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Motion Coherence Across Different Chromatic Axes*

SIMON J. CROPPER,†§ KATHY T. MULLEN,† DAVID R. BADCOCK‡

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It has been reported that equiluminant plaid patterns constructed from component gratings modulated along different axes of a cardinal colour space fail to create a coherent impression of two-dimensional motion [Krauskopf and Farell (1990). *Nature, 348,* 328-331]. In this paper we assess whether this lack of interaction between cardinal axes is a general finding or is instead dependent upon specific stimulus parameters. Type I and Type II plaids were made from sinusoidal components (1 cpd) each modulated along axes in a cardinal colour space and presented at equivalent perceived contrasts. The spatial angular difference between the two components was varied from 5 to 90 deg whilst keeping the Intersection of Constraints (I.O.C.) solution of the pattern constant. Observers were required to indicate the perceived direction of motion of the pattern in a single interval direction-identification task. We find that: (i) When plaids were made from components modulated along the same cardinal axis, coherent "pattern" motion was perceived at all angular differences. As the angular difference between the components decreased in a Type II plaid, the perceived direction of motion moved closer to the I.O.C. solution and away from that predicted by the vector sum. (ii) A plaid made from components modulated along red–green and blue–yellow cardinal axes (cross-cardinal axis) did not cohere at high angular differences (>30 deg) but had a perceived direction of the fastest moving component. At lower angular differences, however, pattern motion was detected and approached the I.O.C. solution in much the same way as a same-cardinal axis Type II plaid. (iii) A plaid made from a luminance grating and a cardinal chromatic grating (red–green or blue–yellow) failed to cohere under all conditions, demonstrating that there is no interaction between luminance and chromatic cardinal axes. These results indicate that there are conditions under which red–green and blue–yellow cardinal components interact for the purposes of motion detection. Copyright © 1996 Elsevier Science Ltd.

Motion detection Colour Luminance Cardinal axes Plaids

INTRODUCTION

A plaid pattern is made by adding two one-dimensional (1D) components at different spatial orientations to form a simple two-dimensional (2D) pattern (Adelson & Movshon, 1982). When an equiluminant chromatic plaid is made from two component gratings of the same chromatic properties, the plaid "coheres" into a 2D pattern (Krauskopf & Farell, 1990) providing the speeds and contrasts are also equivalent. This result indicates that the motion of the second order 2D structure (i.e., the chromatic contrast profile) can be coded by purely chromatic modulation (see also Cropper & Derrington, 1991, 1996; Kooi & DeValois, 1992; Kooi *et al.*, 1992). Furthermore, under some conditions, a Type II chromatic red–green plaid changes its perceived direction of motion with presentation duration in much the same way as a Type II luminance plaid (Yo & Wilson, 1992; Freedland & Banton, 1993). This suggests that there is a purely chromatic input to the motion mechanism(s) encoding Type I and Type II plaids, and that the form of this input may not differ greatly from the luminance input.

If the components are modulated along different cardinal axes (Krauskopf *et al.*, 1982), it has been reported that the plaid fails to cohere into a 2D moving structure (Krauskopf & Farell, 1990). If the percept of coherence requires a common mechanism to process all components of the plaid, the lack of coherence for plaids

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†McGill Vision Research, Department of Ophthalmology, McGill University, 687 Pine Avenue West, Rm. H4-14, Montreal, Quebec Canada, H3A 1A1.

‡Department of Psychology, School of Behavioural Science, University of Melbourne, Parkville, Victoria, Australia, 3052.

§To whom all correspondence should be addressed at School of Psychology, University of Wales College of Cardiff, PO Box 901, Cardiff, Wales, CF1 3YG [*Fax* 1 222 874858; *Email* cropper@cardiff.ac.uk].

made from components modulated along different cardinal axes suggests that motion mechanisms receive inputs specifically from one cardinal axis. This result, which implies that motion in chromatic plaid stimuli is processed only in terms of its cardinal components, is surprising in light of recent neurophysiological evidence which shows that the clustering of the chromatic selectivity of neurones in the macaque lateral geniculate nucleus around the cardinal axes (Derrington *et al.*, 1984) is substantially lost at the cortical level (Lennie *et al.*, 1990; Kiper *et al.*, 1994).

An analogous idea concerning the role of spatial scale in plaid coherence has been investigated which shows that the coherence of plaids composed of disparate spatial frequency components is dependent upon the angle between those components (Kim & Wilson, 1993), and theoretical models of 2D motion detection (Wilson *et al.*, 1992; Kim & Wilson, 1993) take into account an integration of motion signals across spatial scales under certain conditions. It is possible that a similar stimulus dependency exists for motion integration across cardinal axes.

Krauskopf & Farell (1990) used a Type I plaid with component vectors at 45 deg on either side of the Intersection of Constraints (I.O.C.) solution moving at 1 deg/sec. In a similar stimulus arrangement, but with a Type I luminance-only plaid made from different spatial frequency components (1 and 6 cpd), Kim & Wilson (1993) found that one of their observers perceived the plaid as two transparently moving components (their Fig. 2, HRW), whereas two other observers saw the pattern as a coherent 2D moving structure. Thus, it is possible that the failure of cardinal gratings modulated along different axes to cohere, as reported by Krauskopf & Farell (1990), depends upon the precise structure of the plaid, or indeed upon the observer.

The question addressed in this paper is whether this lack of interaction across cardinal axes is a qualitative division in the processing of motion or whether it is a quantitative effect specific to the stimulus conditions. Our experiments study the effect of changing the relative orientation of the components, on the degree of coherence between two component gratings modulated along the same and different axes of a cardinal colour space. Rather than using a "coherent/transparent" judgement task we chose to use the perceived direction of motion of the pattern. When a plaid coheres, observers indicate the direction of motion of the pattern; when the plaid is transparent, observers indicate the direction of one or other component. We find that for both Type I and Type II chromatic plaids composed of components modulated along different chromatic cardinal axes, their indication of pattern direction depends upon the spatial angular difference between the two components. On the other hand, when composed of components modulated in the chromatic and luminance domain, component directions are reported at all angular differences.

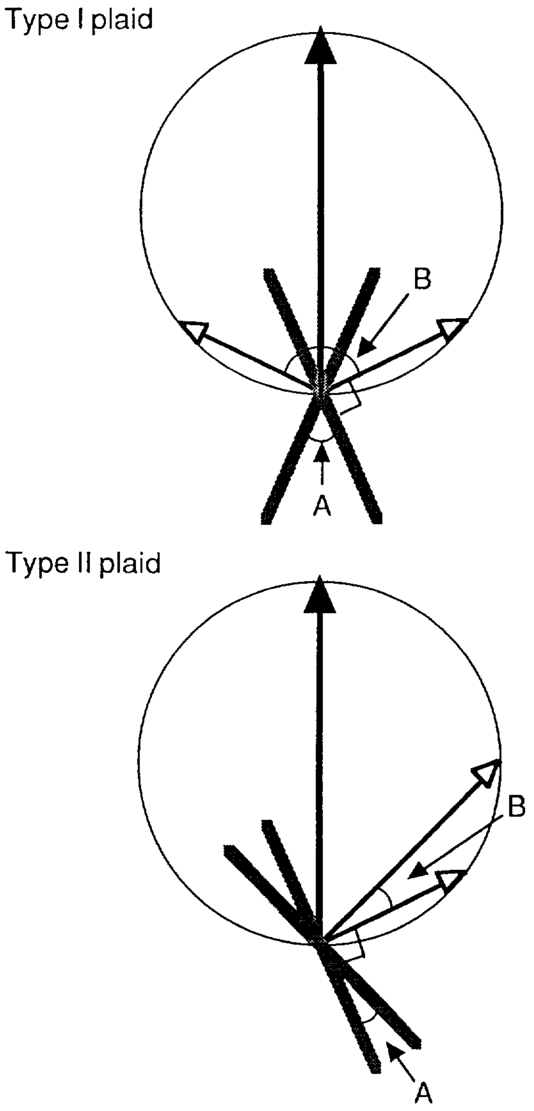

FIGURE 1. Graphical representations of the Type I and Type II plaid stimuli. The broad shaded line represents a single bar of the component gratings. The open-headed arrow normal to the bar represents its direction of motion. The solid arrow gives the Intersection of Constraints solution to the motion of the pattern. Angle A is the spatial angular difference between the components, angle B is the spatiotemporal angular difference. We refer to angle A on the data figures.

METHODS

Stimuli and equipment

The stimuli were sinusoidal gratings combined into 1 or 2D spatial patterns. The stimuli were produced on a Cambridge Research Systems graphics card (VSG2/2) and displayed on a Barco Calibrator 7551 colour monitor running at 120 Hz field-rate and 68 kHz line-rate. One-dimensional stimuli had a contrast resolution of 14-bits, two dimensional stimuli had a resolution of 8-bits. The mean luminance of the display was 18 cd/m^2, the calibrated CIE coordinates of the whitepoint were $x = 0.3116$, $y = 0.338$. Neither the mean luminance nor the mean chromaticity of the display was altered by the presentation of the stimulus. Each 1D component of the stimulus was a sinusoidal function of space and time:

$$L(y,t) = L_{\mathrm{m}}[1 + C\cos\{2\pi(fy + gt) + \phi\}] \qquad (1)$$

where L_{m} is the mean luminance, C is the contrast, f is spatial frequency (cpd), g is the temporal frequency (Hz) and ϕ is the starting spatial phase-angle. Expressed in two spatial dimensions (x and y), the plaid patterns can be described as:

$$L(x,y,t) = L_{\mathrm{m}}[1 + C_1\cos\{2\pi(u_1x + v_1y + g_1t) + \phi_1\} + C_2\cos\{2\pi(u_2x + v_2y + g_2t) + \phi_2\}] \qquad (2)$$

where u and v express the horizontal and vertical spatial frequency components of each grating summed to make the plaid. The contrast C can be expressed independently for each component. As the starting phase was randomised and the patterns were drifted, ϕ is omitted from subsequent equations.

Both Type I and Type II plaids (Ferrera & Wilson, 1990) are represented in Fig. 1. Note that only in the Type I plaid there is an inverse relationship between the spatial angular difference and the angular difference between the component motion vectors: spatial angular differences from 90–10 deg correspond to a spatiotemporal angular range of 90–170 deg, respectively. The data are plotted in terms of the spatial angular difference A, as we found this to be the important independent variable in the study (see Discussion).

It is common to calculate the velocity of a rigid 2D pattern using the Intersection of Constraints (I.O.C.) solution (Adelson & Movshon, 1982; Movshon *et al.*, 1988). In this case, the relationship between the speed and direction of motion of the 1D components and the 2D plaid pattern can be described by:

$$G_1 = P\cos(\alpha) \qquad (3a)$$

$$G_2 = P\cos(\beta) \qquad (3b)$$

where G_1 and G_2 are the velocities of the component gratings in directions described by angular deflections α and β, respectively, away from the direction of motion of the 2D pattern and P is the speed of the 2D pattern. This calculation rests on the assumption that the pattern is subject to a rigid translation in the fronto-parallel plane.

If the plaid is split up into its 1D components, then the simplest solution of recombination is to calculate the vector sum (Ferrera & Wilson, 1990). In this case the speed (VS) is predicted by:

$$VS = \surd[\{G_1\cos(\alpha) + G_2\cos(\beta)\}^2 + \{G_1\sin(\alpha) + G_2\sin(\beta)\}^2] \qquad (4)$$

and the direction (vs degrees away from the I.O.C.) is described by:

$$\tan(vs) = \{G_1\cos(\alpha) + G_2\cos(\beta)\}/\{G_1\sin(\alpha) + G_2\sin(\beta)\} \qquad (5)$$

The behaviour of carrier and envelope properties of the pattern can be expressed by resolving the stimulus into its horizontal and vertical components in space. In a Type I plaid, $u_1 = -u_2$ and $v_1 = v_2$, which simplifies Eq. (2) to:

$$L(x,y,t) = L_{\mathrm{m}}[1 + 2C\cos\{2\pi(ux)\}\cos\{2\pi(vy + gt)\}] \qquad (6a)$$

For a Type II plaid, Eq. (2) becomes:

$$L(x,y,t) = L_{\mathrm{m}}[1 + 2C\cos\{2\pi(u_1 - u_2)x\}\sin\{2\pi((u_1 + u_2)/2)x\} + 2C\cos\{2\pi(v_1 - v_2)y\}\sin\{2\pi((v_1 + v_2)/2)y\}] \qquad (6b)$$

Decomposing the Type II pattern into horizontal and vertical components and examining the spatiotemporal frequencies of each reveals the resultant direction of motion of the 2D envelope to be slightly to the opposite side of the I.O.C. solution to the vector sum.* Stimuli were presented within a raised cosine temporal envelope (Te) of the form:

$$Te(t) = 0.5\{\cos 2\pi(Et) + 1\} \qquad (7)$$

where $-0.5E \leqslant t \leqslant 0.5E$, and zero at all other times, and E is the temporal frequency (Hz) of the envelope. In the case of flickered stimuli, when heterochromatic flicker photometry was being performed, the temporal envelope was a cosine function of time (t):

$$Te(t) = \cos 2\pi(Et) \qquad (8)$$

Contrast detection thresholds for the individual plaid components were measured using a grating counterphased at a temporal frequency of 2 Hz to ensure that the temporal content of the stimulus was similar to that subsequently used as a component for the plaid pattern. In this case the temporal envelope was the product of Eqs (7) and (8), giving a counterphasing grating in a raised cosine temporal envelope. When equiluminance was measured using the method of motion-nulling the temporal envelope was a rectangular function of time. All stimuli were spatially restricted by a circular window 8 deg in diameter centred on the monitor screen (20 deg × 15 deg). The remainder of the screen was constant at the luminance and chromaticity of the whitepoint.

The contrast type (C) of the stimuli was expressed as a vector in a three-dimensional (3D) space, describing deviations from the display's mean luminance and chromaticity using the coordinate system of Derrington *et al.* (1984). The whitepoint was chosen by setting each gun to half its maximum luminance and then altering the blue and red guns to produce a satisfactory white

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*Each grating component of the plaid has the same spatial frequency but different orientation (Fig. 1). When decomposed into horizontal and vertical components [Eq. (6b)], their respective x and y spatial frequencies are unequal: $u_1 < u_2$ and $v_1 > v_2$. This gives the horizontal cosine envelope a negative spatial frequency. Both carrier and envelope have positive temporal frequencies in both x and y dimensions. The carrier motion vectors are both positive in x and y and give the vector-sum solution. The positive spatial frequency component of the horizontal envelope has a negative temporal frequency. Thus, the sum of the envelope motion vectors is to the other side of the vertical to the vector sum.

appearance. The proportional luminance contribution of each gun to the whitepoint was 0.1987 red, 0.7225 green and 0.0788 blue.

Calibration

Luminance response. The voltage to luminance relationship for each gun was measured using a United Detector Technology (UDT) Optometer (Model S370) fitted with a spectrally calibrated silicon photodiode head (No. 260). Relative luminances (Judd $Y_{(\text{rel})}$) were calculated from the meter reading (m_r), the calibrated absolute spectral sensitivity of the photodiode ($s_{(\lambda)}$), the calibrated relative spectral emissions of the R, G and B guns ($p_{(\lambda)}$) and Judd's (1951) modification of the $V(\lambda)$ sensitivity curve ($y_{(\lambda)}$) as follows:

$$\text{Judd}\, Y_{(\text{rel})} = m_r \frac{\int p_{(\lambda)} \cdot y_{(\lambda)} d\lambda}{\int p_{(\lambda)} \cdot s_{(\lambda)} d\lambda} \tag{9}$$

Look-up tables were constructed to linearise the luminance output of the three guns.

Cardinal axes. Best estimates of the cardinal axes were calculated using the cone fundamentals of Smith & Pokorny (1975). The cone excitations were obtained from the Judd (1951) tristimulus values for each gun using the appropriate transform (see Boynton, 1979, Appendix, part III). The Judd tristimulus values (X, Y and Z) were calculated for each gun by substituting the Judd colour matching functions [$x(\lambda)$, $y(\lambda)$, $z(\lambda)$] into Eq. (9). Axes were located initially by calculation of the cone excitations and by subjective equiluminant measures. The accuracy of our selection of the two chromatic axes was measured for two of our observers (DRB and SJC) by testing whether our red–green (RG) and blue–yellow (BY) stimuli are independently adaptable. The results confirmed that our two stimuli showed no cross-adaptation and therefore were "cardinal" according to the criteria of Krauskopf *et al.* (1982).

Psychophysical methods

Subjective equiluminance. The equiluminant plane for each observer was established for the chromatic stimulus to be used. The effects of chromatic aberrations were limited by using a component spatial frequency of 1 cpd (Cavanagh & Anstis, 1991; Bilodeau *et al.*, 1994; Bradley *et al.*, 1992).

For 1D gratings the heterochromatic flicker photometry method was used. Gratings were sinusoidally counterphased at 5 Hz [Eq. (8)] and the contrast was set at approximately 40 times detection threshold. The observer adjusted the luminance angle of the stimulus until the perceived flicker was minimal. The mean of 10 estimates was used as the appropriate correction for all subsequent experiments with that stimulus and observer. For 2D stimuli, equiluminance was measured using a motion-nulling technique (see Anstis & Cavanagh, 1983 for details) for each individual component. Psychometric functions were collected, plotting perceived direction of motion against the luminance angle in the chromatic stimulus. The point of 50% performance (the motion null) was obtained from a fitted Weibull curve and used as the subjective equiluminance estimate.

Detection thresholds. The contrast detection threshold for each grating component was measured with horizontal sinusoids using a staircase procedure (Taylor & Creelman, 1967; Findlay, 1978). This converged on the 75% correct point in a temporal two-alternative forced-choice (2AFC) detection task (see Cropper & Derrington, 1994 for details). The stimulus was cosinusoidally counterphased at 2 Hz [Eq. (8)] and had the temporal form of a raised cosine [Eq. (7)] with a half-envelope width of duration 900 msec. The overall threshold was taken as the mean of four of these estimates. The standard deviation was always less than 0.1 log units.

Direction-identification measurements. The perceived direction of motion of the 2D pattern was chosen as our psychophysical measure. The task was a single-interval direction-identification task. After presentation of the stimuli, observers were required to move a cursor controlled by a mouse so that the vector described by the line between the cursor and the central fixation point indicated the perceived final direction of motion of the pattern. This arrangement allowed an angular resolution around the circumference of the presentation window of approximately 0.2 deg. The orientation of each component was randomised, whilst keeping the angular difference between components the same. The 1D components were temporally interleaved at 60 Hz. It is important to note that for any one type of plaid (i.e., a particular component combination) the components themselves remain exactly the same, only their relative angular separation changes. Because of the randomisation of the actual direction moved there can be no systematic effect of the actual orientation of either component. The observers were instructed to fixate carefully on a central spot and to indicate the perceived direction of the most salient motion of the pattern at the end of the presentation interval.

Coherence or perceived direction of motion?

Preliminary observations, which are supported by our collected data and by other studies (Krauskopf & Wu, 1995), indicated that the percept of coherence or transparency was not categorical in nature. The relative strength of these two percepts may depend on the relative salience of two types of motion vectors elicited by each of the 1D components and the 2D pattern: the latter contributing to perceived coherence, the former to transparency. Using the perceived direction of motion of the pattern allows observers to indicate either component or pattern directions. In those patterns supporting both, data accumulated across trials will include trials where both pattern and component directions are dominant.

If using a metric of direction-identification, one must take into account the change in perceived direction of motion of a Type II plaid that occurs over time and as its contrast changes (Yo & Wilson, 1992; Wilson *et al.*, 1992). These properties of the stimulus made it important that the observers should indicate the direction of motion of the pattern at the end of the observation interval and they were instructed to do so. This procedure ensured that our results reflected the observers' ability to identify the direction of motion of the 2D structure of the pattern, and the effects of contrast and duration on the perceived direction of motion was minimised (Yo & Wilson, 1992; Wilson *et al.*, 1992; Cropper *et al.*, 1994).

Finally, when Type II plaids are described as the product of a carrier grating modulated by a contrast envelope at a different orientation (see Methods) it becomes clear that the carrier and envelope move in different directions. This percept is not one of pattern motion vs component motion but two distinct directions of motion within a single coherent 2D pattern. Observers were instructed to indicate the direction of motion of the contrast envelope (the "pattern" motion) unless otherwise noted below (see also Results section for Type II plaids).

Subjects

The subjects used in this study were the authors and two paid naive observers. Subjects viewed the screen binocularly from a distance of 1 m. They wore their prescribed optical correction and all had normal colour vision.

RESULTS

A note on detection thresholds and perceived contrast

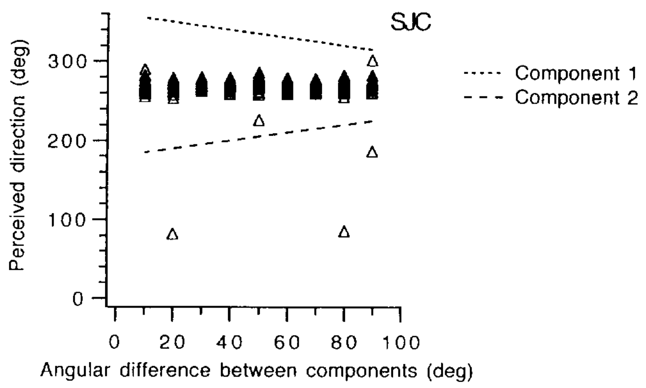
We initially scaled the contrast of the chromatic stimuli to the observers' ability to detect the presence of the individual 1D grating components. This procedure, in conjunction with measurements of independent adaptability of the chromatic cardinal axes, scales the psychophysically defined colour space (Krauskopf *et al.*, 1982) to each individual observer. We also examined the perceived contrast of the cardinal component gratings at suprathreshold levels. We found that there is a marked difference in the perceived contrast of a RG grating and a BY grating when both are presented at the same multiples of their contrast detection threshold. The difference can be explained by a shallower gain-function with increasing input contrast in the BY system, an effect that has been reported for the S-cone system in isolation (Boynton & Kambe, 1980). We found that this difference in perceived contrast had a significant effect on the appearance of the plaid patterns and chose instead to scale the BY grating so that it had the same perceived contrast as a RG grating set to a specific multiple of that grating's detection threshold. The perceived contrast of the BY grating was measured using a two-interval forced choice procedure in which one interval contained the RG grating of constant contrast (as subsequently used for each observer), the other interval contained a BY grating with a variable contrast ranging from perceptually lower to perceptually higher than that of the RG stimulus. The observer indicated which interval had the higher contrast grating. Stimuli were presented for 900 msec in the raised cosine temporal envelope. Psychometric functions were measured and the equivalent perceived contrast for a BY grating calculated for each observer. The mismatch between perceived BY contrast and the perceived RG was at least a factor of 7 and there was little subjective variability. In the subsequent data, the multiples of detection threshold refer to the contrast of the RG grating, the BY grating is presented at the equivalent perceived contrast. The perceived contrasts of the gratings modulated along axes at 45 and 135 deg in the equiluminant plane were similar to each other, so detection thresholds are used as the unit of scale. The Michelson contrasts of the components in the luminance plaid were each 0.5 unless otherwise stated, giving a peak time-averaged contrast in the composite pattern of 0.5.

Perceived direction of type I plaids

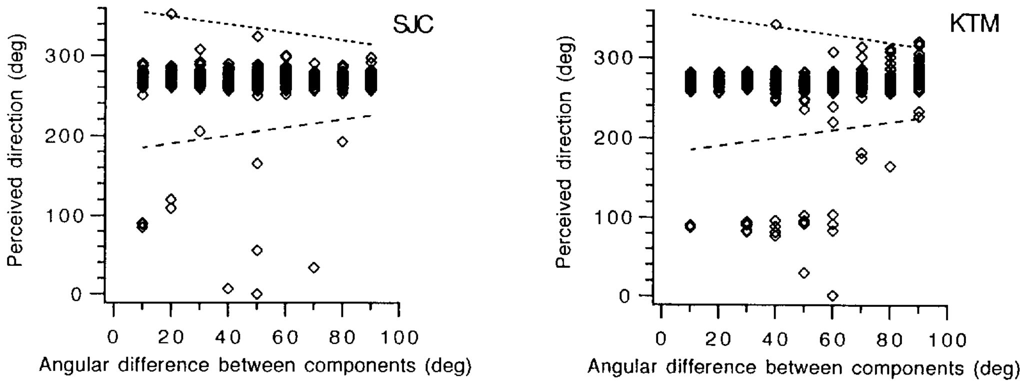
This experiment measures the perceived direction of motion for Type I plaids when the components have a spatial angular difference of between 10 and 90 deg (angle A in Fig. 1). Observers were required to indicate the perceived direction of motion of the pattern. Each observer made 50 direction judgements for each spatial angular difference and each component combination. The contrast of the chromatic component was 1.0 log unit above detection threshold for SJC and 1.2 log units above detection threshold for KTM, AW and DD. The BY grating was matched to the perceived contrast of the RG grating. Lower contrasts were not used for the equiluminant components because the composite stimuli appeared stationary during the presentation (see Cavanagh *et al.*, 1984; Mullen & Boulton, 1992a,b; Teller & Lindsey, 1993). The results for the two observers are plotted for same-axis Type I plaids in Fig. 2 and for cross-axis Type I plaids in Figs 3 and 4. The perceived direction of motion is plotted against the spatial angular difference between the two components. As noted earlier, when the spatial angular difference decreases, the angular difference between the component motion vectors *increases*. This is shown by the dashed lines in the figure.

Figure 2 plots the perceived direction for a Type I plaid made from luminance grating components (A), RG grating components (C) and BY grating components (B). As this is a Type I plaid, both the vector sum and the I.O.C. solutions coincide on a line between these two component motion vectors at 270 deg. The component motions were selected such that the pattern speed was always 4 deg/sec. Each symbol indicates a single direction-identification measurement and all 50 measurements per condition are plotted. Presenting the data in this way reveals the distribution of the perceived direction judgements. The figures show that the perceived direction for each plaid is consistent with the vector sum/ I.O.C. solution and not the motion of either one of the components alone, indicating that all three plaid patterns "cohere". There is slightly greater scatter in the identification of direction associated with the chromatic plaids, particularly at the greater angular separations. This scatter could be simply an effect of the slower perceived speed that is associated with moving equilu-

A) Luminance same-axis Type I plaid



B) Red-Green same-axis Type I plaid



C) Blue-Yellow same-axis Type I plaid

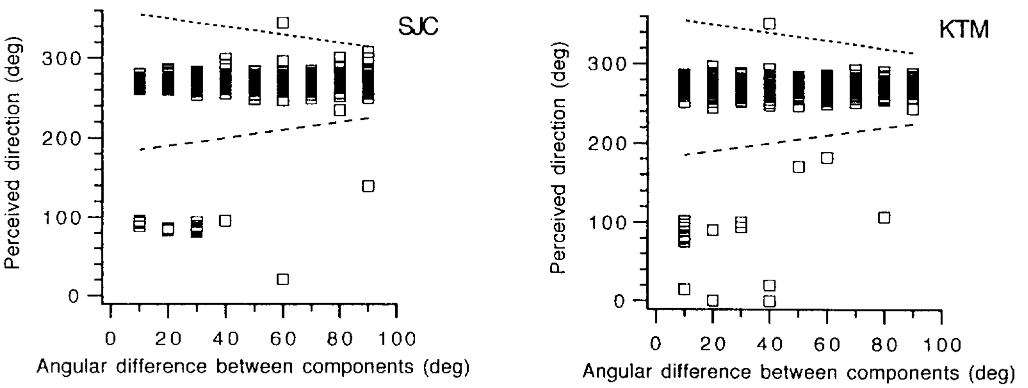


FIGURE 2. The perceived direction of motion of a Type I plaid. The angular difference between the components (angle A in Fig. 1) is plotted against the perceived direction of motion of the pattern normalised to an I.O.C./vector sum solution of 270 deg. Each symbol indicates a single direction of motion estimate and there are 50 such estimates per condition. The dotted lines give the direction of motion of each component (open-headed arrows in Fig. 1).The pattern (I.O.C.) speed was 4 deg/sec and the components were 1 cpd. (A) shows data for a Type I plaid made from two cardinal luminance gratings for observer SJC. In (B) the plaid was made from two RG cardinal gratings. Two observers are shown: SJC and KTM. In (C) the plaid was made from two BY cardinal gratings.

minant patterns (Cavanagh *et al.*, 1984; Mullen & Boulton, 1992b).

The results for a Type I plaid made from components modulated along different cardinal axes in the equiluminant plane are presented in a similar way in Fig. 3. The plaid is made from a RG and a BY equiluminant grating. At an angular separation between the components of 90 deg for observer SJC [represented by the rightmost column of points in Fig. 3(A)], the perceived direction settings fall into two clusters, one around each component direction. This indicates that the observer perceived motion in the direction of an individual component only and perceived no rigid 2D pattern motion. As the spatial angular difference (A; Fig. 1) decreases [correspondingly increasing the difference between the component motion vectors (B)], motion is seen in the component directions

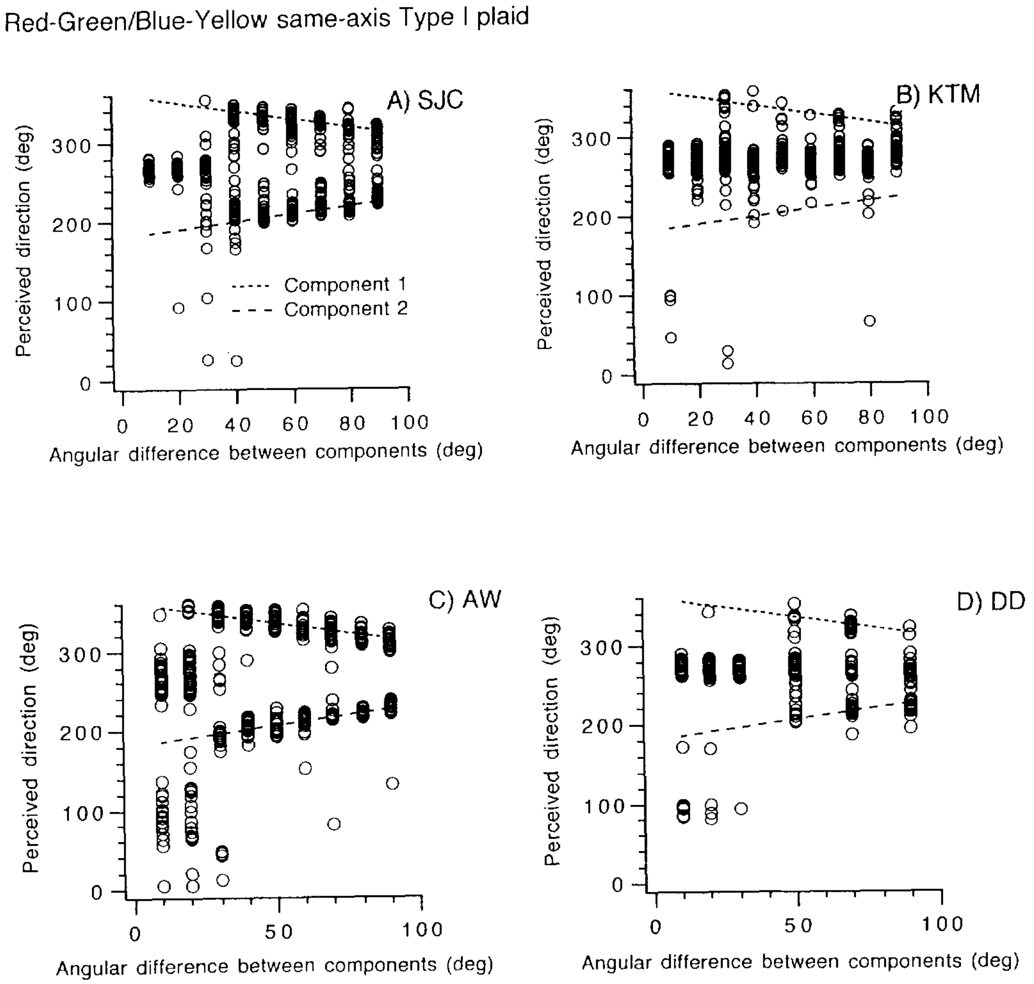


FIGURE 3. As Fig. 2 but the plaid was made from one RG cardinal grating and one BY cardinal grating. Four observers are shown: SJC, KTM, AW and DD.

until an angular difference of 30 deg and below is reached. At this angle, the perceived direction of motion becomes predominantly that predicted by the vector sum or I.O.C. solutions and subjective reports indicate that the pattern is perceived as coherent. The results for observer KTM [Fig. 3(B)] are less clear since more pattern motion is perceived across the full range of angular differences. However, as the spatial angular difference between the components is reduced, the motion of individual components is seen less frequently, and below 20 deg there are no component motion responses. This inter-observer difference, which has also been commented upon previously (Krauskopf & Farell, 1990; Krauskopf & Wu, 1995; Kim & Wilson, 1993; Ferrera & Wilson, 1990), is reflected in the data for two more naive observers AW and DD, shown in Fig. 3(C) and (D), respectively. Observer AW shows a clear component motion response at angular differences above 30 deg, with one of the components (the RG component) dominating the response despite the equivalence of perceived component contrast. At angular differences below this value, the component response is replaced by a response to the pattern similar to that seen for observers KTM and SJC. However, for this condition a significant number of the responses fall at a perceived direction of 90 deg (the opposite direction to that of the pattern) indicating that for some trials the pattern appeared stationary to this observer. This is perhaps not surprising in light of the fact that the pattern was both equiluminant and the envelope temporal frequency was at its lowest (the patterns being equated for velocity at 4 deg/sec). There were few "component" responses below an angular difference of 30 deg, despite the fact that either component alone is above the lower threshold for chromatic motion under these conditions (Cropper & Derrington, 1994). Observer DD [Fig. 3(D)] shows the dissociation of responses between angular differences above and below 30 deg. Below 30 deg pattern motion clearly dominates, above 30 deg the percept may be one of pattern or component motion, mirroring the results of KTM.

Taken as a group, these results indicate that whether a Type I plaid made from cardinal components coheres or not depends upon the spatial structure of the 2D pattern, as determined by the spatial angular difference between the components, and not simply on the individual components.

Figure 4 presents similar data for a plaid made from two component gratings modulated along axes between the chromatic cardinal axes (45 and 135 deg in the

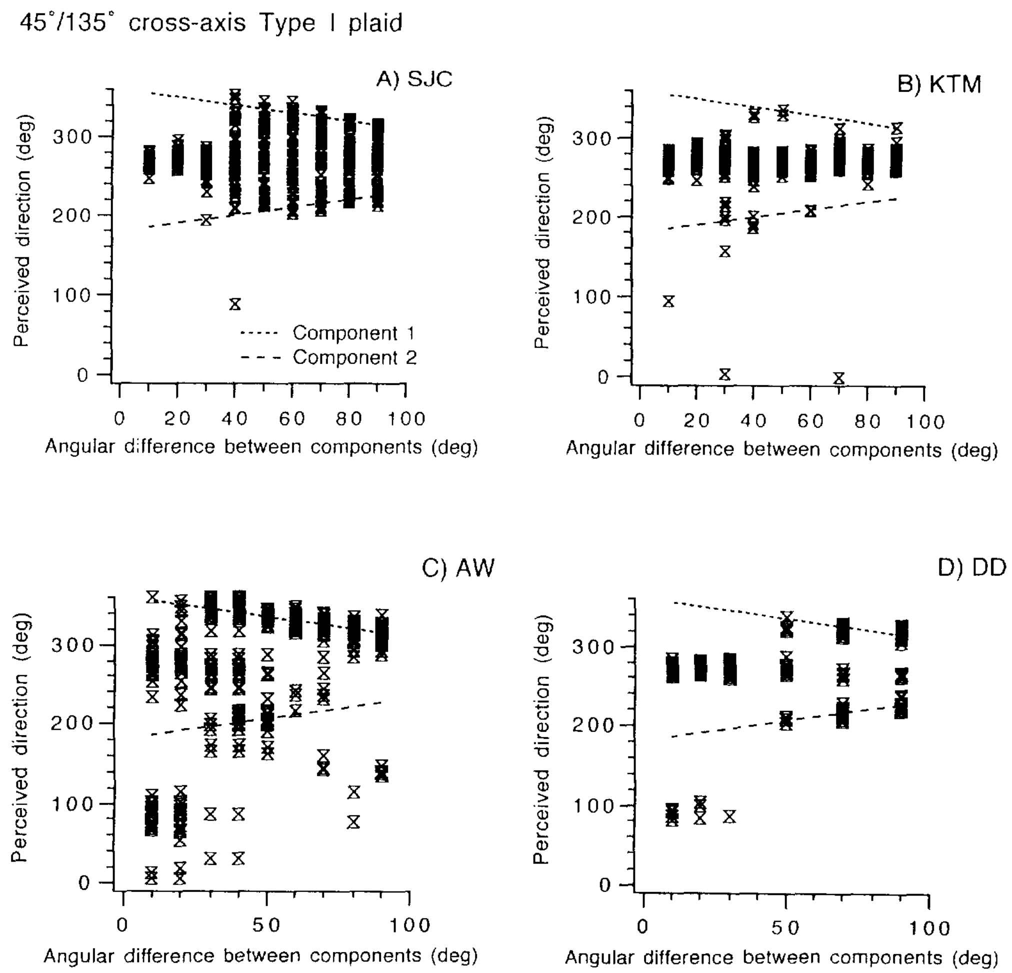


FIGURE 4. As Fig. 3 but the plaid was made from one grating modulated along the 45 deg axis in the observer's equiluminant plane and one grating modulated along the 135 deg axis in the equiluminant plane.

equiluminant plane). It can be seen from Fig. 4(A) (SJC), that the component angular difference of 90 deg (the rightmost column of points) does not elicit a consistent perceived direction, indicated by the large spread of points spanning both component and pattern motion directions. This trend continues until the spatial angular difference has been reduced to 30 deg, at which point pattern motion dominates. Observer KTM [Fig. 4(B)] gives a perceived direction of motion consistent with the vector sum/I.O.C. solution at all angular differences and, therefore, perceives more pattern motion than SJC. Observers AW and DD [Fig. 4(C) and (D)] show results similar to that of SJC in that more pattern motion is perceived overall but at angular differences below 30 deg, this is the dominant percept. Observer AW again shows a split response, which may indicate that although the 2D pattern itself was perceived rather than the components, its direction of motion could not be determined.

Comparisons of Figs 3 and 4 show that at larger angular differences for all observers there is generally a more consistent percept of coherent motion (vector sum/I.O.C. direction) for the inter-cardinal axis plaid (Fig. 3) than the cross-cardinal axis plaid (Fig. 4). Despite the significant inter-observer differences, it is clear that all patterns, whether made from components along the same or different axes in colour space, cohere when the spatial angular difference between those two components is 30 deg or less.

Perceived direction of Type II plaids

One of the problems inherent in a Type I plaid is that the vector sum and I.O.C. solutions coincide, falling between the two component directions. Thus it remains a possibility that observers could perform some kind of averaging of two perceived component motion vectors to give a response resembling the pattern motion direction, even though motion of the two individual components was being perceived. A simple way to dissociate between analysis of the 1D components and of the 2D "blob" structure is to look at the perceived direction of motion of a Type II plaid, which gives different predictions for the vector sum and I.O.C. solutions of the resultant motion (Ferrera & Wilson, 1990; also Fig. 1).

The Type II plaids were made from grating components with a spatial frequency of 1 cpd drifting at a rate such that the pattern velocity in the I.O.C. direction was again 4 deg/sec for each spatial arrangement. The actual pattern orientation was randomised on each presentation and then normalised to an I.O.C. solution of 180 deg to

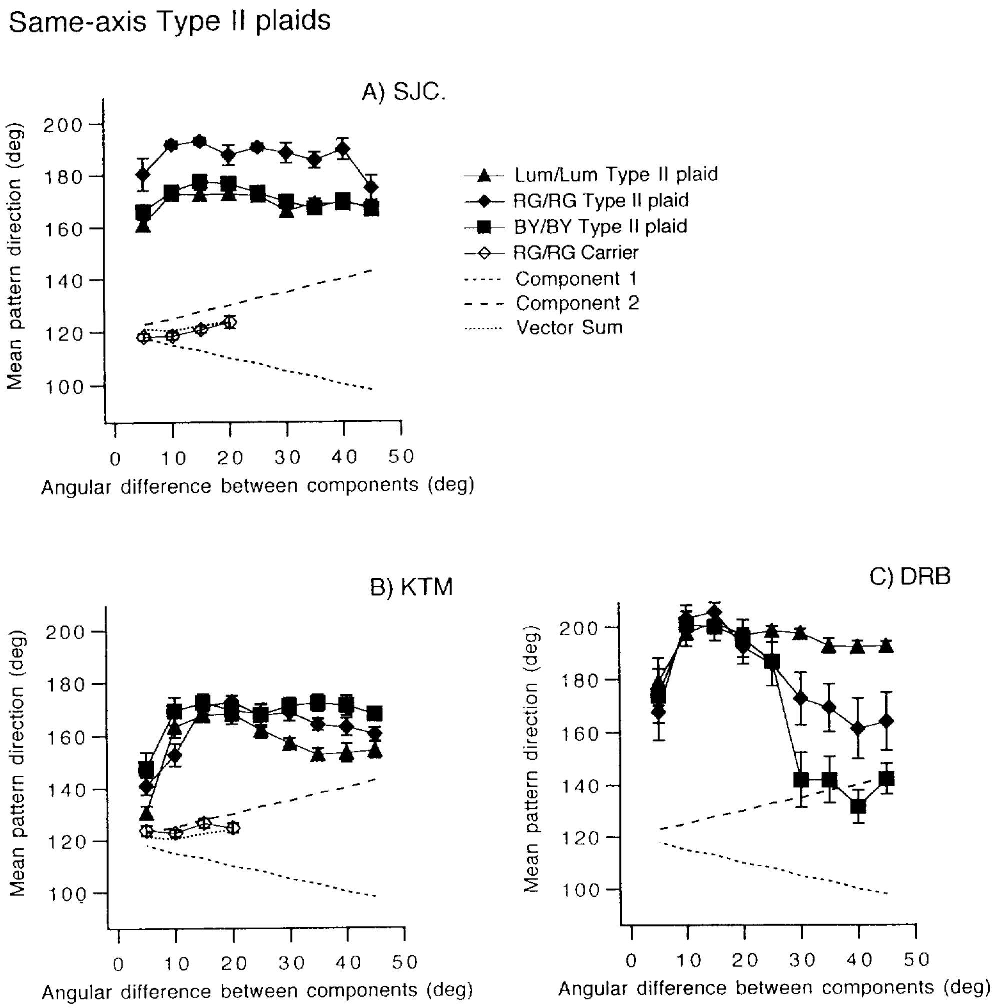


FIGURE 5. Perceived direction of motion of a Type II plaid. As in Figs 2 and 3, the spatial angular difference is plotted against the perceived direction of motion. The results are normalised to an I.O.C. solution of 180 deg. Each symbol now represents the mean (and standard error) of 50 estimates of perceived direction. Different symbols indicate different component combinations. All plaids on this figure are made from components modulated along a common axis of the colour space. The direction of motion of each component and their vector sum are shown by the broken lines. Data for three observers are presented: SJC, KTM and DRB.

present the results. The figures plot the mean and standard error of 50 direction-identification measurements at each angular difference. The dashed lines give the direction of motion of the individual components, the vector sum solution lies between these two component directions for each spatial structure [shown in each of Fig. 5(A) and (B) as fine dotted lines].

Figure 5(A–C) presents the mean perceived direction of the pattern plotted against the spatial angular difference between the components of the Type II plaids, for components modulated along a common axis in colour space. Data for three observers are shown. The contrast was high enough to give each observer a sufficient percept of motion to perform the task (1.0 log units above threshold for SJC; 1.2 log units for KTM and DRB). Although the contrast of a luminance-coded Type II plaid affects the perceived direction of motion (Yo & Wilson, 1992) the contrast is consistent for each observer across the spatial angular difference: the independent variable.

The results show that the perceived direction of motion of a given plaid pattern depends on the angular difference between the components, and performance varies slightly between the observers. Again, this variation between individuals is not uncommon for Type II plaids presented for this duration (Ferrera & Wilson, 1990; Yo & Wilson, 1992; Wilson *et al.*, 1992). Observer SJC [Fig. 5(A)] perceives the direction of pattern motion to be close to the I.O.C. solution of 180 deg at all angular differences. The luminance plaid and the BY plaid give very similar results just below the I.O.C. solution, whereas the RG plaid is perceived as moving slightly above the I.O.C. solution. Observer KTM [Fig. 5(B)] shows results similar to observer SJC and all three patterns have a similar perceived direction over the full range of angular differences. The perceived direction is close to the I.O.C. solution at high angular differences but shifts towards the vector sum at the lowest angular differences. However, it remains consistently outside the range between the two component directions (i.e., between the broken lines). Observer DRB [Fig. 5(C)] shows greater variation with component angular difference and

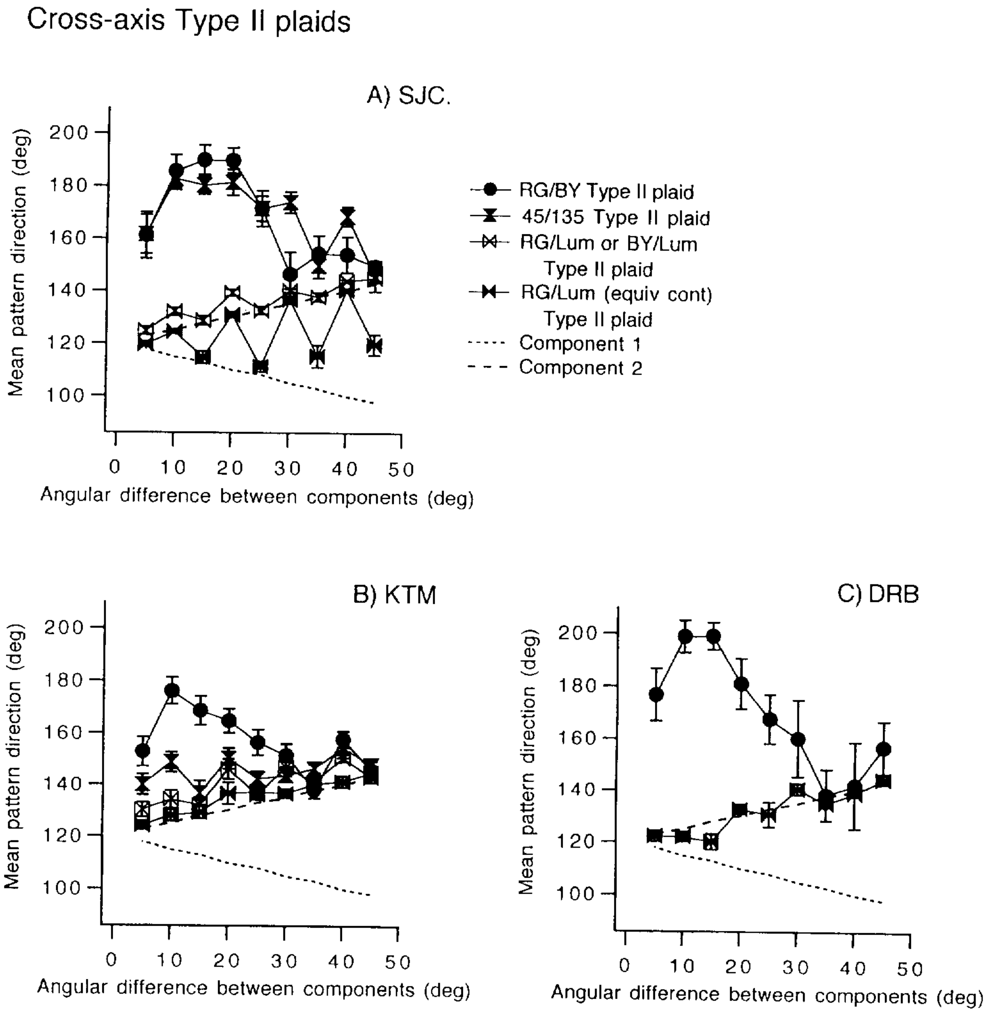


FIGURE 6. As Fig. 5 except each of these Type II plaids are made from components modulated along different axes of the colour space as indicated by the key.

also slightly greater error in the identification. At an angular separation between the components of between 10 and 25 deg, the perceived direction of motion is close to, although slightly greater than the I.O.C. solution, and all three patterns behave similarly. At smaller and larger angular differences, the perceived direction moves towards the vector sum solution and at the larger angular differences the three different patterns show different results.

In summary, Type II plaids formed from components modulated along the same cardinal axes form coherent 2D patterns whose perceived direction of motion is somewhat dependent upon the spatial structure: at most angular differences the perceived direction of motion is close to the I.O.C. solution, but as the angular difference decreases the direction of motion may approach (but not reach) the vector sum solution. This trend is independent of the cardinal axis along which the components are modulated.

As we mentioned in the Methods section, we found that Type II plaids with small angular differences between the components appeared to contain two distinct and simultaneous directions of motion, which we associated with the carrier and envelope forming the pattern (see Derrington *et al.* (1992) and Methods). Note that these plaids are single-axis plaids and always form coherent 2D patterns under our experimental conditions, and observers were required to give the direction of motion of the pattern as whole. For two observers, however, we measured the perceived direction of motion of the carrier in an equiluminant plaid made from two RG components. These results are plotted for SJC and KTM in Fig. 5(A) and (B) as open diamonds. The data show that the envelope and carrier motion were independently discriminable and neither corresponds to component motion. The perceived direction of the carrier corresponds closely to the vector sum solution, shown by the dotted line. As discussed in the Methods section, the calculated direction of motion of the envelope in our Type II plaids is on the opposite side of the I.O.C. solution to that of the carrier, and that the calculated direction of motion of the carrier corresponds to the vector sum solution. This prediction corresponds with the data quite well as, for observer SJC, envelope motion in the RG plaid is seen as just above the I.O.C. solution, and the vector sum approximately predicts the perceived direction of carrier motion in the same pattern.

It is important to note that as the angular difference between the components decreases, and the spatial extent of the "blobs" (Ferrera & Wilson, 1990) increases, so the number of "blobs" present in the 8 deg window also decreases, that is, the envelope spatial frequency decreases. This decrease appears to make it more difficult to extract the direction of motion of the envelope as opposed to the carrier and the perceived direction moves toward the vector sum solution (the carrier direction).

The perceived direction of motion of a Type II plaid made from components modulated along different chromatic cardinal axes (RG/BY) is shown in Fig. 6(A–C) as closed circles for the three observers. At a spatial angular difference between the components of 30 deg or greater, the perceived direction of motion of the pattern is close to that of the faster moving component. Subjects do not indicate the direction of pattern motion, which suggests that these plaids are not perceived as coherent 2D structures. For all subjects, as the angular difference between the components decreases, the perceived direction of motion moves toward the I.O.C. solution, suggesting that the pattern coheres and observers can extract a clear percept of the direction of motion of the 2D structure. This is similar in form to the results presented for a Type I plaid [see Fig. 3(A) for SJC].

The data for a plaid made from components modulated between the cardinal axes (45 and 135 deg in the equiluminant plane), is also presented with vertically opposed arrowheads for observers SJC and KTM in Fig. 6(A) and (B), respectively. The perceived direction of motion is very similar to that measured for the cross-cardinal axis plaid at angular differences below 30 deg and shows that a coherent pattern is perceived. At greater angular differences, more pattern motion than component motion is shown than in the cross-axis condition, showing a greater tendency of these patterns to cohere (Krauskopf & Farell, 1990). However, the perceived direction is closer to the vector sum and component directions at larger angular differences than measured for a plaid made from components modulated along the same cardinal axis. These results are consistent with those for a Type I plaid (Fig. 4) which show that the percept was split between component and pattern motion for spatial angular differences greater than 30 deg.

Is there any role for luminance?

In the final experiment we investigate whether the percept of 2D motion in these plaids is influenced by possible luminance artefacts in the two chromatic gratings. For example, a luminance artefact in each nominally chromatic plaid component might cohere to form a luminance-coded plaid which dominates the purely chromatic contribution to the pattern. We would expect any luminance artefact in the chromatic grating to be at a low Michelson contrast and we, therefore, used a low contrast luminance grating paired with a chromatic grating at the observer's standard contrast.

The solid horizontal arrowheads in Fig. 6 give data collected for a plaid made from one luminance grating and one equiluminant chromatic grating, which was either RG or BY. The luminance grating was presented at a very low Michelson contrast of 0.05, the RG chromatic grating was presented at the standard contrast of 1.0 log unit above its detection threshold for SJC and 1.2 log units for KTM. The BY component was presented at the equivalent perceived contrast to the RG component. The colour of the chromatic component (BY or RG) was alternated between trials and each component could be either chromatic or luminance. The data show that in each plaid, the perceived direction of motion was that of the fastest moving component, which was either luminance, RG or BY. There was no angular difference at which 2D pattern motion was seen.

Another question is whether any interaction between chromatic and luminance cardinal axes can be elicited. To assess this we measured the perceived direction of motion of a plaid made by adding one chromatic component and one luminance component. The luminance component was presented at the same *perceived* contrast as the chromatic component. Thus, the experiment looks for an interaction between the chromatic and luminance axes which may not be evident when the luminance grating is at a much lower perceived contrast. The results are shown in Fig. 6(A) and (B) for observers SJC and KTM, respectively, denoted by open horizontal arrowheads. The perceived direction of motion corresponds to one or other of the components, and no percept of 2D pattern motion is recorded. The interaction across cardinal axes is confined to the equiluminant chromatic plane.

DISCUSSION

The experiments presented in this paper study the effect of the relative spatial orientation of the component gratings on the perceived direction of motion of Type I and Type II plaids, modulated both along and between the cardinal axes of colour space. The motivation for the study was the initial observation by Krauskopf & Farell (1990) that plaids made from gratings modulated along different cardinal axes fail to cohere. This has been taken as evidence for the "cardinal" processing of motion since it suggests that the early spatio-temporal filters in the motion system are sensitive only along the cardinal axes, and that they retain their specificity in connecting to higher-order motion mechanisms. It was suggested that these findings were part of a general "similarity rule", which predicts that only component gratings with similar spatial frequencies, contrasts or velocities will cohere (Adelson & Movshon, 1982; Krauskopf & Farell, 1990). It has recently been reported, however, that plaids made from two luminance gratings of very different spatial frequencies can in fact cohere, and that coherence depends on the relative orientation of the two luminance components (Kim & Wilson, 1993). Thus, although different spatial frequencies may be independently detectable, they can interact for the purposes of motion detection. This conclusion suggests that, before the significance of the results reported by Krauskopf & Farell (1990) in the colour domain can be properly determined, the degree of coherence of cross-cardinal axis plaids over a range of spatio-temporal conditions must be assessed. In particular, we have investigated the dependency of coherence on the spatial orientation of the components.

Our results show that the coherence of Type I and Type II plaids formed from two different chromatic cardinal components is dependent upon the relative spatial orientation of the components. As the two components approach each other in orientation, both Type I and Type II plaids start to cohere, and at an angular difference between the two chromatic components of 10–30 deg the plaids support a pattern motion percept and move with perceived direction of motion consistent with that predicted for a 2D structure. Our results, however, do not contradict the original observation (Krauskopf & Farell, 1990) that a Type I plaid composed of a cardinal RG and cardinal BY grating at a separation of 90 deg (the I.O.C. solution ±45 deg) is generally perceived as two 1D components sliding over each other. Figure 3 shows our results obtained under equivalent conditions to those used by Krauskopf & Farell (1990). Observers SJC and AW indicated the direction of motion of the 90 deg plaid to be in one or other of the component directions, indicating that it was perceived as transparent, with the two component gratings slipping over each other. The responses of observers KTM and DD, on the other hand, indicate that the percept was variable, and was mostly seen to cohere but sometimes perceived as transparent. This suggests that individual variability is an important factor in determining whether plaids cohere or not under these conditions. More importantly, however, our results show that an angular separation between components greater than 30 deg particularly favours a lack of coherence in both Type I and Type II plaids (Figs 4 and 6), and under conditions of lower separations (10–30 deg) coherence occurs reliably between the two different chromatic cardinal components for all subjects.

It is also worth considering whether our data show any differences between the motion obtained from the combination of the two cardinal components as opposed to the combination of the inter-axis chromatic components. For Type 1 plaids at 90 deg, observer SJC showed a higher proportion of directions consistent with coherence for the inter-axis plaids than for the on-axis plaids (compare Figs 3 and 4), supporting the original results of Krauskopf & Farell (1990). Observer KTM, on the other hand, reports directions consistent with coherence for both types of plaid. Comparing the data sets for the cardinal plaids and the inter-axis plaids over all angles and the four observers, the results suggest that there is a somewhat greater tendency for pattern motion to dominate component motion with the inter-axis plaids. The significance of the results for the selectivity of the cardinal processing of motion, therefore, requires reinterpretation, and the idea that chromatic motion is subserved only by selective, independent mechanisms tuned to the two chromatic cardinal directions of colour space cannot be supported.

It is interesting that we found no spatial angular difference at which a luminance grating and a chromatic grating produce a pattern motion percept. When a very low contrast (0.05) luminance component grating is combined with a higher contrast chromatic component grating of either RG or BY modulation, the direction indicated is that of the fastest moving component (Fig. 6, open opposed arrowheads). Subjective reports also indicate that no coherence is seen. When the colour and luminance components are of equivalent perceived contrast (Fig. 6, solid opposed arrowheads) there is also no "pattern" motion, but the direction of the luminance component is always selected, regardless of whether it is the faster or slower component. Thus, like Krauskopf & Farell (1990), we suggest that the chromatic and luminance axes appear to remain fundamentally separate in their contribution to the 2D motion perception of plaids. This is a surprising result since it has been shown that colour and luminance contrast combine in some other aspects of motion perception, most notably in their contribution to the perceived speed of drifting gratings (Cavanagh *et al.*, 1984; Mullen & Boulton, 1992b).

Our conclusion, that there is no fundamental segregation of the chromatic cardinal components in motion perception, is compatible with recent physiological data since the clustering of the chromatic sensitivities of the parvocellular neurones around the cardinal axes found in primate LGN (Derrington *et al.*, 1984) appears to be substantially lost at the striate cortex (Lennie *et al.*, 1990; Kiper *et al.*, 1994). Psychophysical results also suggest that "higher-order" chromatic mechanisms exist which have their greatest sensitivity to the inter-axis colours (Krauskopf *et al.*, 1986; Krauskopf & Gegenfurtner, 1992).

Our results suggest that whether the visual system treats a cross-cardinal axis plaid as a 2D pattern is correlated with the spatial properties of the stimulus. We have shown that for the stimuli with low orientation separations, observers were able to determine two directions of motion in the pattern, neither of which corresponds to the direction of motion of a single component. One direction corresponds to the 2D pattern motion (the direction of the chromatic contrast envelope modulation), and the other corresponds to the carrier which moves in the vector sum direction. We found that observers were able to respond independently to these different aspects of motion. If both percepts were present, observers were specifically instructed to look for the pattern motion. Thus, specific features may emerge in the stimuli when the orientation differences between the component gratings are low (<30 deg), which provide salient cues to the 2D pattern motion of the stimulus. For example, the size of the inter-axis coloured "blob" enlarges at lower component orientation separations. Possibly, this greater area is needed to detect the inter-axis blob as a specific attribute of the pattern, and therefore discriminates its direction of motion in terms of its 2D structure rather than its 1D (cardinal) components. Furthermore, it is not until the blobs become noticeably elongated that the cross-axis plaids become detectable as 2D structures.

The orientation dependence of coherence in cardinal axis plaids is similar to the result reported by Kim & Wilson (1993) for the coherence of luminance plaids between two components of different spatial frequencies. One important difference, however, is that for our results it seems to be the spatial (*xy*) orientation of the components that governs whether the plaid coheres or not in the cross-axis condition, rather than the spatiotemporal (*xt*) orientation of the components, as in the plaid made from components of different spatial frequencies (Kim & Wilson, 1993). Although it is only in our Type I plaids that there is an inverse relationship between the spatial and spatiotemporal vector orientation (see Fig. 1), the results with these patterns imply that it is the 2D spatial pattern analysis that is important in the coherence of these chromatic patterns, and the 1D (component) analysis that is important across spatial scales (Kim & Wilson, 1993).

The distinction between the 1D "component" analysis and the 2D "pattern" analysis is exemplified in Type II plaids. It is thought that the perceived direction of motion of a Type II plaid in a direction close to that predicted by the I.O.C. calculation is due to some form of analysis which extracts the vector describing the direction of motion of the 2D pattern (Wilson *et al.*, 1992; Chubb & Sperling, 1988). This direction of motion (the I.O.C. solution) corresponds closely to the motion of the second-order (contrast) modulation in a same-axis plaid (see Derrington *et al.*, 1992; Wilson *et al.*, 1992). If only the 1D "component" motion was extracted, then the simplest form of recombination would be to sum the two vectors; the vector sum and I.O.C. solutions are different for a Type II plaid. Therefore, the perception of motion in the I.O.C. direction for Type II plaids is strong evidence for analysis of the motion in the pattern itself, rather than a more simple analysis in terms of its components.

When a plaid is made from different coloured components, then the distinction between first- and second-order modulation also corresponds to a distinction between cardinal and non-cardinal processing. If the visual system were only able to process motion along cardinal axes, then one would only be able to identify the 1D component motion vectors in a Type II plaid made from the two different cardinal components. Even if each cardinal component were subject to some form of nonlinear processing to extract a second-order motion vector, the system would not have more information than that given by the direction of motion of the components. As the only property that changes in the stimuli as the spatial angular difference between the components decreases is the 2D structure, the perception of coherence is likely to be due to an increase in the response of the visual system to the interaxis blob *per se*, as the response to the cardinal components will remain the same across all stimuli. Thus, our results for both Type I and Type II plaids support the existence of mechanisms directly analysing the motion of interaxis colours, and indeed may be extrapolated to imply the importance of the 2D analysis of moving patterns rather than the decomposition into the 1D components often assumed (Adelson & Movshon, 1982; Wilson *et al.*, 1992; Burke & Wenderoth, 1993a, b).

In conclusion, the results of this study show that single-axis chromatic and luminance plaids behave very similarly when we are required to perceive their direction of motion. Furthermore, when a cross-axis chromatic plaid coheres into a 2D chromatic pattern, the perceived direction of motion is similar to that shown for single-axis plaids. This suggests that motion processing based on chromatic and luminance contrast is functionally very similar. The most striking qualitative division between chromatic and luminance based motion processing that we find is the complete lack of coherence between luminance and chromatic components.

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