

Isoluminance and Chromatic Motion Perception Throughout the Visual Field

LYNDA BILODEAU,* JOCELYN FAUBERT*

Received 11 July 1995; in revised form 18 April 1996; in final form 19 September 1996

Isoluminance and chromatic motion perception for red/green gratings were measured throughout an 80 deg visual field. Generally, the red/green isoluminance values changed with increasing eccentricity, i.e., observers increased the red luminance contrast for a fixed green luminance contrast. Enlarging the target size (to compensate for the cone density changes with eccentricity) and decreasing the spatial frequency (to compensate for receptive field property changes with eccentricity) did not change the isoluminance values within the central 20 deg, but the isoluminance ratios decreased beyond 20 deg. Our manipulations did not entirely compensate for a given eccentricity, which implies the need for a post-receptoral scaling function for the perception of drifting chromatic stimuli. Further, the results for isoluminance show heterogeneity between the visual field meridians where the red to green luminance ratio tends to be greater in the superior visual field. In our present conditions, chromatic motion was always perceived (up to 40 deg of eccentricity), but sensitivity generally decreased with increasing eccentricity. The inferior visual field was found to be the most sensitive to chromatic motion. We propose that the lower visual field and not the superior visual field is specialized for colour motion information. © 1997 Elsevier Science Ltd.

Peripheral chromatic motion Isoluminance Motion Colour

INTRODUCTION

Several psychophysical studies on chromatic motion indicate that the chromatic system can transmit motion information (Cavanagh, 1991; Cavanagh & Anstis, 1991; Cavanagh *et al.*, 1984 Cavanagh *et al.*, 1985, 1987; Cavanagh & Favreau, 1985; Cropper & Derrington, 1996; Gorea & Papathomas, 1989; Papathomas *et al.*, 1991). Generally, the strength of the motion perception appears degraded, but the chromatic system is capable of achieving motion perception particularly for slower temporal frequencies. However, it has been proposed that the chromatic visual system is unable to relay motion information (Livingstone & Hubel, 1987, 1988; Ramachandran & Gregory, 1978).

Until now, most studies on chromatic motion have focused on the foveal and parafoveal areas of the visual field. Colour motion sensitivity should peak at the fovea, since the majority of cells that respond to colour can be found in that small area. Nevertheless, there are cells sensitive to colour in the peripheral retina. The colour sensitivity in the peripheral visual field is lower than that of the fovea (Abramov *et al.*, 1991; Ferree & Rand, 1919; Stabell & Stabell, 1981) and colours appear desaturated, although it is possible to correctly identify them. Metha *et al.* (1994) compared the contribution of cone-opponent and additive mechanisms to motion in a 24 deg visual field using a 3 deg diameter Gabor patch. They failed to obtain thresholds for a cone-opponent mechanism past 12 deg of eccentricity in the inferior visual field. They concluded that suprathreshold chromatic contrast is necessary to identify correctly the direction of movement in the peripheral visual field. We still have relatively little knowledge of what role the chromatic system plays in the perception of motion throughout the visual field.

Mullen (1985, 1991) demonstrated that with increasing eccentricity, sensitivity to chromatic gratings decreased at a steeper rate than for achromatic gratings. Also, contrast sensitivity for higher spatial frequency gratings decreased more rapidly than for lower spatial frequency gratings in peripheral locations. It might be possible to maximally stimulate the receptive field of peripheral cells by decreasing the spatial frequency of the stimulus and attempt to compensate for cone topography changes by increasing the stimulus size with increasing eccentricity (Noorlander *et al.*, 1983).

The main purpose of this study was to first determine the change in red-green (R/G) isoluminance ratio throughout an 80 deg visual field. A second aim was to assess whether chromatic motion perception is possible throughout the visual field, and if so, to determine

^{*}Ecole d'optometrie and Groupe de Recherche en Neuropsychologie Expérimentale, Université de Montréal, C.P. 6128, Succ. Centre-Ville, Montréal, Quéèbec, Canada H3C 357

whether compensating for the cone density and/or receptive field properties with eccentric viewing had an effect on the perceived motion.

EXPERIMENT 1

The first study assessed the extent to which different parameters influence isoluminance values throughout the visual field. We determined the effect of visual field location, eccentricity, stimulus size and drift rate on isoluminance values using the motion nulling paradigm (Anstis & Cavanagh, 1983).

Methods

Subjects. Three subjects participated in this experiment. Two subjects were the authors (JF and LB) and the third subject was a trained psychophysical observer (AB). They all had normal or corrected to normal vision, as well as normal colour vision.

Stimuli. The stimuli were presented on a 13" Apple colour monitor and generated by a Macintosh IIfx computer. The same general calibration procedures were used as described in Cavanagh et al. (1995). Chromatic and luminance characteristics were measured using a Minolta Chromameter CS-100. The maximum luminance available for red, green, and blue were 19, 57.5, and 9.5 cd/m^2 , respectively. The guns of the monitor had CIE u'v' coordinates of 0.413 and 0.524 for red, 0.124 and 0.556 for green, and 0.170 and 0.157 for blue. The white of the monitor was a standard D-65. The spectral energy functions of the individual guns and the white of our monitor are described in Faubert (1994, 1995). Maximally modulating our red and green guns produced, respectively, approx. 15 and 35% modulation of the Lsensitive and M-sensitive cone fundamentals proposed by Smith & Pokorny (1975). The two stimuli used were circular targets with diameters of 8 and 16 cm, viewed at a distance of 57 cm and subtending visual angles of 8 and 16 deg. The mean luminance of the testing screen was equal to the luminance of the stimuli, which was 19 cd/ m^2 . Random black and white dots served as the background of the monitor to minimize luminance edge



FIGURE 1. (a) A red/dark red sine wave grating drifting in a given direction is superimposed on a (b) green/dark green sine wave grating drifting in the opposite direction. The amount of red contrast necessary to produce a counterphase flicker is the isoluminant ratio for a given condition (c).

artifacts. Dot size was 4 pixels (1 pixel = 8 min of arc). The stimuli were circular targets consisting of red–green (R/G) sine wave vertical gratings. The spatial frequency of the stimuli was 0.5 cycles per degree (cpd). The stimuli were composed of two sine wave gratings, a red/dark red and a green/dark green grating superimposed and drifting in opposite directions (Fig. 1). The contrast of the gratings was preset at 60% of the maximum possible (100%) for each gun. Before every trial a differential of 10% contrast between the two gun outputs was generated so that the guns were not close to isoluminance.

Procedure. All testing was done monocularly. Eccentricity was varied by having subjects fixate at different locations on four axes around the sine wave grating. Observers had to place their head on a chin-rest to help maintain fixation. The task was to adjust the luminance contrast of the red grating (the luminance contrast of the red grating (the luminance contrast of the green grating was fixed) until the observer could no longer identify a clear motion direction. When the observer perceived the bars as counterphase flickering he/she had established the R/G isoluminance for that specific stimulus combination (Anstis & Cavanagh, 1983).

For any given eccentricity (0, 5, 10, 20, and 40 deg) two stimuli sizes, 8 and 16 deg, and three drift rates (2, 4, and 8 Hz) were assessed. For each of the 120 conditions, the observers established their isoluminance equilibrium on the basis of five trials. The isoluminance equilibrium refers to the mean of these five trials for each location and stimulus combination in the visual field.

Results and discussion

Isoluminance values (representing a difference of luminance between the red and the green components) are plotted as a function of eccentricity in Fig. 2. A negative value illustrates a lower red contrast to match the green contrast, whereas a positive value indicates a higher red contrast to match the green contrast, and a zero value (0) indicates that the red and the green component luminance are physically equal (equal contrast). Two ANOVAs with repeated measures were performed (one for each subject who completed all the conditions) and the results reveal a significant four-way interaction of field, eccentricity, size, and temporal frequency (subject F(24,96) = 6.138,P < 0.001;subject LB: JF: F(24,96) = 3.836, P < 0.001). In general, the R/G luminance balance increased with increasing eccentricity. The R/G physically equal contrast (i.e., values approach 0) was generally achieved at 20 deg of eccentricity for the superior visual fields. However, this physical equality between red and green contrast was not achieved before the 40 deg positions for the temporal and nasal visual fields.

Both the 8 and 16 deg stimuli lead to similar results [see Fig. 3(a)]. We have collapsed the data across stimulus size, and have observed that the isoluminance ratios of the 16 deg stimulus tended to be higher than those of 8 deg. This effect is relatively small and probably significant because of the very small variance



FIGURE 2. Isoluminance values for each observer as a function of eccentricity, visual field meridian, stimulus size and temporal frequency. (a) and (b) represent the red–green luminance contrast balance for the nasal meridian; (c) and (d) represent the values for the superior meridian; (e) and (f) represent the values for the temporal meridian; and (g) and (h) represent the values for the inferior meridian. Error bars represent the SEM.

in the data. Only the collapsed curves for the size effect are shown because they represent well the trend observed in each field. The temporal component of the stimuli used in this experiment influenced the isoluminance equilibrium, as illustrated by the collapsed data (across visual field and stimulus size) in Fig. 3(b). In general, the higher the temporal frequency the higher the isoluminance ratios as a function of eccentricity.

Further observations of the data show some common findings between individuals. For instance, the superior and inferior meridian tend to show more dramatic changes as a function of eccentricity. This is particularly



FIGURE 3. Average isoluminance values as a function of eccentricity. Collapsed data across (a) temporal frequency and visual field as a function of eccentricity and stimulus size, (b) stimulus size and visual field as a function of eccentricity and temporal frequency. Error bars represent the SEM.

true for observer JF. To illustrate this point we collapsed the data across stimulus size and temporal frequency and tested a third observer (AB) with one stimulus size (16 dva) and a single temporal frequency (see Fig. 4). Figure 4 demonstrates that for the three subjects there is a relatively greater change in R/G luminance balance values for the superior field than all other fields. These



FIGURE 4. Average isoluminance values as a function of eccentricity for each observer. The values are grouped for each visual field meridian.

data demonstrate that in comparison with the whole visual field, the superior visual field requires an even greater proportion of red relative to green. This may represent one of two things, either there is a greater decrease of L-type receptors in the superior field relative to other areas, or there is a relative increase of M-type receptors in that portion of the visual field. Another possibility could be a weighting of post-receptoral mechanism change with eccentricity.

We can conclude that our results on the nasal-temporal data are similar in nature to Abramov *et al.* (1991), Ferree & Rand (1919), and Stabell & Stabell (1981), as represented by the very minor change in R/G ratio with eccentricity on that particular meridian. However, our results for the superior field show a dramatic change in R/G ratio with eccentricity, which is a novel finding.

EXPERIMENT 2

The purpose of this experiment was to assess the contribution of the chromatic system to motion perception throughout the visual field. We know that the cone distribution decreases with increasing eccentricity (Curcio *et al.*, 1987; Osterberg, 1935), and that colour perception changes with eccentricity, at least along the horizontal meridian (Abramov *et al.*, 1991; Stabell & Stabell, 1981). We also know that the sensitivity to chromatic stimuli in the inferior visual field declines with eccentricity if we do not change the stimulus parameters (Metha *et al.*, 1994). However, we do not know whether it is possible to perceive chromatic motion throughout the visual field, and if so, which areas of the visual field are the most sensitive.

Given that the sensitivity of the chromatic system is low-pass and decreases as we increase the spatial and temporal frequencies (Kelly, 1983; Mullen, 1985) and that chromatic aberration can produce luminance artifacts for spatial frequencies above 0.5 cpd (Faubert et al., 1994) we used spatial frequencies of 0.5 cpd and lower, and a fixed temporal frequency of 4 Hz in order to optimize the input from the chromatic system. If we increase the stimuli sizes and decrease the spatial frequency as we test further in the peripheral visual field (up to 40 deg of eccentricity), we should stimulate more chromatic cells and obtain a better response to colour (Noorlander et al., 1983). Choosing a scaling factor is rather difficult, since many different scaling factors have been proposed thus far and for a given eccentricity the resulting target sizes vary tremendously between models. For instance, Drasdo (1989) proposed a scaling factor which compares the size of the target presented at the fovea to the size which should include the same amount of cells in the periphery. If we were to use this scaling factor, we would have to present a target of 197 deg at a 40 deg eccentricity, as compared with 8 deg in the fovea. Another scaling factor which takes into account the cortical magnification factor is that of Wilson et al. (1990). With this scaling factor, a foveal target of 8 deg would have to be enlarged to 88 deg for an eccentricity of 40 deg. Abramov et al. (1991) have proposed a functional

summation area for colour sensitivity. Their findings indicate that a critical size of 6 deg is necessary at 40 deg eccentricity: further enlarging the target size did not enhance the perception of colour. Our aim was to enlarge the stimuli to enhance the peripheral sensation. Because of the discrepancies between models we arbitrarily decided to use the cone density function as a basis for scaling at the receptor level (Curcio *et al.*, 1987).

Methods

Subjects. The same observers as in Experiment I were tested in the present experiment.

Stimuli. The calibrations were identical to those of Experiment 1. The yellow of the monochromatic grating was a mixture of the equiluminous red and green. All stimuli were circular targets consisting of R/G sine wave gratings. In the two parts of this study (isoluminance and chromatic motion) the stimuli shared the same attributes. The following eight meridians were tested [temporal (0 deg), superior-temporal (45 deg), superior (90 deg), superior-nasal (135 deg), nasal (180 deg), inferior-nasal (225 deg), inferior (270 deg), inferior-temporal (315 deg)]. The eccentricities were created by having the observers fixate at different locations around the sine wave grating, while the stimulus remained exactly in front of the subject. On each meridian, five eccentricities were assessed: 0, 5, 10, 20 and 40 deg. At each point the stimuli were presented perpendicular to the axis (see Fig. 5). We presented the stimuli orthogonal to each axes because there is evidence that humans are more sensitive to motion directed towards them (Raymond, 1994). Presentation of the different stimulus orientations was achieved by inserting the computor monitor in a rotating box, which permitted rotation of the monitor in four orientations. Thus, the stimuli presented on the horizontal meridian were vertical sine wave gratings, those presented on the vertical meridian were horizontal sine wave gratings, those presented on the superior-temporal and inferior-nasal were 45 deg counter-clockwise sine wave gratings, and finally, those presented along the superior-nasal and inferior-temporal meridian were 45 deg clockwise sine wave gratings. Rotating the screen did not affect the screen calibration. The stimuli were



FIGURE 5. Representation of the stimulus positions on the eight meridia of the 80 deg visual field.

respectively 8, 10, 12.5, 16 and 20 deg (viewed at a distance of 57 cm) to compensate approximately for the cone density function changes with eccentricity. All stimuli contained four cycles of red-green bars. Therefore, the spatial frequencies used were 0.5, 0.40, 0.32, 0.25 and 0.20 cpd, respectively. These spatial frequencies were also chosen to minimize the effect of transverse chromatic aberration (TCA). The influence of luminance artifacts is minimized if a spatial frequency of 0.5 cpd or lower is used (Faubert et al., 1994). In a previous study (Faubert et al., 1994) we induced transverse chromatic aberrations with prisms up to the order of 0.40Δ , which is equivalent to natural TCA out to 40 deg eccentricity (Ogboso & Bedell, 1987). We found that the chromatic motion for gratings with spatial frequencies of 0.5 and lower was not affected by the large amount of TCA. In the experiment presented we started with gratings of 0.5 cpd at the fovea and reduced spatial frequency with increasing eccentricity. Therefore, we considerably reduced any possible contamination due to chromatic aberrations.

The subjects had to perform two tasks: an isoluminance and a chromatic motion task. These two procedures followed the motion nulling paradigm as used by Cavanagh & Anstis (1991).

In the chromatic motion perception paradigm, two sine wave gratings each containing opposite motion were generated. An isoluminant grating with a chromatic contrast of 60% (that is 60% of the phosphors' maximum modulation) established from the isoluminance task (see method in Experiment 1) and an achromatic grating (yellow-black) of the same size were drifting in opposite directions. The isoluminant grating was, in fact, composed of the same red/dark red and green/dark green gratings used in Experiment 1 except in this case they were drifting in the same direction superimposed 180 deg out of phase (Fig. 6). The achromatic grating was produced by superimposing inputs from the red and green guns in phase (yellow grating). The achromatic contrast necessary to null the motion (by the method of adjustment) was considered the relative strength of the contribution from the chromatic system. The larger the contrast, the larger was the corresponding contribution of the chromatic system.

Procedure

For each condition, five trials were performed to establish the subject's isoluminance equilibrium. The



FIGURE 6. The chromatic isoluminant grating (see Experiment 1) is superimposed on an achromatic drifting grating. The contrast of isoluminant grating is fixed. The achromatic contrast necessary to produce a counterphase flicker (motion nulling) is the relative contribution from the chromatic system to the perception of motion.



FIGURE 7. Average isoluminance values grouped per subject as a function of retinal eccentricity.

average of these trials was taken as the R/G isoluminance level for a given visual field location. Following this, five trials of the motion nulling task were performed at the same visual field location. Again, the average of these trials was taken as the relative contribution of colour to motion for that specific field location. The observer completed 10 trials (five isoluminance adjustments and five chromatic motion adjustments) for each of the combinations of eight meridians and five eccentricities, for a total of 400 trials.

Results and discussion

Isoluminance. Average isoluminance values for each observer are plotted as a function of eccentricity in Fig. 7.



FIGURE 8. Average isoluminance values as a function of retinal eccentricity for each observer. Thick lines represent the isoluminance values obtained in Experiment 1; dotted lines represent the isoluminance values obtained in Experiment 2 where the stimuli sizes increased with increasing eccentricity.



ISOLUMINANCE AND CHROMATIC MOTION



FIGURE 9. Chromatic motion sensitivity as a function of visual field meridian and eccentricity. The centre represents the fovea, the edge of the map represents 40 deg of eccentricity. The temporal meridian (0 deg) is on the right side, the superior meridian is shown above the map. Sensitivity to chromatic motion is represented by Z-scores. The lighter the area, the more sensitive are the subjects to chromatic motion. Chromatic motion sensitivity measures for (a) subject AB; (b) subject JF; (c) subject LB.

We can see, as in Experiment 1, that there are small differences in the subjects' colour perception baseline. Generally, isoluminance equilibrium changes as we present the stimulus further away from the fovea, however, the change is not as dramatic as found in the first experiment. Only the collapsed data (for visual field) are shown because the trends were the same as in the first experiment. It seems that increasing the stimulus size and decreasing its spatial components have partly compensated for eccentricity (see Fig. 8). The fact that we failed to completely compensate for eccentricity implies that post-receptoral scaling factors might be involved. Still, as compared with the centre of the visual field, the peripheral portion needs, in general, more red relative to green contrast to obtain isoluminance.

Motion. A 5×8 ANOVA (eccentricity and visual field meridian) with repeated measures was performed on the chromatic motion sensitivity measures for each subject (subject AB: F(28,112) = 14.862, P < 0.001; subject JF: F(28,112) = 9.904, P < 0.001; and subject LB: F(28,112) = 27.009, P < 0.001). In all cases, the results indicate a significant interaction of eccentricity and visual field meridian.

The measures in relative sensitivity to motion show that the chromatic system responded to motion throughout the visual field. As we tested further in the periphery, motion sensitivity decreased. We can examine the results in more detail by mapping each observer's motion sensitivity across the visual field on a grayscale. Figure 9 illustrates the normalized scores (Z-scores) of each observer's motion sensitivity as a function of eccentricity and visual field meridian. Since the relative sensitivity baseline to chromatic motion differs between the three subjects (as observed at the fovea), and since we used a finite number of gray levels, we chose to use Z-scores to emphasize the relative changes of motion sensitivity for each observer. The Z-scores were calculated from the average obtained for 200 trials. The 40 Z-scores of subject AB were calculated from the mean of all AB's motion values (6.278 and a SD of 1.753), and so on for the two remaining subjects. Subject JF's Z-scores were based on a mean of 6.131 and a SD of 2.250, whereas subject LB's Z-scores were based on a mean of 4.330 and a SD of 1.323.

The data of subject AB show a decrease in motion sensitivity for the superior and temporal axes and also on

the inferior-nasal axis starting at 20 deg of eccentricity. Subject JF obtained a smooth decrease of sensitivity across the visual field, with a steeper slope for the superior and temporal portions of the visual field. At 20 deg of eccentricity and beyond, subject LB showed a steeper function decrease of chromatic motion sensitivity for the superior and temporal parts of the visual field. At 10 deg of eccentricity, two of the three observers (AB and LB) also showed diminished chromatic motion sensitivity on the oblique axes (superior-temporal and inferiornasal).

CONCLUSION

Isoluminance

The results of Experiment 1 indicate that, without changing the target size, the R/G isoluminance equilibrium was relatively constant for the nasal, temporal, and inferior meridians, except for 40 deg of eccentricity where the subjects significantly increased the red luminance contrast relative to the green luminance contrast to obtain a perception of isoluminance. For the superior meridian, a marked change in R/G isoluminance equilibrium was present at 20 and 40 deg of eccentricity. One implication could be that the superior meridian contains relatively less L-type vs M-type receptors than other visual areas. Another possible explanation is that the post-receptoral weighting of the two colours involved in our study changes with increasing eccentricity and/or between visual field areas.

The findings of Abramov et al. (1991) and Weitzman & Kinney (1969) state that if we sufficiently increase the stimuli size, it is possible to obtain similar identification thresholds from the fovea to 20 deg of eccentricity. At further eccentricities, thresholds for colours could not be obtained even with an increased stimulus size. However, our findings indicate that when we scaled the target according to the cone density function (Curcio et al., 1987) in Experiment 2, the R/G isoluminance equilibrium was similar to Experiment 1 in the central visual field and up to 10 deg of eccentricity. A slight difference in R/G ratio was observed at 20 deg and beyond. The isoluminance ratios decreased in the peripheral visual field, thus suggesting that we had only partially compensated for the lower cone density in the periphery, implying the need for a post-receptoral scaling function for red-green isoluminance ratios.

Studies have reported that it is possible to perceive colours beyond 40 deg of eccentricity (Abramov *et al.*, 1991; Ferree & Rand, 1919; Stabell & Stabell, 1981). Therefore, we still need to know how the peripheral cells code chromatic information (qualitative), and we also need to establish an appropriate scaling factor (quantitative). It was reported that thresholds for green and yellow are greatly reduced in peripheral locations (Abramov *et al.*, 1991; Weitzman & Kinney, 1969), making the peripheral retina more sensitive to short wavelengths (blue) and to long wavelengths (red). Our results clearly show that more red contrast was required to set

isoluminance for drifting sinusoidal gratings. This gives us a reason to believe that there must be a post-receptoral mechanism involved in setting isoluminant conditions.

Chromatic motion

First and foremost, we have demonstrated that it is possible to perceive chromatic motion across an 80 deg visual field at each position tested. Even though each observer established his/her isoluminance equilibrium prior to performing the motion nulling task, we obtained relative chromatic motion measures indicating interindividual differences in the motion sensitivity baseline (as obtained in the fovea). Some observers were more sensitive than others, but they all were able to perceive chromatic motion across the 80 deg visual field.

Secondly, the perception of R/G chromatic motion in the periphery was weaker than that observed in the central visual field, as we expected. For further eccentricities (i.e., 20 and 40 deg), a motion sensitivity asymmetry becomes more apparent. The superior visual field seems to be the least sensitive to colour motion, whereas the inferior field appears to be the most sensitive. Previous findings (on cell distribution) suggested that the inferior visual field was specialized for motion, and that the superior field was more specialized for colours (Previc, 1990). The results obtained in this study clearly indicate that the inferior field is better than the superior field for processing chromatic motion information under isoluminant conditions.

Do the chromatic and achromatic systems stimulate the same motion mechanisms?

We know that the middle temporal (MT) cortical area is the center responsible for motion processing (Maunsell & Van Essen, 1983). Much of the information feeding this area are luminance signals, whereas chromatic information feeds area V4 (Lueck et al., 1989). There is also evidence that MT receives input from the chromatic system (Ferrera et al., 1994). A recent psychophysical study has demonstrated that there are two independent entries in the motion centre, one for colour and another for luminance signals (Cropper & Derrington, 1996). Other researchers have proposed that V4 must be linked to MT for higher chromatic motion processing (Cavanagh et al., 1984, 1985). Because we obtain better chromatic motion sensitivity in the inferior visual field it follows that the chromatic motion mechanisms show the topographical specialization pattern for motion (inferior visual field) as opposed to colour (superior field) as proposed by Previc. Therefore, another possibility is that the chromatic motion perception we obtain may be via a portion of the chromatic system which goes directly to MT. It may also imply that the chromatic system for motion stimuli may be primarily localized in the lower visual field, which contrasts Previc's assumptions about P and M visual field distribution.

Finally, we observed that the peripheral mechanisms do not seem to respond as strongly to chromatic motion

as the foveal mechanisms. Perhaps the respective mechanisms operate on different motion cues. Further research will explore the difference between foveal and peripheral chromatic mechanisms for the perception of local vs global features of motion.

REFERENCES

- Abramov, I., Gordon, J. & Chan, H. (1991). Color appearance in the peripheral retina: effects of stimulus size. *Journal & the Optical Society & America A*, 8, 404–414.
- Anstis, S. M. & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In Mollon, J. D. & Sharpe, L. T. (Eds), *Colour vision: physiology and psychophysics* (pp. 155–166). London: Academic Press.
- Cavanagh, P. (1991). Contribution of colour to motion. In Valberg, A. & Lee, B. B. (Eds), From pigments to perception: advances in understanding visual processes (pp. 151–164). New York: Plenum Press.
- Cavanagh, P. & Anstis, S. M. (1991). The contribution of color to motion in normals and color-deficient observers. *Vision Research*, 32, 2109–2148.
- Cavanagh, P., Boeglin, J. & Favreau, O. E. (1985). Perception of motion in equiluminous kinematograms. *Perception*, 14, 151–162.
- Cavanagh, P. & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research*, 25, 1595–1601.
- Cavanagh, P., MacLeod, D. I. A. & Anstis, S. M. (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., Saida, S. & Rivest, J. (1995). The contribution of color to depth perceived from motion parallax. *Vision Research*, 35, 1871–1878.
- 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.
- Cropper, S. J. & Derrington, A. M. (1996). Rapid colour-specific detection of motion in human vision. *Nature*, 379, 72–74.
- Curcio, C. A., Sloan, K. R. Jr., Packer, O., Hendrickson, A. E. & Kalina, R. E. (1987). Distribution of cones in human and monkey retina: individual variability and radial asymmetry. *Science*, 236, 579–582.
- Drasdo, N. (1989). Receptive field densities of the ganglion cells of the human retina. *Vision Research*, 29, 985–988.
- Faubert, J. (1994). Seeing depth in colour: more than just what meets the eyes. *Vision Research*, *34*, 1165–1186.
- Faubert, J. (1995). Colour induced stereopsis in images with achromatic information and only one other colour. *Vision Research*, 35, 3161–3167.
- Faubert, J., Bilodeau, L. & Simonet, P. (1994). Colour motion sensitivity and transverse chromatic aberration. In *Ophthalmic and Visual Optics/Noninvasive Assessment of the Visual System Technical Digest*. Optical Society of America, Washington, D.C., s2, 102–105.
- Ferree, C. E. & Rand, G. (1919). Chromatic thresholds of sensation from center to periphery of the retina and their bearing on color theory. *Psychology Reviews*, 26, 16–41.
- Ferrera, V. P., Rudolph, K. K. & Maunsell, J. H. (1994). Responses of neurons in the parietal and temporal visual pathways during a motion task. *Journal of Neuroscience*, 14, 6171-6186.
- Gorea, A. & Papathomas, T. V. (1989). Motion processing by chromatic and achromatic visual pathways. *Journal of the Optical Society of America A*, *6*, 590–602.
- Kelly, D. H. (1983). Spatiotemporal variation of chromatic and achromatic contrast thresholds. *Journal* of the Optical Society of America, 73, 742–750.

- Livingstone, M. S. & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and stereopsis. *The Journal of Neuroscience*, 7,3416–3468.
- Livingstone, M. S. & Hubel, D. H. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, 240, 740–749.
- Lueck, C. J., Zeki, S. M., Friston, K. J., Deiber, M. P., Cope, P., Cunningham, V. J., Lammertsma, A. A., Kennard, C., Frackowiak, R. S. *The colour center in the cerebral cortex of man. Nature*, 340, 386–389.
- Maunsell, J. H. R. & Van Essen, D. C. (1983). Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey: I. Selectivity for stimulus direction, speed and orientation. *Journal of Neurophysiology*, 49, 1127–1147.
- Metha, A. B., Vingrys, A. J. & Badcock, D. R. (1994). Detection and discrimination of moving stimuli: the effects of color, luminance, and eccentricity. *Journal of the Optical Society of America A*, 11, 1697–1709.
- Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings. *Journal of Physiology*, 359, 381-400.
- Mullen, K. T. (1991). Color vision as a post receptoral specialization of the central visual field. *Vision Research*, 31, 119–130.
- Noorlander, C., Koenderink, J. J., den Ouden, R. J. & Edens, B. W. (1983). Sensitivity to spatiotemporal color contrast in the peripheral visual field. *Vision Research*, 23, 1–11.
- Ogboso, Y. U. & Bedell, H. E. (1987). Magnitude of lateral chromatic aberration across the retina of the human eye. *Journal of the Optical Society of America A*, *4*, 1666–1672.
- Osterberg, G. (1935). Topography of the layer of rods and cones in the human retina. Acta Ophthalmologica (Suppl.), 6, 11–102.
- Papathomas, T. V., Gorea, A. & Julesz, B. (1991). Two carriers for motion perception: color and luminance. *Vision Research*, 31, 1883– 1891.
- Previc, F. H. (1990). Functional specialization in the lower and upper visual fields in humans: its ecological origins and neurophysiological implications. *Behavioral and Brain Sciences*, 13, 519–565.
- Ramachandran, V. S. & Gregory, R. L. (1978). Does colour provide an input to human motion perception? *Nature*, 275, 55–56.
- Raymond, J. E. (1994). Directional anisotropy of motion sensitivity across the visual field. *Vision Research*, 34, 1029–1037.
- Smith, V. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research*, 15, 161– 171.
- Stabell, B. & Stabell, U. (1981). Absolute spectral sensitivity at different eccentricities. Journal of the Optical Society of America, 71, 836–840.
- Weitzman, D. O. & Kinney, J. A. S. (1969). Effect of stimulus size, duration, and retinal location upon the appearance of color. *Journal* of the Optical Society of America, 59, 640–643.
- Wilson, H. R., Levi, D., Maffei, L., Rovamo, J. & Devalois, R. (1990). The perception of form: retina to striate cortex. In Spillman, L. & Werner, J. S. (Eds), *Visual perception: the neurophysiological foundations* (pp. 231–272). San Diego: Academic Press.

Acknowledgements — This research was supported by grants NSERC OGP0121333 and FCAR 93NC0903 to JF. LB was supported by an FCAR pre-doctoral fellowship. A partial report was presented at the ARVO annual meeting, 1993 (IOVS, 34, 1032). We wish to thank Patrick Cavanagh for providing an earlier version of the software, Anne Bellefeuille for participating in the experiment, François Bellavance for the help provided on the statistical analyses and Andrew Metha and an anonymous reviewer for constructive comments on the earlier draft.