

THE CONTRIBUTION OF COLOUR TO MOTION

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INTRODUCTION

Anstis (1970) and Ramachandran and Gregory (1978) showed that the motion normally visible in random dot kinematograms could not be seen when the dots were presented in equiluminous colours. Based on this evidence, Ramachandran and Gregory suggested that colour and motion analyses were functionally independent and that the motion pathway responded only to luminance information. However, more recent studies (Cavanagh, Tyler & Favreau, 1984; Cavanagh, Boeglin & Favreau, 1985; Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Gorea & Pappathomas, 1989; Mullen & Baker, 1985) have shown that this may not be the case. There is a motion response, although somewhat degraded, to equiluminous coloured stimuli. In this chapter, I shall review several experiments that have examined the contribution of colour to motion in an attempt to identify whether the contribution is mediated through the magnocellular (M) or parvocellular (P) stream.

First, despite the dramatic examples of loss in motion perception at equiluminance (Moreland, 1982; Cavanagh, Tyler & Favreau, 1984), the visual system actually shows a high degree of sensitivity to the motion of chromatic stimuli when the stimulus strength is expressed in terms of cone contrast (Stromeyer, Eskew, & Kronhauer, 1990). A major factor in the losses at equiluminance may be due to the restricted contrast range available for chromatic stimuli.

Second, in collaboration with Stuart Anstis, I have measured the relative contributions of colour and luminance to motion (Cavanagh & Anstis, 1990). These results demonstrate that the contribution is based on opponent-colour mechanisms.

Third, we also tested the phase lag in the relative contributions of red and green to motion at equiluminance (Cavanagh & Anstis, 1990). These phase lags were similar to those for P units in the retinal ganglia and very different from those for M units.

Finally, motion can be seen for drifting patterns defined by attributes other than colour which do not stimulate luminance-based motion detectors (Cavanagh & Mather, 1989). In particular, stereo-defined (random dot stereograms) and texture-defined stimuli are detected only by the parvocellular stream (Schiller, Logothetis, & Charles, 1990), so

that the perception of the motion for these stimuli must rely on signals carried by the parvocellular stream. Since the parvocellular stream can contribute to the perception of motion for these stimuli, it would be reasonable to assume that it also contributes to motion in the case of colour stimuli. In fact, it would be unreasonable to assume the opposite.

PATHWAYS

The luminance pathway takes its input from the sum of the long- and medium-wavelength sensitive cones (R- and G-cones, respectively) although some psychophysical studies indicate that the short-wavelength sensitive cones (B-cones) may also contribute to some extent (Drum, 1983; Lee & Stromeyer, 1989; Stockman, MacLeod, & DePriest, 1987). The chromatic signals arise from the differences between cone signals: R-G and B-(R+G) for the red/green and blue/yellow opponent-colour pathways, respectively. An equiluminant stimulus is one that varies in colour but not in luminance. The purpose of such a stimulus is to provide information to the chromatic pathway but not the luminance pathway in order to test the capacities of the chromatic pathways in isolation.

The notion of equiluminance presumes one luminance pathway that has a single null, that is, one relative luminance between any two colours for which there is no response of the luminance pathway. In truth, however, there may be many luminance pathways. Image information from separate spatial frequency bands pass through separate units in the visual system — each of these could be considered a separate luminance pathway (low-pass, high-pass, etc.) with potentially a different equiluminance point. Many physiological studies have revealed a variation in the equiluminance points of M units that project to the directionally selective cells in the cortex. In particular, Shapley and Kaplan (1989) and Lee, Martin, and Valberg (1988) have shown that individual M units do show a null activity point at a particular luminance ratio between the two colours of the stimulus and that this null ratio varies somewhat from unit to unit. Given that many pathways may be contributing to a final luminance stream, it is remarkable that there is a fairly well defined equiluminance point around which performance is degraded.

There have been many attempts to link the luminance and chromatic pathways identified psychophysically to the magnocellular and parvocellular streams (DeYoe & van Essen, 1988; Livingstone & Hubel, 1987; Maunsell & Newsome, 1987) of the primate visual system. The units in the magnocellular stream have little colour sensitivity and respond best to low spatial and high temporal frequencies whereas those in the parvocellular stream generally have colour-opponent responses and prefer high spatial and low temporal frequencies (see Schiller, Logothetis, & Charles, 1990; and Shapley, 1990, for reviews). However, there is no simple relationship between these properties and those of the luminance and chromatic pathways. For example, it has been argued (De Valois & De Valois, 1975; Ingling, & Martinez-Urigas, 1985; Schiller et al, 1990) that both magnocellular and parvocellular streams are involved in carrying luminance information: The magnocellular stream is principally non-opponent but the parvocellular stream, although carrying colour-opponent information for low spatial and low temporal frequencies, also carries non-opponent (luminance) information at high spatial and temporal frequencies. Moreover, units in the magnocellular stream exhibit colour-opponency for large stimuli (Type IV units, Wiesel & Hubel, 1966). Several studies have revealed residual, opponent-colour responses in the magnocellular stream both in the retina (Gouras & Eggers, 1982) and in the magnocellular layers of the LGN (Krueger, 1979; Schiller & Colby, 1983; Derrington, Krauskopf & Lennie, 1984). No physiologically distinct structures have yet been identified whose properties correspond in a straightforward way to those of the luminance and chromatic pathways (see for example, Lennie, Krauskopf, & Sclar, 1990).

Schiller et al (1990) have directly tested the role of the magnocellular and parvocellular streams of macaque monkeys in various visual tasks. They made small lesions in the lateral geniculate in the magnocellular and parvocellular layers destroying cells that responded to different spatial areas in the two systems. They then presented tests to areas subserved by both magnocellular and parvocellular units, by only magnocellular or by only parvocellular. Two of their findings are of particular interest for this review. First, within areas subserved only by parvocellular units, motion detection was very poor if the temporal frequency was greater than 6 Hz but was little affected at lower rates. This indicates that the parvocellular stream can mediate motion responses although only for lower temporal frequencies. Second, areas subserved only by magnocellular units were unable to support the perception of either texture or random-dot stereograms. This will be important when we consider the substrate responsible for the perception of motion of stimuli defined by texture and by stereo.

CONTRAST THRESHOLD FOR MOTION

In collaboration with Stuart Anstis (Cavanagh & Anstis, 1990) I measured thresholds for one normal observer (colour-deficient observers were also tested but their results are not discussed here) on two threshold tasks. We collected the contrast thresholds for detection and for direction discrimination with chromatic stimuli (red/green), and luminance stimuli (yellow/black).

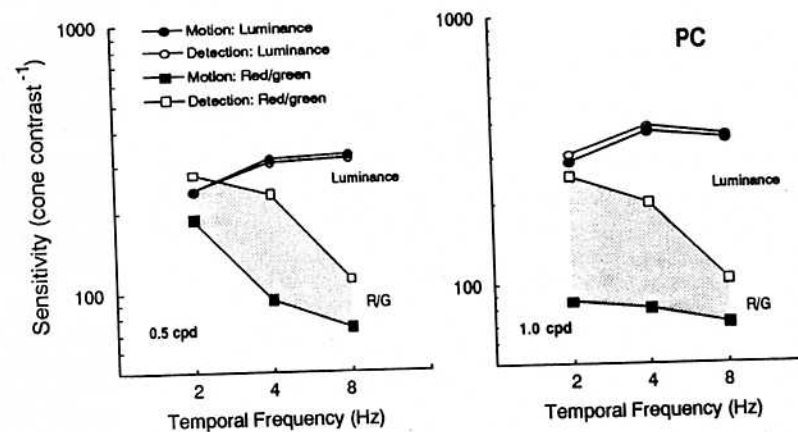


FIG. 1. Sensitivity (reciprocal of threshold cone contrast) for detection and direction discrimination as a function of spatial and temporal frequency. (Adapted from Cavanagh & Anstis, 1990.)

As has been reported previously for comparable stimuli, there is no difference between detection and motion thresholds for the achromatic stimuli and sensitivity increases with temporal frequency between 2.0 and 8.0 Hz (Kelly, 1979). The red/green detection sensitivity drops with increasing temporal frequency, as expected (Kelly, 1983), and the motion sensitivity drops with temporal frequency as well suggesting that the motion threshold is based on chromatic mechanisms. The sensitivity for direction discrimination is lower than that for detection and between these two thresholds, in the shaded area on the graphs, the colour bars could be seen but did not appear to move.

When expressed in terms of cone contrasts, the sensitivity to chromatic stimuli is quite high, comparable to that for luminance stimuli at the lowest spatial and temporal frequencies. Stromeyer et al (1990) measured even higher sensitivity to chromatic stimuli (as much as four times higher than to luminance stimuli) in a direction discrimination experiment. The difference between their results and those of our one observer may simply be that our observer (myself) falls on the low end of normal colour vision. Among the four normal observers in the next experiment to be described, my results were next to lowest in strength of contribution of colour to motion (Cavanagh & Anstis, 1990).

How can we reconcile this high sensitivity to chromatic stimuli with the many reports of degraded motion response at equiluminance? The explanation lies in the contrast available in chromatic and luminance stimuli. Luminance stimuli can modulate each cone class by as much as 100%, whereas the maximum differential modulation of the R- and G-cone classes attainable on a colour monitor is between 15 and 25%. In other words, the biggest loss for chromatic stimuli may be a stimulus factor and not a processing factor: luminance modulation drives the cones more effectively than chromatic modulation.

Our data (Cavanagh & Anstis, 1990) and the data of Stromeyer et al (1990) demonstrate that the visual system is in fact quite sensitive to chromatic stimuli but these data do not identify definitively the pathway that mediates the response. In the next experiment that I shall describe, the characteristics of the response help to identify the source.

OPPOSING MOTION

The contrast of an unknown grating can be measured by varying the contrast of an otherwise identical grating moving in the opposite direction. The direction of perceived motion of the combined gratings is determined by the grating with the higher contrast. When the two gratings have equal contrast, a motion null—counterphase flicker—is obtained. This same technique can be used to compare the relative contributions of luminance and colour to motion.

To do so, a red/green grating drifting in one direction was superimposed on a light yellow/dark yellow grating drifting in the opposite direction (Cavanagh & Anstis, 1986). Four normal and nine colour-deficient observers were tested. Observers nulled the motion of a drifting luminance grating of fixed contrast by varying the luminance contrast of a colour grating (the contrast between the luminances of the red and green components of the colour grating) that drifted in the opposite direction. At motion null, the total effective contrast of the colour grating is equal to that of the luminance grating whose motion it has nulled. In Fig. 2, the total effective contrast of the colour grating is shown as a function of its luminance contrast. Results for two observers — a normal observer, SA, and a deutan observer, BA, — are given for tests at 0.5 cpd and 2 Hz. The V-shaped dotted lines of unit slope rising from the origin indicate the effective contrast that the colour grating would have if colour made no contribution to the perception of motion. In this case, the effective contrast of the colour grating would be equal to its luminance contrast. The lines plotted through the data points indicate the observed effective contrasts in these two examples. The shift of these lines from the dotted lines indicates an increase in the effective contrast and the amount of the shift, shown as a vertical arrow, is the contribution of the colour: We labeled this the equivalent luminance contrast of the colour in the colour grating. Note that the equivalent luminance contrast is substantial, more than 10%, for the normal observer (note also that there is only one data point per line in this example!), but very small, less than 1%, for the colour-deficient observer.

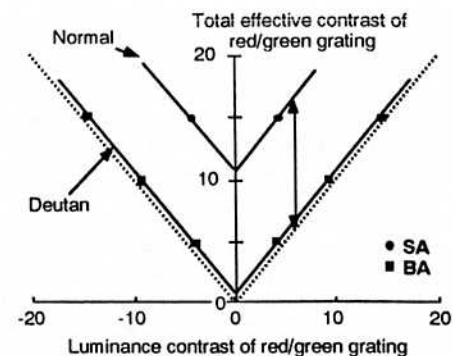


FIG. 2. Total effective contrast as a function of the luminance contrast between the red and green in the colour grating. Data from two observers, SA and BA, for 2 Hz, 0.5 cpd, red/green stimuli. The equivalent contrast of the colour in the grating is the difference (shown as a vertical arrow) between the luminance contrast of the colour grating (the dotted V rising from the origin) and the total effective contrast. (Adapted from Cavanagh & Anstis, 1990.)

What should we expect to see if the response to the colour grating is a residual response of a luminance pathway, due to the variation of equiluminance points among the units in the pathway? The left panel of Fig. 3 shows the response of a single unit in a luminance pathway to a drifting red/green grating as a function of its luminance contrast. The response function is given by the grating's absolute luminance contrast. At the centre of the horizontal scale, the red and green have equal luminance as measured by a photometer and the unit "sees" a uniform field with no contrast. At the right end of the horizontal scale, the grating is bright red and dark green while at the other end it is bright green and dark red. In both cases, however, the unit merely detects an identical light and dark grating.

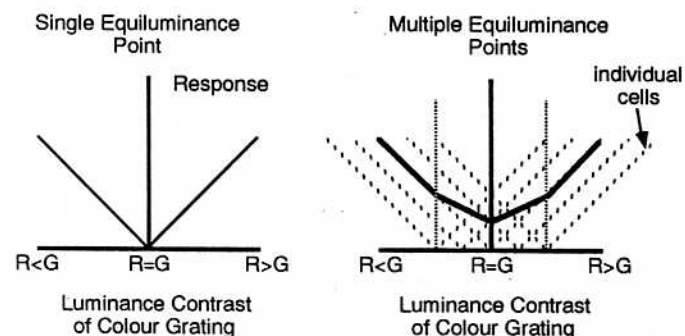


FIG. 3. The response of luminance-based units to a colour grating as a function of the luminance contrast between the two colours in the grating. On the left, the response for a single unit is shown and the response function follows the absolute value of the luminance contrast. On the right, different units have different equiluminance points. The total response is shown for graphical convenience as the average of the individual responses and indicated by the heavy curve. The curve has a minimum but the response is greater than zero at the minimum value.

We assumed that the contrasts sensed by individual units are summed to produce the net contrast. If all units had the same null point, there would be a single, true response null in the luminance pathway and the overall function would look like that of the single unit shown on the left in Fig. 3. On the other hand, in righthand panel of Fig. 3, we have the more likely situation of variable null points for individual units and overlapping functions. If we take the response to be the sum of the activity of the individual units (thick, curved line in right panel of Fig. 3 shows the average value for graphical convenience), we see that there is no longer a true null. The mean function dips to a minimum at photometric equiluminance but this minimum response is not zero. The shape of the actual function depends on the response characteristic of the individual units (shown as linear in Fig. 3) and the distribution of equiluminance points. We do not know either of these factors exactly, but we do know that M units have a moderate degree of scatter (probably not more than $\pm 10\%$ around the population average, Shapley & Kaplan, 1989; Lee et al, 1988). This allows us to predict that the V-shaped functions should be rounded off at the bottom within $\pm 10\%$ of equiluminance but should follow the V-shaped curve of the luminance contrast outside that range. That is, the net effectiveness of the colour grating in a *luminance pathway* only deviates from its luminance contrast within the range of scatter where the responses from some units are rising while others are falling.

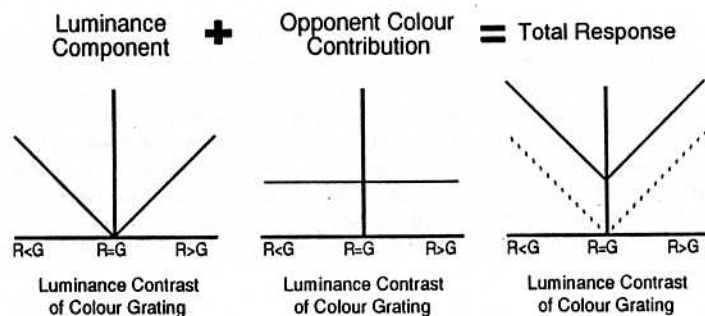


FIG. 4. The total response to a colour grating as the sum of luminance and opponent-colour contributions. Since the chromatic contrast and, therefore, the opponent-colour response, is fairly constant over the moderate range of luminance contrasts of the colour grating that were tested, the total effective contrast will be an elevated, V-shaped curve.

What would the total effective contrast look like if colour made a contribution to motion through an opponent-colour pathway and not through residual activation of a luminance pathway (i.e. if there were no interunit variation in equiluminance points)? We can assume that a contribution from an opponent-colour pathway would be a function of the chromatic contrast of the stimulus and this is fairly independent of its luminance contrast, at least over the range we looked at (maximum of $\pm 30\%$). Assuming a simple linear model in which the colour contribution sums with the luminance contrast to produce the total effective contrast, the function would just be a V-shaped curve that is raised everywhere by the same amount (Fig. 4).

The data of Figure 2 are sufficient to state that, as expected, the colour-deficient observer gets no contribution from colour so that the response is purely determined by a luminance pathway. However, there are insufficient data in Figure 2 to draw any conclusions about the normal observer. In order to see the pattern of response for a normal

observer across a wider range, we extended the luminance contrasts tested to $\pm 25\%$ and included a test at the equiluminance point. We used only one spatial and one temporal frequency (1 cpd and 8 Hz). Fig. 5 shows the total effective contrast of the red/green grating as a function of its luminance contrast. The data again appear to be V-shaped over this larger range.

There appears to be a fairly constant contribution of colour to motion at all the physical contrast values measured producing an elevated, V-shape curve that does not rejoin the dotted luminance contrast function. This behavior is more like that of a chromatic contribution than that of a luminance pathway with scattered equiluminance points.

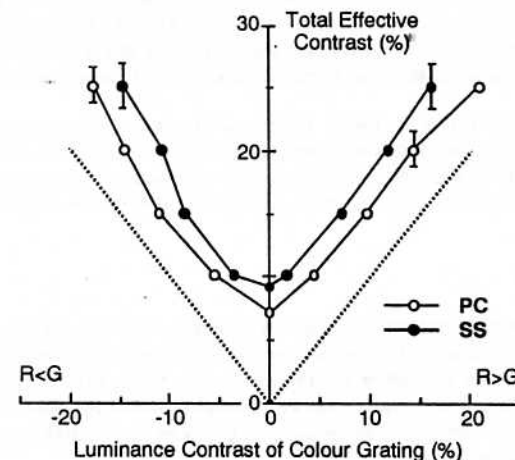


FIG. 5. Total effective contrast of a red/green grating at 1.0 cpd and 8 Hz as a function of the luminance contrast of the grating for two observers. The dotted lines show the total effective contrast the colour grating would have if its contribution to motion were determined solely by its luminance contrast. Vertical bars show standard errors (± 1 S. E.) where they are larger than the data symbols. (Adapted from Cavanagh & Anstis, 1990.)

Could the contribution have resulted from some luminance artifact due to display alignment or calibration or to the optics of the eye? Any luminance artifact in the colour stimulus will add directly to its effective contrast, increasing it uniformly within a fairly wide range of luminance contrasts around equiluminance — a pattern very similar to that which we had measured. However, the luminance artifact sets a lowest possible value for the contribution of colour that will be present in all the measurements and, for colour-deficient observers who have little or no colour-opponent response, it must be the main or only contributor to the measured equivalent contrast of the colour. Figure 6 shows the equivalent contrast of a red/green grating (the difference between its total effective contrast and its luminance contrast) for normal and colour-deficient observers as a function of spatial frequency (averaged over the two temporal frequencies tested, 0.5 and 1.0 Hz). Note that the colour-deficient observers had little or no equivalent contrast for the colour stimuli at 0.5 and 1.0 cpd. We can conclude that the stimuli at these low spatial frequencies produce luminance artifacts of less than 1% and that the readings for the normal viewers are true readings of the contribution of colour to motion.

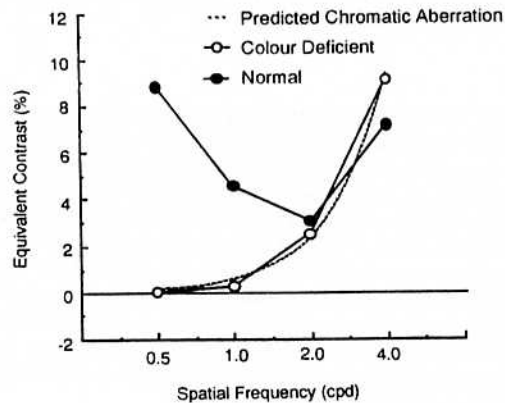


FIG. 6. Equivalent contrast of colour for red/green gratings as a function of spatial frequency for normal and colour-deficient observers. The curved line is the predicted luminance artifact produced by chromatic aberration.

The theoretical value of the luminance contrast generated by chromatic aberration increases with the square of the spatial frequency (Cavanagh & Anstis, 1990) and the data of colour-deficient observers for spatial frequencies covering the range of 0.5 to 4 cpd (averaged over the three temporal frequencies) showed this squared increase. The normal observers show a U-shaped curve resulting from two factors: 1) the colour contribution to motion that decreases with spatial frequency; and 2) the chromatic aberration artifact that increases with spatial frequency.

To summarize, the data showed a motion response to colour that did not arise from display or optical artifacts and was not due to interunit variability in equiluminance points in a luminance pathway. The evidence supported an opponent-colour source for the contribution of colour to motion.

PHASE LAG

Although the magnocellular pathway is characterized as broad-band or non-opponent (see Schiller et al, 1990), it is capable of colour-opponent responses. In particular, Type IV retinal ganglion cells (Wiesel & Hubel, 1966) show colour-opponency between centre and surround. Could this colour-opponency in the magnocellular stream account for the results described in previous sections? I shall use the phase characteristics of responses to chromatic stimuli to examine this point.

Cushman and Levinson (1983), deLange (1958), von Grünau (1977), Lindsey, Pokorny, and Smith (1986) and Swanson, Pokorny and Smith (1987) have reported that the relative phase between red and green producing minimum flicker sensitivity can deviate from the expected 180° by as much as 180° . We measured phase lags in the motion response using quadrature motion techniques (Cavanagh & Anstis, 1990; Cavanagh, Anstis & MacLeod, 1987; Shadlen & Carney, 1986) where a counterphasing luminance stimulus is positioned as a lure so that it will generate a moving stimulus when combined with the luminance artifact produced by the phase lag.

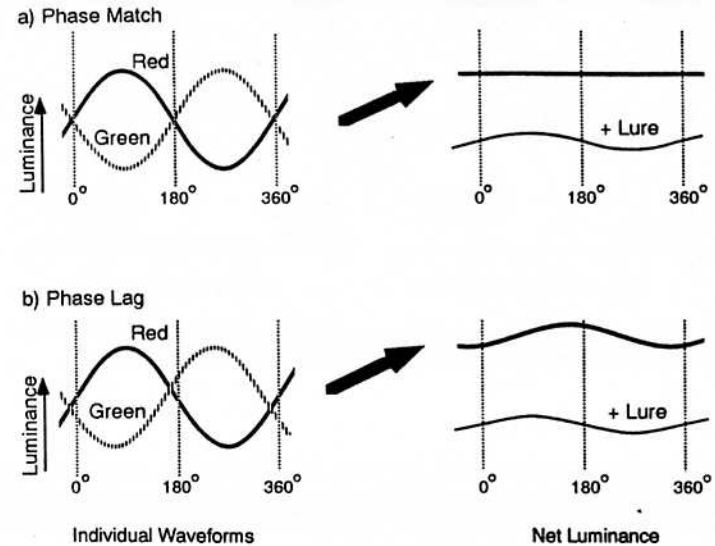


FIG. 7. a) The sum of red and green sine-waves, 180° out of phase, produces no net luminance modulation if the amplitudes of the two sine-waves are equal and the phase offset is exactly 180° . b) The sum of red and green sine-waves having the same amplitude produces a net luminance modulation if their phase difference is not exactly 180° . The luminance waveform is a sine-wave with the same frequency as the colour waveforms and its phase is the mean of the phases of the two colour waveforms, about 90° as shown here. A luminance lure combined in quadrature phase will produce motion only when the luminance artifact is present.

A stationary red/green stimulus is set in counterphase temporal modulation and a stationary luminance lure is introduced having the same spatial and temporal frequencies but 90° out of phase with the chromatic stimulus in space *only* (Fig. 7). Since it is not in quadrature phase with the red/green stimulus, it does not produce any motion. However, any phase lag between the red and green waveforms in the red/green stimulus will produce a luminance component at 90° from the peaks and troughs of the red and green waveforms (Fig. 7). This artifact will then be in quadrature phase with the luminance lure that we have introduced in the stimulus and the combination of the two will produce motion. If there is a phase lag between the two colours in the neural response at some point, it can be canceled by introducing the opposite phase lag in the stimulus. When it has been exactly canceled, no motion will be visible and when it has been overcompensated, the motion will reverse direction. The motion reversal point can therefore be used to accurately measure phase lag in the pathways responding to counterphasing gratings.

The measured phase lags (Fig. 8) were much smaller than those reported for minimum flicker settings by Cushman and Levinson (1983), deLange (1958), von Grünau (1977), Lindsey et al (1986) and Swanson et al (1987). This may be due to the direct measurement technique that involves only the response of the motion pathway. There may be additional phase lags in a form pathway that contribute to flicker judgements especially at low temporal frequencies.

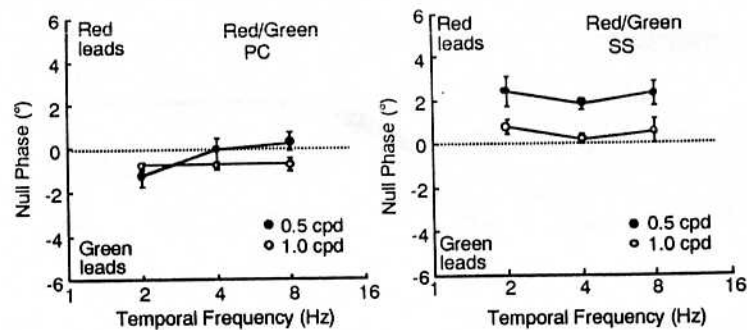


FIG. 8. Temporal phase lag for red/green stimuli as a function of spatial and temporal frequency for two observers. Vertical bars show standard errors.

The lags are comparable to those for parvocellular stream units reported by Smith, Lee, Pokorny, Martin, and Valberg (1989). M-stream units generate much larger phase lags at low temporal frequencies (Smith et al, 1989). These data argue strongly for the participation of the parvocellular stream in the contribution of colour to motion.

MOTION PERCEPTION FOR OTHER EQUILUMINOUS STIMULI

The typical motion detector in area V1 of visual cortex responds principally to drifting luminance contours. However, there are several motion phenomena that cannot be explained by these motion detectors. Ramachandran, Vidyasagar and Rao (1973) reported the perception of apparent motion in a two-frame display consisting of two completely uncorrelated dot patterns. The perception of motion in the absence of correlated luminance information has also been reported for stimuli defined by relative motion (Petersik et al., 1978; Anstis, 1980; Prazdny, 1986a, 1986b, 1987), random-dot stereograms (Julesz, 1971; Prazdny, 1986a, 1986b, Papathomas, Gorea, Julesz & Chang, 1988), flicker (Lelkens & Koenderinck, 1984; Mather, Cavanagh & Anstis, 1985; Prazdny, 1986a, 1986b, 1987; Chubb & Sperling, 1988) and texture (Cavanagh & Mather, 1989; Pantle, 1978; Turano & Pantle, 1989).

In collaboration with Martin Arguin and Michael von Grünau, I have replicated and extended these observations (Cavanagh, Arguin & von Grünau, 1989). The stimulus consisted of two disks which alternated at 2.0 Hz. Each disk could be defined by a difference in luminance, colour, binocular disparity, texture, or motion with respect to the random dot background. The observer's task was to decrease the separation between the two disks until motion was just visible. This separation was taken as an indication of motion strength. When the two disks that alternated were defined by the same attribute, the motion strength was comparable for all attributes, varying by at most a factor of 2. Motion could also be seen between disks defined by any two different stimulus attributes and the motion strength showed no systematic variation as a function of the attributes involved.

According to Schiller et al (1990), at least two of these stimulus types — texture and random dot stereograms — are detected entirely by the parvocellular stream (a lesion of the parvocellular layers drastically reduces texture and random dot stereo detection while a magnocellular lesion does not affect either). Since moving texture or random dot stereo borders produce impressions of motion, the parvocellular stream must be capable of

mediating the motion responses for at least these stimuli. It seems illogical to propose that in the case of colour stimuli, but not texture or stereo, the parvocellular stream somehow becomes incapable of mediating motion responses.

CONCLUSIONS

The data reviewed here indicate that the visual system is quite sensitive to motion of chromatic stimuli. On the other hand, the restricted contrast range available in physical chromatic stimuli reduces their effective strength compared to luminance stimuli. The results of the opposing motion experiment showed that the contribution of colour is mediated by opponent-colour mechanisms and the phase lag data linked the mechanisms in question to the parvocellular stream. The evidence of motion perception for texture and random dot stereogram contours — stimuli detected by the parvocellular stream — also supported the motion capabilities of the parvocellular stream. Since the directionally selective units of MT have been shown to respond to drifting equiluminous stimuli defined by colour or texture (Albright, 1987; Charles & Logothetis, 1989; Saito, Tanaka Isono, Yasuda, Mikami, 1989) these responses may be mediated by signals projecting to MT from structures in the parvocellular stream such as area V4.

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