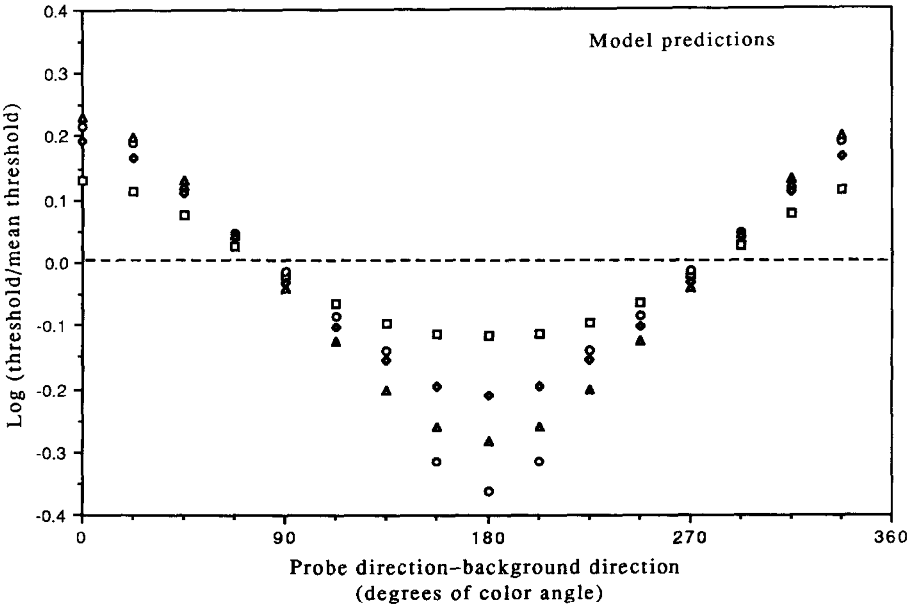

FIGURE 14. Predictions of the model for normalized discrimination thresholds plotted against the angular difference between the directions of background and probe changes. Different symbols are for different amplitudes of the background change.

(ii) If the number of directional-color mechanisms is reduced from 16 to just 4 that are maximally sensitive to changes along the cardinal axes, i.e. 0, 90, 180 and 270 deg, then the model predicts maxima for probes at one or two of the cardinal directions irrespective of the background direction. Even though the variance in the data does not allow a precise estimate of the number of directional-color mechanisms, it is apparent that the number has to be > 4 to account for the systematic shift in the peaks to approx. 90 deg plus the background phase in Fig. 10.

(iii) The discrimination rule generates the predictions in Fig. 14 because the projection of C_B on C_P is proportional to the cosine of the angle between them. The predicted thresholds are thus equal to some constant criterion level plus the cosine of the angular difference. One prediction of this model is that any orthogonal pair of color changes from a steady mid-white background will be discriminable from each other at detection threshold, where detection threshold is equal to the amplitude of change that is just discriminable from no change in the steady background. This prediction conforms to Krauskopf *et al.*'s (1986) results on the detection and discrimination of orthogonal color changes on steady mid-white backgrounds.

The detection and discrimination results of Krauskopf *et al.* (1986) can also be explained by a different type of discrimination model in which the response of each rectifying directional-color mechanism to one color change minus the response to the second change is computed independently. If any of these independent differences is greater than a criterion level, then the two changes are discriminable. Both an independent-differences model and our model predict that all those pairs of color changes from a steady background will be discriminable at detection threshold whose directions differ by more than 90 deg but less than 270 deg. The two models, however, differ in predicting the effect of modulated backgrounds. Whereas, the present model predicts cosinusoidal results like Fig. 14, a discrimination model based on comparing the differences in the independent outputs of directional-color mechanisms predicts that for every background change, normalized thresholds will be similar for all probe directions more than 90 and less than 270 deg from the direction of background change. This is almost never the case in the empirical results. The present experiment, based on discrimination between pairs of color changes, thus provides a more stringent test for models than experiments that measure discrimination from steady backgrounds.

SUMMARY

The main empirical result of this study is that based on the average of a large variety of conditions, the threshold for discriminating between a pair of color changes is approximately proportional to the cosine of the color angle between them. The main theoretical result is the evidence for parallel directional-color mechanisms, maximally tuned to many different directions in color space and responsive to change in one direction but not its opposite. The results of this study provide support for a visual capacity to sense the direction of temporal changes in color *per se*.

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