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# Evidence that luminant and equiluminant motion signals are integrated by directionally selective mechanisms

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Abstract. Three experiments tested whether motion information for nonequiluminant (luminant) and equiluminant dots affects direction judgments when both types of stimuli are moving simultaneously in the same display. The motion directions for the two sets of dots were manipulated to produce four direction differences  $(0^{\circ}, 30^{\circ}, 60^{\circ}, and 90^{\circ})$ . The equiluminant dots were moved in a perfectly correlated fashion, but the percentage of correlated motion for the luminant dots was varied. When subjects judged whether the directions of the equiluminant and luminant dots were the same or different, performance for the conditions with  $0^{\circ}$ ,  $60^{\circ}$ , and  $90^{\circ}$ difference improved as the percentage of correlated luminant motion increased. The same result occurred for a control display that contained two sets of luminant dots. However, for the  $30^{\circ}$  difference, performance was at chance level for the control display, but dropped below chance for the equiluminant – luminant display. When subjects indicated just the direction of the luminant dots, judgments were not affected by equiluminant motion. Judgments for the equiluminant dots also were accurate, except for the conditions with 30° difference; these responses were biased by the luminant motion, indicating some form of motion capture. The interactive effects are discussed in terms of a directionally selective mechanism that combines equiluminant and luminant motion signals.

#### **1** Introduction

There are profound differences in the perception of nonequiluminant (luminant) and equiluminant stimuli. Stationary equiluminant stimuli are captured easily by moving luminance contours, and drifting equiluminant gratings appear slower than luminant gratings moving at the same speed. For some tasks, information for equiluminant motion appears to be degraded or available only for a restricted range of stimulus parameters (Carney et al 1987; Cavanagh et al 1984, 1985; Livingstone and Hubel 1987; Ramachandran 1987; Ramachandran and Gregory 1978). These characteristics suggest that motion information for purely chromatic stimuli is not processed in the same way as motion information for luminant stimuli (cf Mullen and Boulton 1992).

One explanation for these differences is that the motion system is color-blind, or that chromatic stimuli cannot provide sufficient signals to motion processes (eg Livingstone and Hubel 1987; Ramachandran and Gregory 1978; Srinivasan 1985). To the contrary, a sizable body of psychophysical research indicates that motion mechanisms can be driven by chromatic stimuli (eg Cavanagh and Anstis 1991; Cavanagh and Favreau 1985; Cavanagh et al 1984; Cropper 1994; Cropper and Derrington 1994; Derrington and Badcock 1985; Gorea and Papathomas 1989; Kooi and DeValois 1992; Mullen and Baker 1985; Troscianko and Fahle 1988).

What remains unclear is whether chromatic and luminant motion signals are processed by a common motion system, because different measures suggest different answers. For example, Krauskopf and Farell (1990) asked subjects to judge the coherence of plaids composed of orthogonal luminant and equiluminant components. Subjects consistently reported that the grating components appeared to slip, rather than cohere. Krauskopf and Farell inferred that for the conditions used in their study, luminant and equiluminant signals are analyzed by separate motion mechanisms. Kooi and DeValois (1992, experiment 3) also found that plaids containing equiluminant and luminant components did not cohere, but subjects were able to report a single motion direction for the plaid stimulus. Direction judgements showed a bias that depended on the contrast of the luminant grating. On the basis of this finding and data from other experiments in the study, Kooi and DeValois concluded that for motion processes underlying plaid-direction perception, color and luminant motion signals initially are processed in parallel, and then are integrated by a motion system that heavily weights the luminant input.

Other studies also have indicated a shared motion process [eg Cavanagh and Anstis 1991; Cavanagh and Favreau 1985; Troscianko and Fahle 1988; but see Cropper (1994) and Cropper and Derrington (1994) for a different approach]. According to Cavanagh and Anstis (1991), color-opponent mechanisms, which respond to equiluminant stimuli, provide independent inputs to the same motion processes that operate on luminant inputs (although color-opponent signals are likely to be limited to spatial frequencies of less than 2 cycles  $deg^{-1}$ ); furthermore, motion processes that combine the two types of signals are directionally selective.

To test this hypothesis, we determined whether direction information for equiluminant stimuli would remain veridical or become distorted when luminant stimuli moving in a different direction were shown simultaneously in the same display. The rationale for using this type of display is as follows: by definition, a directionally selective process that combines equiluminant and luminant signals should be tuned to a limited range of directions, so that the process does not integrate information for motion in all directions. If equiluminant and luminant motion signals are processed independently and are not integrated by a common mechanism, then direction information for the two signals should remain intact. However, if direction information for one stimulus is perturbed by the other stimulus moving in a different direction, then the two types of signals must be combined at some stage of processing. Evidence that equiluminant and luminant information interact when the directions of motion differ by a small angle, but not when the difference is large, would support the proposition that the two sources of information contribute to the same directionally selective process (cf Cavanagh and Anstis 1991; Cavanagh and Favreau 1985).

#### 2 Experiment 1

The purpose of the first experiment was to determine whether subjects could discriminate differences in direction of motion for equiluminant and luminant dots, displayed simultaneously in a random-dot stimulus, when a strong equiluminant motion signal was presented. The equiluminant dots always moved in a perfectly correlated fashion; however, the percentage of correlated motion for the luminant dots varied systematically, providing a measure of direction discrimination as a function of the strength of the luminance motion signal. As a control, the procedure used in experiment 1 was repeated, but the stimuli were modified so that the equiluminant dots were no longer equiluminant with the background. This allowed us to assess direction discrimination for two sets of luminance-varying dots, and compare performance with that for the equiluminant-luminant-dot conditions.

#### 2.1 Method

2.1.1 *Materials and apparatus*. Stimulus generation and data collection were under the control of a Macintosh IIci computer, equipped with a video board that permitted two monitors, one for the display and the other for parameter specifications. The stimuli used for all of the experiments were a series of random-dot patterns presented on an Apple High Resolution RGB monitor with a 66.7 Hz raster rate. For this type of monitor, the standard CIE x-coordinates and y-coordinates for the red and green guns are 0.623 and 0.330, and 0.318 and 0.590, respectively. The blue gun was set to zero at all times.

2.1.1.1 Test stimuli. Each random-dot stimulus contained thirty circular elements. presented on a uniform background. Half of the elements, referred to here as equiluminant dots, appeared as greenish dots equiluminant with the reddish-orange background. The remaining fifteen elements, referred to here as *luminant dots*, appeared as yellowish dots on the same background. Heterochromatic flicker photometry (HFP) established the red-green equiluminance ratio for each subject, and generated values used to modify the luminances of the red and green phosphors (Anstis and Cavanagh 1983). The HFP task required the subject to set the point of minimum flicker for a 7.3 cm  $\times$  7.3 cm (7.3 deg  $\times$  7.3 deg) test field embedded in a surround. The test field and the surround were made to flicker, at a rate of 15 Hz, by rapidly alternating two colors, designated here as the background color and the foreground color. To create the background color, the intensities for the red and green guns were set at constant values. To construct the foreground color, the intensity of the red gun was set at a constant value (different from the one used for the background color). while the intensity of the green gun was adjusted, so that it corresponded to the subjective point of minimum flicker. The luminance values for the background and foreground colors determined the red hue of the stimulus background and the green hue of the equiluminant dots, respectively. To create the uniform hue of each luminant dot, an increment was added to the red and green luminances for the foreground color; but the intensities were modified so that the brightness of the luminant dots perceptually matched that of the equiluminant dots.<sup>(1)</sup>

The space-average luminance level was 25 cd m<sup>-2</sup> (Minolta Chromameter CS-100). Cone contrasts, defined as the ratio of incremental cone excitation for the stimulus relative to excitation for the background, were calculated with formulas including CIE *x*-values and *y*-values, luminance levels, and Smith and Pokorny (1975) fundamentals (Cole and Hine 1992; cf Cropper and Badcock 1994). For three observers, the average L-cone and M-cone contrasts were 6.4% and 14.7%. Chromatic contrast, determined from an equiluminant red–green sine-wave grating with a spatial frequency of 0.5 cycles deg<sup>-1</sup>, was above detection threshold by a factor of approximately 15. Luminance contrast was above detection threshold by a factor of approximately 8.

The display monitor, positioned 57 cm from the viewer, was covered with a circular mask (17.5 cm in diameter) and a blur screen that filtered out high spatial frequencies. There were no apparent spatial inhomogeneities across the display either before or after the blur screen was in place. The blur screen was added as a control because the axial chromatic aberration of the lens of the eye produces luminance contrast artifacts for equiluminant red-green stimuli that are significant at high spatial frequencies (Cavanagh and Anstis 1991; Cavanagh and Favreau 1985; Cavanagh et al 1987; Gur and Akri 1992; Thibos et al 1990). However, luminance artifacts can be minimized by employing equiluminant stimuli that contain very low spatial frequencies (Cavanagh and Anstis 1991). For example, Cavanagh and Favreau (1985) estimated that less

<sup>(1)</sup> Most programs that are designed to generate luminant and equiluminant sinusoidal gratings will linearize a range of voltage-luminance values and include a gamma corrrection for each gun. This is done to ensure that proportional, linear increments can be used to create variations in luminance or chrominance across the gratings (eg Cropper 1994; Cropper and Derrington 1994). Neither a linearizing table nor gamma corrections were necessary for the experiments reported here, because the stimuli did not contain chromatic or luminant variations. However, linearizing lookup tables and gamma corrections were used to generate stimuli for the contrast threshold measurements. Maximum luminance values utilized for the red and green guns (approximately 50%) were well within linear ranges.

than a 1% shift in the red-green luminance ratio would result for a red-green equiluminant sine-wave grating of 1.6 cycles  $deg^{-1}$ , when the greatest possible change in accommodation occurs. To ensure that the blur screen effectively filtered high spatial frequencies, contrast-sensitivity functions for three subjects were derived. Each subject viewed a series of monochromatic, contrast-modulated sine-wave gratings varying in spatial frequency from 0.10 to 2.5 cycles  $deg^{-1}$ . For each trial, the subject correctly identified the orientation of the grating, horizontal or vertical, and then adjusted the contrast so that the lines of the grating were barely visible. This produced a value defined by a standard Michelson contrast. Ten contrast settings per spatial frequency were averaged to determine each contrast threshold. The three contrast-sensitivity functions were bandpass, with peak sensitivities in the range of 0.2 to 0.3 cycles  $deg^{-1}$ , and poor sensitivities for higher frequencies. For a 2.0 cycles  $deg^{-1}$  grating, contrasts had to be increased by a factor ranging from 7 to 13. None of the subjects were able to discern orientations for spatial frequencies beyond 2.0 cycles  $deg^{-1}$ , even when luminance contrasts were set to maximum.

Two additional aspects of the blur screen need to be considered. The filter may have differentially transmitted light at different wavelengths. However, this would not have introduced a confound, because the same blur screen was used during the HFP procedure and the test trials. Therefore, any differential effects of the filter would have remained constant across subjects and test conditions. Second, the blur screen reduced the contrast of the stimuli, which affected the apparent size of the dots. We chose to match perceptually the sizes of the two types of stimuli, under the assumption that a small size difference would not affect direction discrimination. The luminant dots were made larger than the equiluminant dots, 1.0 deg diameter compared with 0.9 deg diameter, as computed without the blur screen.

The initial position of each dot was randomly determined on each trial. For the few trials in which a luminant and equiluminant dot overlapped, the luminant dot occluded the equiluminant dot. The speed of each dot was 7.4 deg s<sup>-1</sup>, which created the impression of smooth motion, according to solicited reports from the observers (ie subjects did not mention any jerky motion, but smoothness per se was not measured).

2.1.1.2 Control stimuli. The stimuli were identical to the test stimuli described above, except that the equiluminant dots were modified so that the green color no longer was equiluminant with the reddish background. These dots were created by reducing the red and green luminance values, determined from HFP to generate the equiluminant dots, by a small decrement. Essentially, this produced a set of dark green dots, which were distinguished by color from the other, yellow luminant dots. The sizes of the yellow and dark green dots were 1.0 deg and 0.9 deg in diameter, corresponding to the sizes used for the test stimuli. Again, it was assumed that the size difference was inconsequential.

2.1.2 Design. In this experiment a  $5 \times 4 \times 2$  repeated-measures design was used. The first manipulated variable was correlated luminant motion, defined as the percentage of correlated motion across successive frames for the luminant dots: 0%, 25%, 50%, 75%, and 100%. Dots that did not move in a correlated fashion were displaced in different directions randomly selected from a range of  $360^{\circ}$ . To ensure a strong equiluminant motion signal, the motion of the equiluminant dots always was correlated 100%. The second variable was direction difference, or the angular difference in direction for the two sets of correlated dots:  $0^{\circ}$ ,  $30^{\circ}$ ,  $60^{\circ}$ , and  $90^{\circ}$ . Figure 1 shows an example of luminant dots, with 100% correlated motion, moving to the right and equiluminant dots moving upward in a direction that differs by  $30^{\circ}$ . The third variable was dot display; the first level corresponded to the test stimuli, a display containing equiluminant and luminant dots, and the second level corresponded to the

control stimuli, a display containing two sets of luminant dots. All conditions were randomly interleaved.

For each type of dot display, twenty test conditions were presented across four randomly ordered blocks of trials. For each block, two equiluminant-dot directions were factorially combined with two luminant-dot directions to create the four direction differences. Using all possible combinations across four blocks of trials, we were able to analyze performance as a function of direction difference and absolute direction of motion.



Figure 1. The stimulus display containing equiluminant and luminant dots, where the percentage of correlated motion is 100%. The direction difference for these two sets of dots is  $30^{\circ}$ .

2.1.3 Subjects. One of the authors (SH), and two undergraduates, not aware of the hypotheses being tested, voluntarily participated in the experiments. The subjects, ranging in age from 20 to 40 years, had normal or corrected-to-normal vision.

2.1.4 *Procedure*. Each subject viewed the screen binocularly, with her head positioned in a chin rest 57 cm from the display screen. Prior to each testing session, the subject repeated the HFP task, so that the mean of twenty settings established the red and green luminances for the test stimuli (Anstis and Cavanagh 1983; Cavanagh et al 1987). After a three-tone 'ready' signal, the stimulus was presented for 1000 ms. The subject was instructed to fixate the center of the display and note the general direction of motion for both sets of dots, without tracking any single dot. A fixation cross was not used.<sup>(2)</sup> The subject indicated whether the two streams of dots moved

<sup>(2)</sup> Although each subject was instructed otherwise, the subject may have tracked one set of dots on any given trial. If this were the case, any directional difference would have produced a difference in retinal velocity for the two sets of dots; this, in turn, may have affected discrimination performance for that trial. This would have been problematic if the probability of tracking one set of dots differed for the two dot displays (ie the display containing equiluminant and luminant dots vs the display containing two sets of luminant dots), or for any of the four direction differences. We assumed that tracking was a random factor that varied equally across all conditions. Note that this assumption has to exist for all relative-motion studies that do not stabilize the retinal image or monitor eye movements. Furthermore, data from a pilot study showed that when one set of dots. So, tracking one set of dots would not have been an optimal performance strategy. in the same or different directions by depressing one of two keys on the keyboard. No error feedback was provided. A total of 400 trials, 20 per test condition, were presented during a 35 min session.

#### 2.2 Results and discussion

Data collapsed across three subjects are shown in figure 2. Figure 2a represents the data for the test conditions, in which equiluminant and luminant dots were presented in the same display. Here the percentage of trials for which the subjects correctly identified the two dot directions is plotted as a function of the percentage of correlated luminant motion and direction difference (ie the data for the  $30^\circ$ ,  $60^\circ$ , and  $90^\circ$  conditions show the percentage of "different" responses, and the data for the  $0^\circ$  conditions represent the percentage of "same" responses). Each data point indicates the average for three subjects, based on 80 trials per subject per test condition. In figure 2b the same graphing conventions are used to illustrate the data for the control stimuli conditions, in which two sets of luminant dots were presented simultaneously. The group data are generally representative of the individual subject data.

Note that for the trials with 0% correlated motion, luminant direction information was nonexistent (ie the luminant dots moved in random directions), so the discrimination task was ambiguous. Thus, data for the conditions with 0% correlated motion reflect the percentage of times the subject responded "different" for the  $30^{\circ}$ ,  $60^{\circ}$ , and  $90^{\circ}$  conditions or "same" for the  $0^{\circ}$  conditions. As such, these values do not provide a measure of direction discrimination. If judgments were completely unbiased, responses should have been approximately 50%. As seen in the data for 0% correlated motion for the equiluminant –luminant display (figure 2a), responses were within one standard error of 50%. However, in the corresponding data for the luminant –luminant display (figure 2b), responses appeared to be biased. The raw data indicate that at least one subject was more likely to report "different" when two distinct directions were not discernible, which may reflect a shift in decision criterion under ambiguous conditions.

A repeated-measures analysis of variance (ANOVA) included responses only for the conditions with 50%, 75%, and 100% correlated luminant motion, because the data for the 0% and 25% conditions were more variable. The analysis showed a significant



Figure 2. Experiment 1. (a) Mean judgments for three subjects presented with the equiluminantluminant-dot display. Responses for the four direction differences are plotted as a function of percentage correlated motion for the luminant dots. (b) Mean judgments for three subjects shown the display containing two sets of luminance dots. Responses for the four direction differences are plotted as a function of percentage correlated motion for one set of luminant dots. For both graphs, the gray line indicates chance performance. Error bars represent  $\pm 1$  SEM.

direction difference × dot display interaction  $(F_{3,6} = 6.80, p \le 0.05)$ , a significant main effect for direction difference  $(F_{3,6} = 45.66, p \le 0.001)$ , and a significant main effect for dot display  $(F_{1,2} = 37.12, p \le 0.05)$ . However, there was no significant three-way interaction, no other two-way interactions, and no significant effect for correlated luminant motion (for all, p > 0.05). Planned chi-square comparisons indicated that subjects did not show a bias for vertical or horizontal directions (p > 0.05); that is, performance did not differ as a function of the absolute direction of the equiluminant or luminant dots.

Two interesting findings emerged. First, for equiluminant-luminant displays containing a 60° or 90° direction difference, direction judgments improved as the strength of the luminant motion signal increased. In other words, direction information for the equiluminant dots was not affected by robust luminant motion. According to the logic outlined earlier, the evidence suggests that the two motion signals were not integrated under these test conditions (cf Krauskopf and Farell 1990). This result differs from the Kooi and DeValois (1992, experiment 3) finding, which showed direction biases for plaids comprising orthogonal luminant and equiluminant components. One reason for the discrepancy may be task demands: subjects in the Kooi and DeValois study judged a single direction, whereas subjects in our experiment were told to note and compare two directions of motion. Second, a dot display × direction difference interaction occurred. For the 30° direction difference trials in which two sets of luminant dots were shown, performance was approximately at chance. (See section 5 for an elaboration of this point.) However, for equiluminant and luminant dots separated by 30°, as the percentage of correlated luminant motion increased, judgment performance dropped below chance. This is evidence for motion capture, suggesting that information for one or both sets of dots was distorted.

#### 3 Experiment 2

For conditions in which subjects could not discern two directions of motion for equiluminant and luminant dots, one question that remained was whether direction information for one set of dots was perturbed, or whether the signals for the two directions were averaged. To differentiate between these alternatives, subjects were asked to view the equiluminant-luminant dot display and then judge the direction of motion for just the luminance dots. The complementary task of judging the direction for the equiluminant dots was completed in experiment 3.

#### 3.1 Method

3.1.1 Materials and design. The same test stimuli from experiment 1 were used here, with the following exceptions. A  $3 \times 4$  repeated-measures design was used; three levels of correlated luminant-dot motion, 50%, 75%, and 100%, were factorially combined with four levels of direction difference, 0°, 30°, 60°, and 90°. The twelve test conditions were presented across twelve randomly ordered blocks of trials, so that each block of trials was defined by one level of correlated luminant-dot motion and one direction difference. As in experiment 1, the percentage of correlated motion for the equiluminant dots was held constant at 100%.

3.1.2 Procedure. Ten heterochromatic flicker settings were used to determine the red-green equiluminant ratio prior to each test session. The stimulus display containing thirty equiluminant and luminant dots was presented for 1000 ms. Immediately afterwards, the dots were extinguished and a black pointer appeared in the center of the reddish background. The subject adjusted the position of the pointer, which rotated through a  $360^{\circ}$  range, to indicate the perceived direction of the luminant dots. Twenty-five trials per test condition were averaged to provide a measure of luminant-dot-direction judgment.

#### 3.2 Results and discussion

Data collapsed across three subjects are shown in figure 3. The vertical axis indicates the direction error for luminant dots, computed as the difference between the true direction and the perceived direction. These values are plotted as a function of the percentage of correlated motion for the luminance dots. Here a zero value indicates no bias, a negative value indicates a bias in the direction of the equiluminant dots, and a positive value suggests bias in the direction opposite the equiluminant dots. The data for each subject showed the same pattern as represented in figure 3.

A repeated-measures ANOVA produced no significant effect for direction difference ( $F_{3,6} = 0.90$ , p > 0.05), no effect for correlated luminant-dot motion, ( $F_{2,4} = 4.59$ , p > 0.05), and no direction difference × correlated luminant-dot motion interaction ( $F_{6,12} = 0.61$ , p > 0.05). The data clearly indicated that direction information for the luminant dots was not affected by the equiluminant-dot motion.



Figure 3. Experiment 2. Direction error for luminant dots (true direction minus perceived direction) as a function of percentage correlated motion for luminant dots and direction difference. Data are collapsed across three subjects. A zero response indicates accurate performance, whereas a negative value indicates a bias in the direction of the equiluminant dots. Error bars represent  $\pm 1$  SEM.

#### 4 Experiment 3

#### 4.1 Method

The materials, design, and procedure used here were identical to those employed in experiment 2, except that subjects adjusted the pointer to indicate the perceived direction of the equiluminant dots.

#### 4.2 Results and discussion

Data collapsed across three subjects are shown in figure 4, where the vertical axis indicates the direction error for equiluminant dots, or the difference between the true and perceived direction. Here a zero value indicates no bias, a positive value indicates a bias in the direction of the luminant dots, and a negative value suggests bias in the opposite direction. Again, this pattern was consistent for all subjects. A repeated-measures ANOVA showed a significant main effect for direction difference  $(F_{3,6} = 123.31, p < 0.001)$ , but no effect for correlated luminant-dot motion  $(F_{2,4} = 1.12, p > 0.05)$ , and no direction difference  $\times$  correlated luminant-dot motion interaction  $(F_{6,12} = 1.82, p > 0.05)$ . The strong judgment bias only for the 30° direction difference indicates some form of motion capture, in which equiluminant motion is distorted by luminant motion. The implications are elaborated below.



Figure 4. Experiment 3. Direction error for equiluminant dots (true direction minus perceived direction) as a function of percentage correlated motion for luminant dots and direction difference. Data are collapsed across three subjects. A zero response indicates accurate performance, whereas a positive value indicates a bias in the direction of the luminant dots. Error bars represent  $\pm 1$  SEM.

#### 5 General discussion

To summarize, the results from three experiments showed that when luminant and equiluminant dots moved in very different directions, neither stimulus influenced the perceived direction of the other. The demonstration that direction information for each stimulus remained veridical suggests that equiluminant and luminant signals differing by more than  $30^{\circ}$  were not integrated by a common process. Second, when a smaller direction difference was used, judgments for the equiluminant stimuli were biased in the direction of the luminant stimuli. The biasing effect was asymmetrical, because there was no indication that chrominant motion influenced the perceived direction of luminant motion.

One might argue that poor direction discrimination for equiluminant stimuli resulted because the luminant signal reduces the visibility of the equiluminant dots (ie some form of masking occurred). However, a masking argument cannot explain why performance was very good when the two sets of stimuli were presented with a direction difference greater than 30°, and the subject had to attend to both sets of stimuli (see experiment 1). Furthermore, the present results cannot be explained just in terms of an equiluminant signal that is too weak to drive a directional mechanism. Tangentially related psychophysical evidence indicates that direction discrimination for equiluminant gratings is not affected unless the stimulus contrast approaches detection threshold (Cavanagh and Anstis 1991; Derrington and Henning 1993; Mullen and Boulton 1992).

Rather, we contend that the data provide evidence for a directionally selective process that combines chrominant and luminant motion signals. The process can be modeled by a higher-order mechanism (ie not a first-order motion detector) that integrates motion information across greater spatial and temporal extents than low-level motion detectors (cf Cavanagh 1992). The present results indicate that the mechanism has a bandwidth between  $30^{\circ}$  and  $60^{\circ}$ . This estimate coincides with others derived from psychophysical studies employing luminant-varying stimuli (Raymond 1993; Williams et al 1991). For one study, Raymond used an adaptation procedure with random-dot stimuli to measure interactions among directionally selective processes. Subjects first adapted to unidirectional motion, and then judged whether a test stimulus contained coherent, global motion or incoherent noise. Thresholds for

motion coherence were bandpass, showing an elevation when the direction of the test stimulus approximated the direction of the adapting stimulus. The results disconfirmed models of opponent-direction mechanisms, because there was no enhanced sensitivity to motion in the opposite direction after adaptation. On the basis of the evidence, Raymond proposed a multiple-analyzer model, composed of independent, directionally selective units with  $\pm 35^{\circ}$  to  $40^{\circ}$  bandwidths.

This estimate is supported by our results for the luminant-luminant dot display (ie the control condition) employed in experiment 1. When the directions of two sets of luminant stimuli differed by  $60^{\circ}$  or more, direction discrimination was very accurate; but when the direction difference was  $30^{\circ}$ , discrimination performance was at chance. One reviewer noted that there are at least three possible explanations for chance performance. First, the small direction difference generated spurious matches across the two types of dots. Matching failures (which may be defined as a correspondence problem) would have produced very weak motion signals, and reduced the probability of detecting any direction for either set of dots. This explanation is unlikely, given the strong impression of coherent motion for the two streams of dots. Second, the two directions were indistinguishable because an identical direction signal was generated for each stimulus. This implies that direction information for each stimulus was very imprecise, as would occur if each set of dots activated the same broadly tuned motion detector at a very early stage of processing. The data from experiment 2 showed that direction information for a single luminant-motion stimulus was exact; this finding disconfirms any hypothesis based on imprecision at a low level of processing. Third, the two stimuli created distinct motion signals that were averaged by a directionally selected process, with a bandwidth encompassing the two directions. The difference between the second and third options (ie one direction signal compared with an averaged signal) is the level of the operation. If only one signal is generated initially, then information for two distinct directions never can be ascertained. However, if separate signals interact at some later stage, then an experimental paradigm may unravel the two. One way to do this may be to reduce the effective input for one of the two stimuli, possibly by using an adaptation paradigm.

We propose a qualitative model of a directionally selective integrator, with a given directional bandwidth, that averages chrominant and luminant motion signals. We assume the luminant channel inputs, which are determined by the contrast and speed of the luminant stimulus, are weighted more heavily than chrominant channel inputs (cf Kooi and DeValois 1992). A differential weighting of signals can explain why the direction information for equiluminant motion was biased toward a strong luminant stimulus when the direction difference was small, and why the direction information for luminant stimulus affects the integrative mechanism in a manner akin to a low-contrast stimulus (Troscianko and Fahle 1988). Stone et al (1990) showed that direction judgments for a plaid stimulus, comprising two luminant grating components with different contrasts, were biased by as much as  $20^{\circ}$  in the direction of the higher-contrast component.

The question of whether the equiluminant signal operates as a low-contrast input is an empirical one that was anticipated by Kooi and DeValois (1992). If this is the case, then an increase in equiluminant contrast would strengthen the equiluminant input and improve discrimination performance (cf Cropper and Derrington 1994), while a decrease in contrast would weaken the input and worsen performance. A test of this hypothesis would be whether direction discrimination for equiluminant stimuli, presented with luminant stimuli separated by a small direction difference, improves when the contrast of the luminant stimuli is decreased. This test is being conducted currently. Acknowledgements. We wish to thank Jim Dannemiller and three anonymous reviewers for their constructive criticism and invaluable help. Portions of this work were presented at the 1993 meeting of the Association for Research in Vision and Ophthalmology. This work was partially supported by a grant from NSF/LEQSF (1992–1993)-ADP-04 to Lee Zimmerman.

#### References

- Anstis S, Cavanagh P, 1983 "A minimum motion technique for judging equiluminance", in Colour Vision: Physiology and Psychophysics Eds J D Mollon, LT Sharpe (London: Academic Press) pp 155-166
- Carney T, Shadlen M, Switkes E, 1987 "Parallel processing of motion and colour information" Nature (London) 328 647-649
- Cavanagh P, 1992 "Attention-based motion perception" Science 257 1563-1565
- Cavanagh P, Anstis S, 1991 "The contributions of color to motion in normal and color-deficient observers" Vision Research 31 2109-2148
- Cavanagh P, Favreau O E, 1985 "Color and luminance share a common motion pathway" Vision Research 25 1595-1601
- Cavanagh P, Boeglin J, Favreau O E, 1985 "Perception of motion in equiluminous kinematograms" *Perception* 14 151-162
- Cavanagh P, MacLeod D I A, Anstis S, 1987 "Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones" Journal of the Optical Society of America A 4 1428-1438
- Cavanagh P, Tyler C W, Favreau O E, 1984 "Perceived velocity of moving chromatic gratings" Journal of the Optical Society of America A 1 893-899
- Cole G R, Hine T, 1992 "Computation of cone contrasts for color vision research" Behavior Research Methods Instruments & Computers 24 22-27
- Cropper S J, 1994 "Velocity discrimination in chromatic gratings and beats" Vision Research 34 41-48
- Cropper S J, Badcock D R, 1994 "Discriminating smooth from sampled motion: chromatic and luminance stimuli" Journal of the Optical Society of America A 11 515-530
- Cropper S J, Derrington A M, 1994 "Motion of chromatic stimuli: first-order or second-order?" Vision Research 34 49-58
- Derrington A M, Badcock D R, 1985 "Separate detectors for simple and complex grating patterns?" Vision Research 25 1869-1878
- Derrington A M, Henning G B, 1993 "Direction-of-motion discrimination and detection of luminance and colour gratings" Vision Research 33 799-813
- Gorea A, Papathomas T V, 1989 "Motion processing by chromatic and achromatic pathways" Journal of the Optical Society of America A 6 590-602
- Gur M, Akri V, 1992 "Isoluminant stimuli may not expose the full contribution of color to visual functioning: Spatial contrast sensitivity measurements indicate interaction between color and luminance processing" Vision Research 32 1253-1262
- Kooi F L, DeValois K K, 1992 "The role of color in the motion system" Vision Research 32 657-668
- Krauskopf J, Farell B, 1990 "Influence of colour on the perception of coherent motion" Nature (London) 348 328-331
- Livingstone M S, Hubel D H, 1987 "Psychophysical evidence for separate channels for perception of form, color, movement and depth" *Journal of Neurosciences* 7 3416-3468
- Mullen K T, Baker C L, 1985 "A motion aftereffect from an isoluminant stimulus" Vision Research 25 685-688
- Mullen K T, Boulton J C, 1992 "Absence of smooth motion perception in color vision" Vision Research 32 483-488
- Ramachandran V S, 1987 "Interaction between color and motion in human vision" Nature (London) 328 465-467
- Ramachandran V S, Gregory R L, 1978 "Does colour provide an input to human motion perception?" *Nature (London)* 275 55-56
- Raymond J E, 1993 "Movement direction analysers: Independence and bandwidth" Vision Research 33 767-775
- Smith V C, Pokorny J, 1975 "Spectral sensitivity of the foveal cone pigments between 400 and 500 nm" Vision Research 15 161-171
- Srinivasan M V, 1985 "Shouldn't directional movement detection necessarily be 'colour-blind'?" Vision Research 25 997-1000

- Stone L S, Watson A D, Mulligan J B, 1990 "Effect of contrast on the perceived direction of a moving plaid" Vision Research 30 1049-1067
- Thibos L N, Bradley A, Still D L, Zhang X, Howarth PA, 1990 "Theory and measurement of ocular chromatic aberration" Vision Research 30 33-49
- Troscianko T, Fahle M, 1988 "Why do isoluminant stimuli appear slower?" Journal of the Optical Society of America A 5 871-880
- Williams D, Tweten S, Sekuler R, 1991 "Using metamers to explore motion perception" Vision Research 31 275-286