

INDEPENDENT ORIENTATION-SELECTIVE MECHANISMS FOR THE CARDINAL DIRECTIONS OF COLOUR SPACE

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Abstract—Simultaneous, oppositely tilted, aftereffects were obtained for pairs of equiluminant gratings (e.g. magenta/cyan vs purple/greenish-yellow) and pairs of equiluminant and luminant gratings (e.g. magenta/cyan vs dark-grey/light-grey, or purple/greenish-yellow vs dark-grey/light-grey). Maximum aftereffects occurred for gratings whose colours were modulated along the principle axes of the colour space of Krauskopf, Williams and Heeley (1982): an axis of short-wavelength cone activation (B-cone axis), the difference between long- and medium-wavelength cone activation (R - G cone axis), and an axis of a contrast ratio of long-, medium- and short-wavelength cone activation (R + G + B cone axis). The results indicate that selectivity for orientation occurs independently in at least two chromatic channels and one achromatic channel.

Colour-contingent tilt aftereffects Orientation Equiluminance Colour selectivity Cone
excitations Colour space

INTRODUCTION

The tilt aftereffect (Gibson & Radner, 1937) is now taken as evidence for the orientation selectivity of mechanisms in the human visual system. Although the original studies of the tilt aftereffect employed stimuli defined by luminance (e.g. with black and white contours), more recent studies have shown that colour can also be used to code orientation. McCollough (1965) showed that the perceived colour of a pattern of stripes could be made contingent on their orientation, while Held and Shattuck (1971) showed the converse effect: perceived orientation could be made contingent on contour colour. Both of these studies used contours which were defined by both luminance and colour differences (McCollough used orange/black and blue/black stripes and Held and Shattuck used red/black and green/black gratings). There is also evidence that contours defined by colour-only differences will produce orientation-selective aftereffects (Bradley, Switkes & De Valois, 1988; Day, 1959; Elsner, 1978). Although all these studies show that coloured contours can support orientation

aftereffects, indicating that orientation-selective mechanisms respond to contour colour, they do not provide direct evidence that mechanisms responding to the colour of contours are independent from those that respond to contours defined only by luminance differences. These colour-related tilt effects could be generated in orientation-selective mechanisms that respond principally to luminance but also have some colour biases. In addition, these studies do not provide information about the colour selectivities of the underlying orientation-selective mechanisms.

We have used tilt aftereffects to investigate the colour and luminance specificities of orientation-selective mechanisms and find evidence for two types. One type is selective for the colours and luminances defining the contours, and the principal mechanisms of this type are selective for the cardinal directions of colour space described by Krauskopf et al. (*Vision Research*, 22, 1123-1131, 1982). A second type responds non-selectively to contours, whether defined by colour differences, by luminance differences, or by both. Our results are consistent with those of Bradley et al. (1988) who showed independent, orientation-specific threshold elevations following adaptation to colour-defined (equiluminant red/green) and luminance-defined (yellow/black) gratings.

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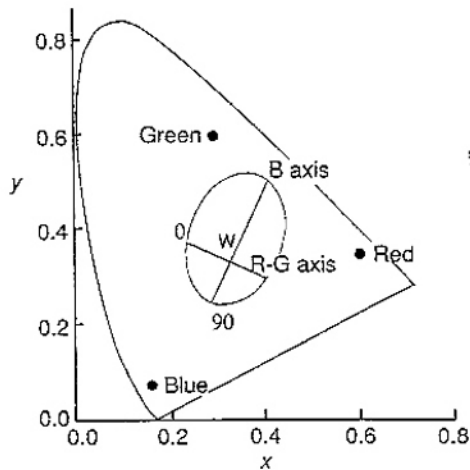


Fig. 1. Positions on CIE chromaticity diagram of: the phosphor primaries of monitor, the R-G and B axes (of MacLeod & Boynton, 1978); the circumference of the equiluminant plane (of the colour space in Fig. 2); and the equal-energy white (W) for the CIE standard observer.

METHOD

Observers

Three observers (PF, SS and LM) participated in two conditions, and two of these (PF and LM) participated in a third. All had normal colour vision and normal or corrected-to-normal acuity.

Stimuli and apparatus

The stimuli were sine-wave gratings presented on a high-resolution colour monitor. The grating stimuli were constructed by varying the proportions of red, green and blue phosphor primaries (see Fig. 1) such that the colours of the gratings were modulated sinusoidally between the two endpoints of a diameter of the colour sphere of Derrington, Krauskopf and Lennie (1984), and shown in Fig. 2. This colour space is based on the chromaticity diagram of Macleod and Boynton (1978) and is characterized by three axes: an R + G + B cone axis (which indicates equal ratios of activation in long-, medium- and short-wavelength selective photopigments), an R - G cone axis (which indicates the difference in activation of long- and medium-wavelength selective photopigments), and a B-cone axis (which indicates

activation in short-wavelength selective photopigments). The R - G and B axes together define an equiluminant plane (the horizontal plane of Fig. 2), whereas stimuli defined along the R + G + B axis, are achromatic. These three axes are also the cardinal directions of colour space of Krauskopf et al. (1982).

In this colour space a diameter along the R - G axis is cyan at one end and magenta at the other; appropriate variation of the phosphor primaries along this diameter produces a cyan/magenta grating with a mean chromaticity corresponding to white. Similarly, a grating formed by modulation of the phosphor primaries along a diameter at the B axis is light-purple and greenish-yellow in appearance. Modulation of the phosphors along the R + G + B (or achromatic) axis produces a grating that is dark grey and light grey.

Following Derrington et al. (1984), the chromaticity of a stimulus was defined as a position in the colour space and described as a colour direction, measured in degrees.* In the colour sphere, changes in colour but not in luminance (or directions in the equiluminant plane) were specified by a colour angle, which varied from 0 to 360°, in which 0° was assigned to the

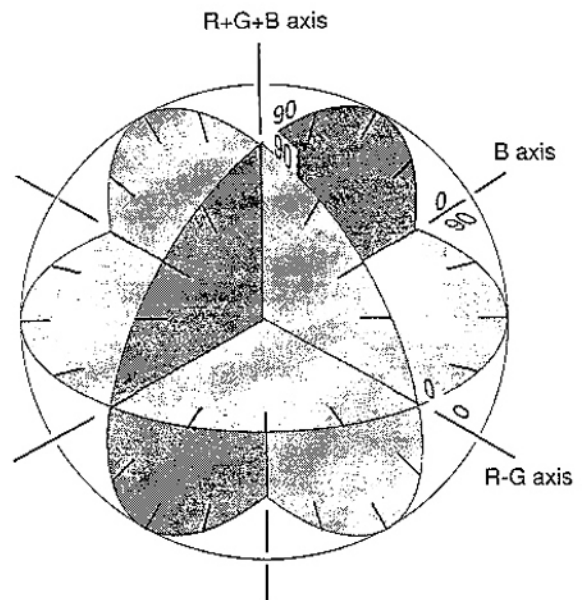


Fig. 2. Representation of spherical colour space of Derrington et al. (1984). R - G, B and R + G + B axes in this space, taken in pairs, define the three shaded planes shown: R - G & B, R - G & R + G + B and B & R + G + B. Stimuli were spatially modulated sinusoidal gratings whose colour and luminance were described as colour directions. (See Method for details.) An alternative representation of this colour space is described in the Appendix and illustrated in Fig. A1.

*Since we were studying tilt aftereffects, two variables were measured in degrees: directions of tilt of the adapt and test gratings and directions in colour space. To avoid confusion, the tilt of the adapting gratings and the apparent tilt of the vertical test gratings, following adaptation, will be indicated by "°". A direction in the colour space will be indicated by "°_{cs}".

R – G axis, and 90°_{cs} was assigned to the B axis. Likewise, changes in direction out of the equiluminant plane, or changes toward the achromatic axis, were specified by an angle (a luminance angle) which also varied from 0 to 360°_{cs} . For these luminance angles, 0°_{cs} was assigned to colour directions in the equiluminant plane and 90°_{cs} was assigned to colour directions along the achromatic axis. These two angles, a colour angle and a luminance angle, may be used to describe the chromatic properties of grating at any direction in the colour space. All stimuli used in the experiment were defined along directions in the three planes formed from pairs of axes of the colour space (i.e. R – G & B, R – G & R + G + B and B & R + G + B planes, the three shaded planes of Fig. 1).

The proportions of R, G and B cones of individuals often differ somewhat from those of the CIE standard observer, and so the equiluminant plane (defined by a constant level of activation in the sum of R and G cones) had to be adjusted for each of our three observers, individually. To determine the proportions of red, green and blue phosphor primaries that define the position of the equiluminant plane, for individual observers, we used the method of Cavanagh, Macleod and Anstis (1987) to null the motion of 1 cycle deg^{-1} gratings for colours along the R – G axis and repeated this procedure for gratings along the B axis. These two settings were sufficient since, once made, the motion nulls were found to hold for other directions around the equiluminant plane. The individual differences in these settings tilt the achromatic axis and shift the equiluminant plane with it. As a result of these slight differences in the position of the achromatic axis, there were small differences in the white point of the colour sphere used for each observer. The CIE x, y coordinates of the white points for the three observers were: 0.337 and 0.334 for PF; 0.362 and 0.340 for LM; and 0.348 and 0.326 for SS. The space-averaged luminance of the gratings depends on the equiluminance settings of the individual observers, but was approx. 100 cdm^{-2} (for both chromatic and achromatic gratings). The Michelson contrast of the achromatic grating was 15%.

We took a number of precautions to minimize the effects of optical factors, chromatic aberration and the filtering effects of the macula, in particular, on the properties of adapt and test gratings. Because chromatic aberration increases with spatial frequency, we used 1 cycle

deg^{-1} gratings for which the theoretical "worst-case" luminance artifact has less than 0.5% contrast (Cavanagh & Anstis, 1986). In addition, a high-contrast bull's-eye fixation target was used to provide a spatially structured achromatic stimulus which, by encouraging constant accommodation, would reduce the luminance artifact due to chromatic aberration to less than 0.5%. This bull's-eye was also used to occlude the central 2.7° of the visual field at the fixation point and below, therefore, by covering part of the adapt and test gratings, avoiding the effects of macular filtering on short-wavelength stimuli.

Experimental design

To examine whether there is independent orientation selectivity for chromatic and achromatic stimuli, we used the opposed aftereffects paradigm (e.g. Held & Shattuck, 1971). In two *opposed* adaptation conditions, observers were adapted to pairs of oppositely tilted gratings in which the colours of the gratings were defined along pairs of directions in the colour space, and, following this opposed adaptation, we measured the tilt aftereffect on vertical test gratings which varied in their chromatic and luminance properties.

In the first condition, the two oppositely tilted adapting gratings were defined at colour directions along pairs of the axes in each of the three planes of Fig. 1 (0 and 90°_{cs}). Therefore, in this condition, observers were exposed to three sets of opposed adaptation gratings: two in which the oppositely tilted gratings were colour and luminance (R – G vs R + G + B and B vs R + G + B), and one in which the oppositely tilted gratings were both equiluminant (R – G vs B). The effects of simultaneous adaptation to these pairs of oppositely tilted gratings were examined with vertical test gratings at eight colour directions (-45 to $+112.5^\circ_{cs}$, at 22.5°_{cs} intervals) in the plane containing the pair of adapting colour directions.

In a second condition, by adapting observers to pairs of gratings whose colours were defined at colour directions between these axes, we determined whether these tilt aftereffects were specific to colours along the axes of the colour space. Observers were adapted to pairs of oppositely tilted gratings at directions in the colour sphere halfway between the main axes (-45 and $+45^\circ_{cs}$). In this condition there were again three sets of opposed adaptation gratings: two in which the oppositely tilted gratings contain colour and luminance differences (between the

R - G and R + G + B axes and between the B and R + G + B axes), and one in which the oppositely tilted gratings were both equiluminant (between the R - G and B axes). The effects of opposed adaptation of gratings at these intermediate directions were examined with vertical test gratings at eight colour directions (-67.5 to $+90^\circ_{cs}$, at 22.5°_{cs} intervals) in the plane containing the pair of adapting colour directions.

In a third condition (a *simple* adaptation condition), the magnitude of the tilt aftereffect was measured following adaptation to a *single* tilted grating which was defined at a colour direction along each of the three axes of the colour space (the R - G, B and R + G + B axes). The effects of this adaptation to single gratings were measured on vertical tests at eight colour directions (spanning 180°_{cs} , at 22.5°_{cs} intervals) in the two planes that pass through the single adapting colour direction.

Procedure

Testing took place in darkened room in which the only source of illumination was that provided by the display monitor. The observers viewed the square monitor screen from a distance of 193 cm, at which it subtended 8° of visual angle. Viewing was binocular with natural pupils, and head position was restrained by a chin rest and forehead bar. The screen was divided horizontally into two rectangular windows, each $7.5 \times 3.5^\circ$, separated by a 0.5° horizontal strip. The bull's-eye fixation target was positioned in the centre of the strip between the two windows and was truncated at the bottom edge of the top window while intruding into the lower window. A (0.25° wide) frame of high-contrast black and white random dots ($7.5'$ of arc square) enclosed the lower window (including the lower half of horizontal strip between the windows), whereas a plain white frame enclosed the upper window. The dimensions of the display, and the appearance of the screen during the adapt sequence are shown in Fig. 3a. The appearance of the display screen during a subsequent test/adjust sequence is shown in Fig. 3b.

Opposed adaptation. The observers were tested individually and fixated the bull's-eye while two adapting gratings (e.g. 0 and 90°_{cs} in the R - G and B plane), each tilted 15° either side of vertical, were displayed in alternation in the lower window. The adapting gratings alternated every 2 sec and, while visible, drifted back

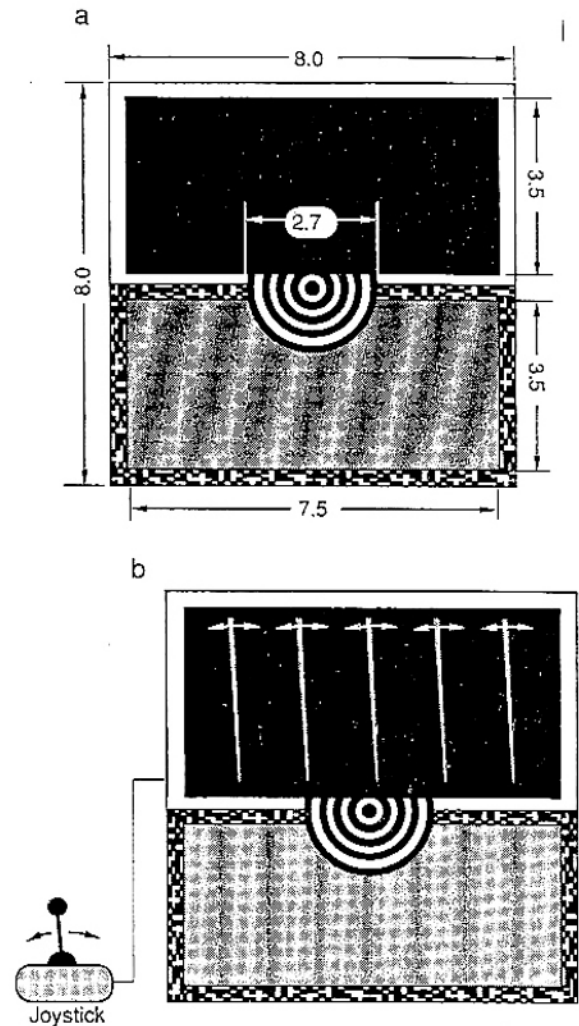


Fig. 3. Appearance of display and dimensions (in degrees of visual angle) when viewed from 193 cm: (a) during adapt sequence; and (b) during subsequent test/adjust sequence. (See Method for details.)

and forth at a rate of 1 cycle sec^{-1} . The initial adapting period was 2 min. During the adapting period, the top window remained dark ($<2 \text{ cdm}^{-2}$). On completion of the adapting period, a warning tone sounded and a coloured vertical test grating, at one of eight test colour directions (i.e. spanning 180°_{cs} at 22.5°_{cs} intervals) in the plane containing the pair of adapting colour directions, replaced the adapting grating for 330 ms. Simultaneously with the onset of the test grating, an adjustment stimulus (composed of five white lines each 3.5° high and $3'$ of arc average width) was shown in the top window. These white lines (with a maximum luminance of 120 cdm^{-2}) were distributed at equally spaced intervals (1.3° apart) across the otherwise dark upper window, and could be rotated synchronously up to 15° either side of vertical, around the bottom end of their long axes, by a

joystick control. The observer's task was to use the joystick control to adjust these comparison lines, so that the long axes of the comparison lines matched the perceived orientation of the vertical, coloured test. The comparison lines were visible for 1.5 sec (for the 330 msec during which the test grating was visible, plus a further 1270 msec after removal of the test grating). During this 1270 msec period, a uniform field of mean luminance was displayed in the lower window.

If a match between the orientation of the test and the orientation of the comparison lines could not be achieved in the time available, there was an additional 8 sec period of readaptation, followed by another test and adjustment period. This sequence of 8 sec adaptation, 330 msec test, and 1.5 sec adjust, continued until the observer accepted (by pressing a button) the orientation match between the comparison lines and the test grating. The button press caused the observer's setting to be stored and the orientation of the comparison lines to be reset to an arbitrary value around vertical (in preparation for the next test). Another test-colour direction was chosen randomly (without replacement) from the untested directions, and following a further 8 sec readaptation, testing continued as before. When one match of the orientation of the comparison lines and the vertical test grating had been completed for each of the eight test-colour directions the observer rested for a few minutes. The session continued until the observer had made six orientation matches at each of the eight test colour directions. There was only one session per day for each observer. To control for response bias, each of the two adapting colour directions was paired with one direction of tilt in one session, and the pairing was reversed in the second session. Each observer required six sessions (all combinations of right and left tilt from vertical of the oppositely tilted gratings in each of the three planes) to complete each of the opposing-adaptation conditions.

Simple adaptation. Observers were adapted to one grating at a time; the second adapting grating of the opposing-adaptation condition was replaced by a uniform screen of the same mean luminance as the other colour displays. The single adapting grating, at each of the three cardinal colour axes, was tilted 15° to the left of vertical in one session and 15° to the right of vertical in a second session. The colour directions of the test spanned 180° at 22.5° intervals

in each of the two planes passing through the adapting colour direction. Each observer required 12 sessions (all combinations of right and left tilt from vertical, three adapting-colour directions and two test planes for each) to complete this condition. In all other respects, the procedure was the same as for the two opposing-adaptation conditions.

RESULTS

Opposing adaptation

Figure 4 shows the magnitude of the tilt aftereffect, as a function of test-colour direction, that results from opposed adaptation to gratings at 0 and 90° colour directions in the R - G & B, R - G & R + G + B and B & R + G + B planes. The form of the curves describing the change in magnitude of the tilt aftereffects with change in test colour direction are similar for adapting gratings defined in the equiluminant plane and for adapting gratings defined in the two planes that pass through the achromatic axis. In all three cases the tilt aftereffect changes in sign with change in colour direction of the vertical test grating. The change in sign of the tilt aftereffect, with change in test-colour direction, indicates that the direction of the perceived

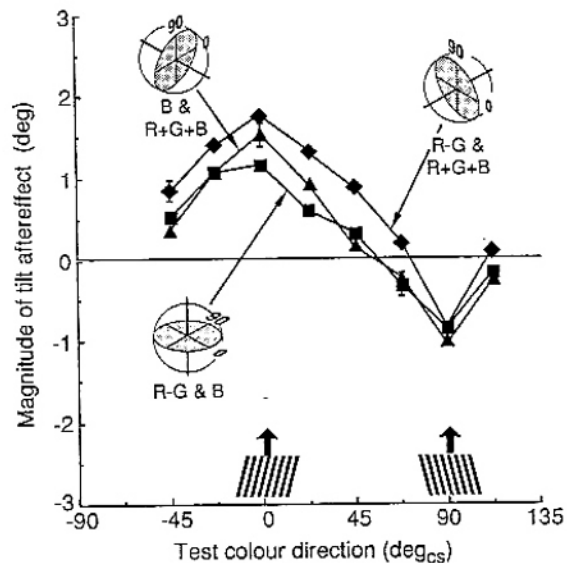


Fig. 4. Magnitude of tilt aftereffects for opposed adaptation at 0 and 90° , for tests from -45 to 112.5° in each colour plane. Symbols and shaded plane in small spheres identify results for each plane (triangles, R - G and R + G + B; diamonds, R - G & R + G + B; squares, R - G & B). Each point average for three observers. Vertical lines indicate median size of standard errors of means. Arrows and grating patterns, on horizontal axis, indicate colour direction and direction of tilt from vertical of adapting grating.

deviation from vertical of the test depends on the colour of the vertical test grating. In addition, the largest (positive and negative) deviations from vertical occur when the colour directions of the test correspond to the colour directions of the adapting gratings and declines with deviation of the test colours from the adapting colours.

Figure 5 shows the magnitude of the tilt aftereffect, as a function of test-colour direction, following opposed adaptation between pairs of intermediate colour directions (-45 and 45°_{cs}) in the R-G & B, R-G & R+G+B and B & R+G+B planes. The tilt aftereffects are smaller than those obtained for adapting colour directions along the axes of the colour space, and the maximum tilt aftereffect does not always occur at the adapting colour directions; but the aftereffects obtained are still significantly different from zero (as can be inferred from the error bars in Fig. 5).

Simple adaptation

The three panels in Fig. 6 show the magnitude of the tilt aftereffects obtained, as a function of the colour direction of the vertical test, following adaptation to single tilted gratings whose colours are defined along the 0 or 90°_{cs} colour directions in the R-G & B plane (top panel), the R-G & R+G+B plane (middle panel) and the B & R+G+B plane (bottom panel). The two curves in each panel, and the two horizontal scales, show the results for the 0°_{cs} (the filled symbols and the upper scale) and 90°_{cs} (the

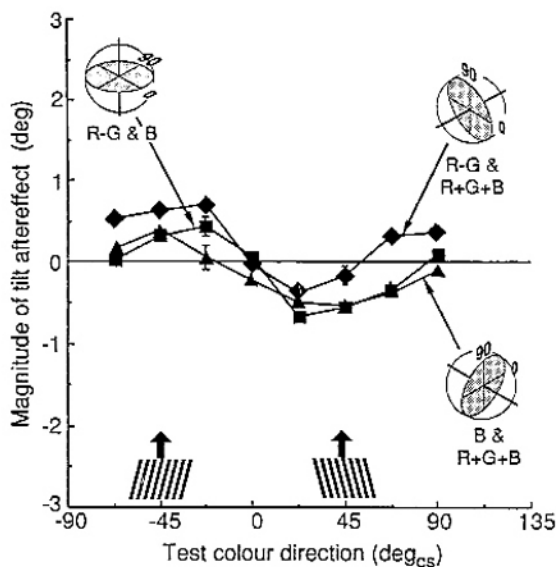


Fig. 5. As for Fig. 4, except -45 and 45°_{cs} adapting colour directions and tests from -67 to 90°_{cs} .

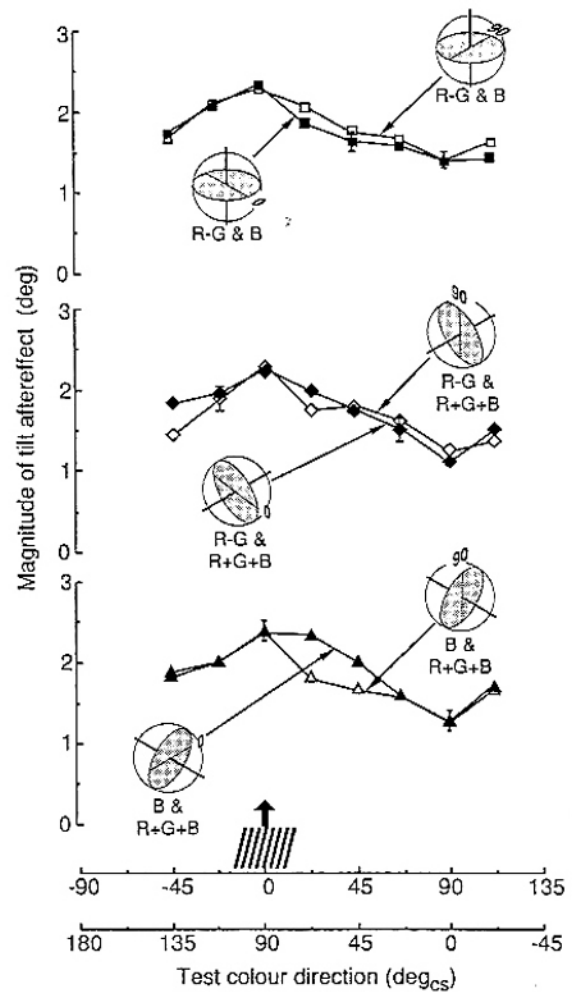


Fig. 6. Magnitude of tilt aftereffect obtained following adaptation to single tilted gratings defined along 0 or 90°_{cs} colour directions in R-G & B plane (squares, top panel), R-G & R+G+B (diamonds, centre panel) and B & R+G+B plane (triangles, bottom panel) for vertical tests from -45 to 112.5°_{cs} . Curves in each panel, and two horizontal scales, show results for adapt grating at 0°_{cs} (the filled symbols and the upper scale) and 90°_{cs} (the open symbols and the lower scale). Results for adaptation to 90°_{cs} directions (and the lower scale) have been reversed (left to right) in order to superimpose 0 and 90°_{cs} directions on horizontal axis. Each point average for two observers. Vertical lines indicate median size of standard errors of means.

open symbols and the lower scale) adapting colour directions. The results for adaptation to the 90°_{cs} directions (and the lower scale) have been reversed (left to right) in order to superimpose the results for the two adapting-colour directions in each plane.

As can be seen in Fig. 6, the maximum tilt aftereffect obtained following adaptation to single gratings at either 0 or 90°_{cs} varies between 2 and 2.5° , or not quite twice the magnitude of tilt aftereffects obtained in the opposing adaptation

condition (to oppositely tilted gratings at both 0 and 90°). The tilt aftereffects obtained with single gratings do not fall to zero at any test-colour direction, however, but have a minimum value of about 1 to 1.5°. Superimposed on this minimum (or baseline) tilt aftereffect, there is again a modulation in the magnitude of the aftereffects that varies with the colour direction of the test. Furthermore, in all cases, the tilt aftereffect has its maximum for tests at, or very near, the colour direction of the adapting grating, and its minimum for tests at, or very near, a direction 90° from the adapting colour direction.

DISCUSSION

Separate oppositely tilted aftereffects were produced following adaptation to an equiluminant grating, tilted one direction from vertical, and an achromatic luminance-defined grating, tilted the opposite direction from vertical. The coexistence of these separate and opposite effects for equiluminant chromatic gratings and achromatic gratings demonstrates that there are mechanisms which respond independently to the orientation of equiluminant colour-defined contours and to the orientation of achromatic contours. The tilt aftereffects observed with chromatic tests could not be mediated by residual luminance in the chromatic adapt or test stimulus, since it would have been overwhelmed by the aftereffect in the opposite direction produced by the oppositely tilted achromatic grating. These findings are consistent with the evidence of Bradley et al. (1988) for the orientation-specificity of elevations in threshold contrast following adaptation to red/green equiluminant gratings as well as yellow/black luminance gratings. The tilt aftereffects, we report, also varied in magnitude with variation in the colour direction of the test, indicating that the mechanisms responding to the adapt and test gratings are selective for the colour and luminance properties of the stimulus gratings.

Separate tilt aftereffects were also obtained following adaptation to pairs of oppositely tilted equiluminant gratings, at the 0° (red/green) and 90° (tritanopic) colour directions, suggesting that there are orientation-selective mechanisms that respond independently to equiluminant gratings defined along these colour directions. The variation in the magnitude of the tilt aftereffect, with the deviation of the test-colour direction from the colour directions of the adapting gratings, indicates

that the underlying orientation-selective mechanisms are also selective for the colours defining equiluminant gratings.

Overall, these results indicate that orientation-selectivity occurs in two chromatic mechanisms and one achromatic mechanism. The colour selectivities of these orientation-selective mechanisms correspond to the proposed cardinal directions in colour space (Krauskopf et al., 1982).

The smaller, but still substantial, aftereffects produced following opposed adaptation at intermediate colour directions (as observed in the second condition and illustrated in Fig. 5) indicate that the two chromatic mechanisms and one achromatic mechanism (at the cardinal directions) are not the only adaptable orientation-specific mechanisms, and suggest the possibility of additional orientation-selective mechanisms at other directions in colour space (Zeki, 1980). These mechanisms appear to be either weaker or less adaptable than orientation-selective mechanisms at the cardinal directions. Mechanisms selective for colours at non-cardinal directions have also been reported in studies of adaptation to temporally-modulated chromatic pulses (Krauskopf et al., 1982; Krauskopf, Williams, Mandler & Brown, 1986).

Finally, following adaptation to single tilted gratings, the aftereffects appeared to be the sum of two components: one which was constant for all colour directions of the vertical test, and another that varied with the colour direction of the vertical test. The presence of this constant component suggests that some orientation-selective mechanisms are non-selective for colour direction and respond to contours whether defined by luminance contrast, colour contrast or a combination of luminance and colour contrast. These non-selective mechanisms may be the psychophysical correlates of the generalized contour detectors of Gouras (1974) or the multiple-colour cells of De Valois and De Valois (1975). The second variable component of the simple aftereffects indicates, once again, the presence of adaptable colour- and orientation-selective mechanisms. The maxima and minima of the variable component of the aftereffects are separated by 90°, which suggests that the axes of the colour space that we used, are functionally orthogonal for the underlying orientation-selective mechanisms, at least to a first approximation (see Appendix).

Recently, Livingstone and Hubel (1987, 1988) have claimed that colour and form are pro-

cessed in separate pathways in the visual system; they suggest that orientation is one aspect of form that is analyzed by mechanisms in a luminance pathway, but not by mechanisms in a colour pathway. In contrast, our findings, and those of Bradley et al. (1988), imply that the encoding of orientation also occurs in pathways selective for colour, and that the nature of the encoding is similar to that which occurs in pathways selective for luminance. Several electrophysiological studies have identified colour- and orientation-selective cells in cortical area V1 of the monkey (e.g. Dow & Vautin, 1987; Gouras, 1974; Gouras & Krüger, 1979; Hubel & Wiesel, 1968; Michael, 1978a,b; Thorell, De Valois & Albrecht, 1984). On the other hand, Livingstone and Hubel (1984) and Lennie (1987) claim that cells in area V1 which respond best to colour stimuli all have concentric receptive fields. If this is the case, the mechanisms underlying the chromatic tilt aftereffects that we report are located elsewhere; a likely site is cortical area V4 where a large proportion of cells are selective for colour (Zeki, 1980) and form (Desimone, Schein, Moran & Ungerleider, 1985). Our findings suggest that the colour preferences of these orientation-selective mechanisms should be characterized principally by one achromatic axis and two chromatic axes, corresponding to the proposed cardinal directions of colour space (Krauskopf et al., 1982). In addition to these principal mechanisms, we also found evidence for mechanisms at off-axis directions in colour space, as well as for non-specific mechanisms which respond to oriented contours defined by colour, by luminance, or both colour and luminance.

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APPENDIX

Our stimuli have been described in terms of three axes of a colour sphere, the $R - G$, B and $R + G + B$ (achromatic) axes, and these have been drawn as orthogonal axes in Fig. 2. Although the two axes of the equiluminant plane are mutually orthogonal in the linear cone-activation space—the space defined by orthogonal axes of R , G and B cone activation—the achromatic axis is not, in fact, orthogonal to either of the two colour axes. It is the luminance axis (the $R + G$ axis) that is orthogonal to the equiluminant plane, and the luminance axis is not an achromatic axis; $R + G$ varies along the luminance axis but B does not, and therefore hue must change.

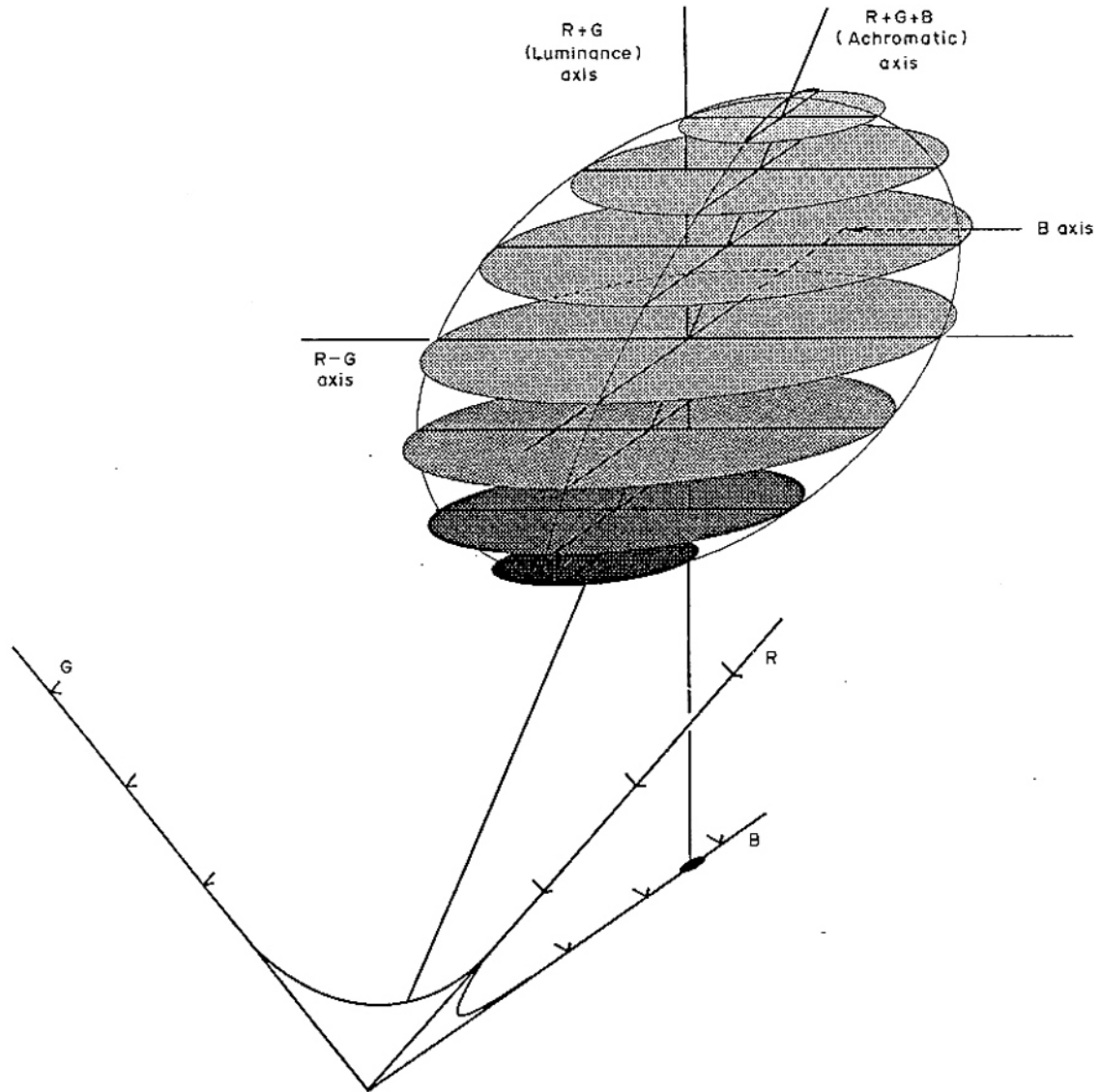


Fig. A1. Linear representation of the cone activation space. Directions of R , G and B cones are shown by three lines intersecting at bottom left of figure (the origin of cone-activation space); R , G and B directions are orthogonal in this representation. Luminance (or $R + G$) axis, passes through central white point and intersects B axis at $B > 0$, illustrating assumption that B cones make little contribution to luminance. In now skewed sphere, each horizontal plane is a plane of constant $R + G$, hence a plane of equiluminant colours; increasing lightness indicates increasing luminance (increasing sum of $R + G$). Planes' central achromatic points do not fall along vertical ($R + G$, luminance) axis but along diagonal $R + G + B$ (achromatic) axis. In spherical representation of Fig. 2, the achromatic points (and $R + G + B$ axis) are aligned vertically.

Why did we use the achromatic axis as the third axis of the colour space and not the more geometrically appropriate luminance axis? First, data from Krauskopf et al. (1982) indicated that it was not the luminance axis but the achromatic axis that was functionally orthogonal to the equiluminant plane and our data have supported their finding. Second, we wished to use a colour sphere comparable to that of Derrington et al. (1984), Krauskopf et al. (1982) and Krauskopf et al. (1986).

Why did we not use a transform of the linear cone activation space in which the achromatic axis is orthogonal to the equiluminant plane? This transform must necessarily be nonlinear and can take only two forms: a luminance-contrast transform; where the R - G and B axis values are divided by luminance (or R + G) at all points, where the achromatic axis has ill-defined units; or a log transform of the cone-activation space, with axes of $\log R - \log G$, $2 \log B - \log R - \log G$ and $\log R + \log G + \log B$. These two colour spaces would produce idiosyncratic nonlinearities in various visual tasks. Since it has not yet been established whether human performance is best described by a linear colour space or one of these non-linear spaces, and, since the appropriate colour space is undoubtedly task-dependent, we chose to use the space of Krauskopf and his colleagues.

Figure A1 shows the colour sphere when the luminance (R + G) axis is represented as being orthogonal to the equiluminant plane. As this figure shows, the achromatic axis which is defined by fixed proportions of R-, G- and B-cone activation, like all lines of constant hue, must pass through the origin of the cone activation space (R, G, and B = 0). The horizontal planes of the skewed sphere indicate equiluminant planes, or planes of constant R + G cone activation, each centred at the achromatic axis. These planes would be stacked vertically in the representation of Fig. 2.

Stimulus values in the experiment were expressed by a colour angle and a luminance angle, that defined the position of the two endpoints of a diameter on the colour sphere (centred at equal-energy white). These angles determined the luminance, w , of the stimulus and the deviation of the R - G and B cone activations from the achromatic point of the stimulus' equiluminant plane (the plane of $w \text{ cdm}^{-2}$ luminance). These values, and the R-, G- and B-cone activations of the achromatic point at $w \text{ cdm}^{-2}$, then specify

the R-, G- and B-cone activations of the stimulus. These are then transformed into the red, green and blue phosphor values through a linear transform, based on the Smith and Pokorny (1975) cone fundamentals (with the B-cone function scaled according to Boynton, 1979, p. 404) and the CIE coordinates of our monitor's phosphors (as determined by spectroradiometry). The lengths of the R - G, B and R + G + B diameters of our sphere (in units of cone activation) were adjusted to produce the largest volume of stimulus values within those permitted by our phosphors. The modulations in R, G and B cones, for the CIE standard observer, between the endpoints of the diameter of the stimulus space along the R-G axis, were 8.8, 17.6 and 0%, respectively; those between the endpoints of the diameter along the B axis were 0, 0 and 85.3%. For individual subjects, the cone modulations along the R - G and B axes would differ slightly from values calculated for the CIE standard observer. These unequal modulations in cone activations, along the axes of the colour space, result in the spherical colour space ending up as a skewed, squashed ellipsoid in linear cone-activation space.

It is interesting to consider some of the important directions in colour space, in terms of the angles of the spherical space. The projection of the luminance (R + G) direction on to the R + G + B & R - G plane is at 113° while its projection on the R + G + B & B plane is at 86° . It is clear from the data in Fig. 6 (centre panel), that neither a maximum nor a null effect occurs near the 113° point on the R + G + B & R - G plane. The luminance direction is so close to the achromatic direction in the R + G + B & R - G plane, however, that it is not possible to distinguish between them in this plane. In the equiluminant plane, the direction corresponding to Hurvich and Jameson's (1957) unique-blue/unique-yellow occurs at an angle of 64° , while unique-green/unique-red is coincident with the R - G axis. These directions are the null points of Hurvich and Jameson's (1957) red/green and blue/yellow mechanisms, respectively. We can see from the data in Fig. 6 (top panel, filled squares), that the minimum response of the mechanism, whose maximum effect is at the R - G axis (0°), lies at 90° , not 64° . Thus the null of the R - G mechanism appears to coincide with the peak of the B mechanism, not with the unique-blue/unique-yellow direction, at least in the case of those mechanisms that are selective for orientation.