

CODING OF POSITION OF ACHROMATIC AND CHROMATIC EDGES BY RETINAL GANGLION CELLS

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Introduction

In studies concerning vernier performance, achromatic stimuli have been used much more often than chromatic targets (e.g. Levi and Klein 1982; Levi 1996; McKee 1991; Morgan *et al.* 1983; Morgan and Aiba 1985*a,b*; Westheimer and Hauske 1975; Westheimer and McKee 1975, 1977*a,b*; Westheimer 1979, 1981). However, Morgan and Aiba (1985*a,b*) measured vernier thresholds for two bars with varying chromaticity and luminance. They found a deterioration of vernier threshold with bars set in an equiluminant surround, and showed vernier thresholds displayed properties consistent with photometric additivity when lights of different chromaticity were combined, as might be expected if a luminance channel mediated performance. For another hyperacuity task, Rüttiger and Lee (2000) showed that for displacement thresholds of edges with incremental chromatic and luminance contrasts, performance was strictly determined by luminance contrast, consistent with magnocellular (MC-) pathway cells playing a more important role than parvocellular (PC-) cells in this task. On the other hand, Krauskopf and Farell (1991) measured vernier thresholds for either luminance or equiluminant chromatic Gaussian and Gabor patterns. They found that, except for narrow Gaussian patterns, vernier thresholds were approximately equal when the modulation contrasts were equal multiples of detection threshold. Their results imply that chromatic and luminance channels can be equally effective in providing a vernier signal.

It has been shown that the spatial precision of MC-cells' responses to achromatic targets, analyzed with a template matching procedure, is independent of target velocity over a wide range (Rüttiger and Lee 1998). We ask here how accurately ganglion cells carry positional information about chromatic and achromatic moving edges, and compare results with psychophysical thresholds to similar stimuli. We do not suggest that mechanisms for vernier performance are located at the retinal level; we are only concerned here with the accuracy of the spatial signal a single ganglion cell can deliver.

We used edges of different luminance and chromatic contrasts. The physiological data showed that spatial precision of MC-cells' responses was determined solely by luminance

contrast, but that of PC-cells was dependent on chromatic contrast. Psychophysical vernier thresholds for edges of the same luminance, but different chromatic contrasts were similar when plotted as a function of luminance contrast, but were different when plotted in detection threshold units. Taken together, the physiological and psychophysical data suggest that positional information delivered by MC-cells is important for vernier performance.

Methods

Physiology

Stimuli

Visual stimuli were generated with a Cambridge Research VSG 3 System controlled by a Macintosh 950 computer, and presented on a Barco CRT video display (frame rate: 195 Hz, luminance resolution of RGB gun: 15 bit) 2.6 m away from the monkey. The stimulus was a horizontal edge moving downwards at a speed of $2^\circ/\text{s}$. The luminance of the background was fixed at 40 cd/m^2 , and the luminance of the test, which was added to the background, was varied to change either the luminance contrast alone (when chromaticities of the test and background are the same) or both the luminance and chromatic contrasts (when chromaticities of the test and background are different) of the edge. For the pure-luminance condition (edges with luminance contrast alone), the chromaticity of both test and background was (0.45, 0.47) in CIE (x, y) coordinates, which appeared yellowish to observers with normal color vision. For the luminance–chromatic conditions (edges with both luminance and chromatic contrasts), the chromaticity of the test or background was one of the following (0.625, 0.34), (0.28, 0.595) or (0.153, 0.07), which appeared reddish, greenish or bluish to observers with normal color vision. The following test/background combinations were chosen in order to favor different cone opponent cells; red-on-green (a reddish test on a greenish background for +L–M cells), green-on-red (a greenish test on a reddish background for +M–L cells), and blue-on-red (a bluish test on a reddish background for +M–L and +S–ML cells). For all conditions, the luminance contrast was varied from about 1–33 per cent (Weber contrast). For luminance–chromatic edges, at the maximal luminance contrast the L- and M-cone contrasts were about (39, 18 per cent) and (28, 52 per cent) for red-on-green and green-on-red edges, respectively, and the L-, M-, and S-cone contrasts were (20, 50, 95 per cent) for the blue-on-red edge.

Procedure

Ganglion cell responses to edge stimuli were recorded from the retinae of three anesthetized macaques (Lee *et al.* 1989). Receptive field eccentricities were between 4° and 8° . Times of spike occurrence were recorded to an accuracy of $100 \mu\text{s}$. Binwidth in histograms was 6 ms, with 20 or 40 sweeps for each histogram.

The spatial precision of a cell's impulse trains was estimated using a template matching procedure (Rüttiger and Lee 1998). For each edge condition, the response histogram at

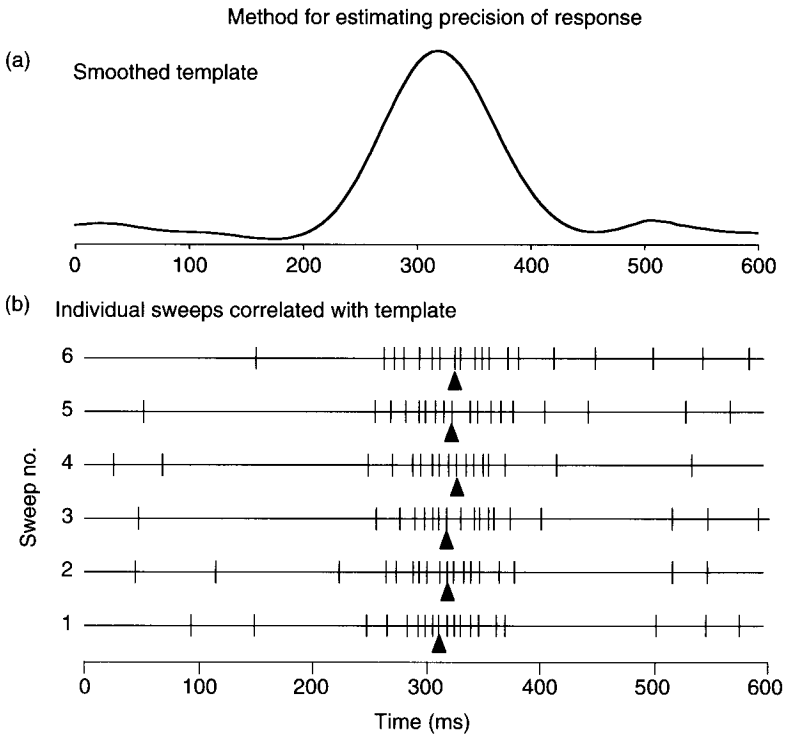


Figure 9.1 (a) The template matching procedure. A matching template was obtained by smoothing the cell's response histogram at maximal contrast; the same template was used at different contrast levels of the same edge condition. (b) The impulse train was shifted over the template until the matching positions (arrows) that gave maximal correlation between impulse train and template were found. This procedure was repeated for each individual impulse train. The standard deviation of the matching positions was a measure of the reliability of spatial localization by the cell.

maximal contrast was smoothed, and used as a template for that edge condition at all contrast levels. Each impulse train was shifted over the template to find the matching location that gave maximal correlation between the impulse train and the template. This procedure was repeated for each individual impulse train, and the standard deviation of the matching locations was taken as a measure of the reliability of spatial localization by the cell. The method is illustrated in Fig. 9.1.

Psychophysics

Stimuli

The same display system was used as in the physiological experiments. The viewing distance was extended to 11.4 m by means of two surface-silvered mirrors. The vernier stimulus consisted of two vertical edges (separated by 4 arcmin), moving rightward or

leftward for 188 ms. The luminance, chromaticity, and speed of the edge were the same as in physiological experiments.

To achieve a sub-pixel resolution (theoretically 0.1 arcsec at a physical CRT pixel size of 10.7 arcsec), the intensities of a row of pixels at the border of the edge were adjusted so as to shift the contour of the edge by the required amount (Morgan and Aiba 1985*b*). To ensure that relative positional information could not be derived from stimulus onset or offset locations, a 50 ms masking edge was presented at both onset and offset of the stimulus in some sets of experiments. For our experimental conditions, presence or absence of the masks had no effect on thresholds.

Procedure

The vernier threshold was measured with staircase method. The observer viewed the visual target monocularly. A fixation point was presented before each trial; at the onset of each trial, the fixation point disappeared and the stimulus appeared, and the observer's task was to indicate if the top edge was to the left or right of the bottom one. An auditory feedback was given after each trial. Each run included two randomly interleaved staircases. The direction of movement was leftward in one staircase and rightward in the other. Threshold of each staircase was the average of six reversals. Thresholds plotted were the averages of six staircases.

We also measured detection thresholds for each edge condition using a four-alternative forced-choice procedure. A moving edge was presented in one of the four quadrants. The observer's task was to indicate in which quadrant the stimulus was presented. Thresholds were estimated with the same staircase method as in the vernier experiment.

Observer

Two observers participated in the experiments, both with normal color vision as assessed with Neitz Anomaloscope, Ishihara pseudoisochromatic plates and Farnsworth-Munsell 100-Hue Test. Both observers are myopic and wore contact lens during experiments.

Results

Physiology

Responses of macaque ganglion cells were measured for 6 MC-cells, 14 L/M cone opponent PC-cells, and 2 +S-ML cells. For each cell, we recorded responses to four types of edges at five luminance contrasts. Figure 9.2 shows response histograms at ~33 per cent luminance contrast. The MC-cells gave similar transient responses to all drifting edges. +L-M PC-cells gave strong sustained responses only to red-on-green edges, and were suppressed by green-on-red edges. +M-L cells gave strong sustained responses to green-on-red and blue-on-red edges, and were suppressed by red-on-green edges. +S-ML cells responded only to blue-on-red edges.

Figure 9.3a shows the standard deviations of the maximal correlation loci (the measure of spatial reliability) as a function of luminance contrast. Four plots represent data

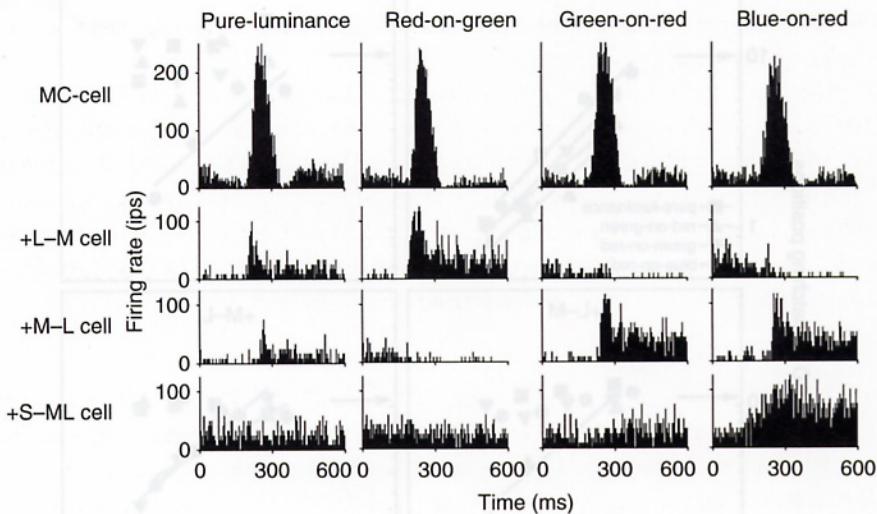


Figure 9.2 Histograms of ganglion cells' responses to different types of edges at ~ 33 per cent luminance contrast. Four rows show responses of MC-, +L-M, +M-L, and +S-ML cells. Four columns represent responses to pure-luminance, red-on-green, green-on-red, and blue-on-red edges, respectively. The binwidth was 6 ms, with 20 or 40 sweeps each histogram.

for MC-, +L-M, +M-L, and +S-ML cells. Data are shown for pure-luminance (squares), red-on-green (erect triangles), green-on-red (inverted triangles) and blue-on-red (circles) edges. Lines represent linear fits. Arrows indicate the standard deviation of the maximal correlation positions in the absence of stimulation, that is, at 0 per cent contrast, and data points near this level indicate chance performance by the neurometric algorithm.

For PC-cells, only excitatory responses yielded positional information. Inhibitory responses did not provide any spatial cue. This was also the case for MC-cells, for example, off-center cells gave little spatial information as to the location of the incremental edges used here (data not shown). The spatial precision of MC-cell spike trains was similar for all four types of edges. This is expected for stimuli of the same luminance contrasts. The spatial precision increased with contrast; the slopes of linear fits were between -0.83 to -1.0 . L/M opponent PC-cells and +S-ML cells gave spatial information only with edges with the appropriate chromatic components.

Psychophysics

There is evidence that MC- and PC-pathways form the physiological basis for psychophysical luminance and chromatic channels (Crook *et al.* 1987; Kaiser *et al.* 1990; Lee *et al.* 1988). If so, we expect psychophysical vernier thresholds for edges of the same luminance but different chromatic contrast to be similar if the luminance mechanism underlies vernier performance, but vernier thresholds may differ if chromatic pathways

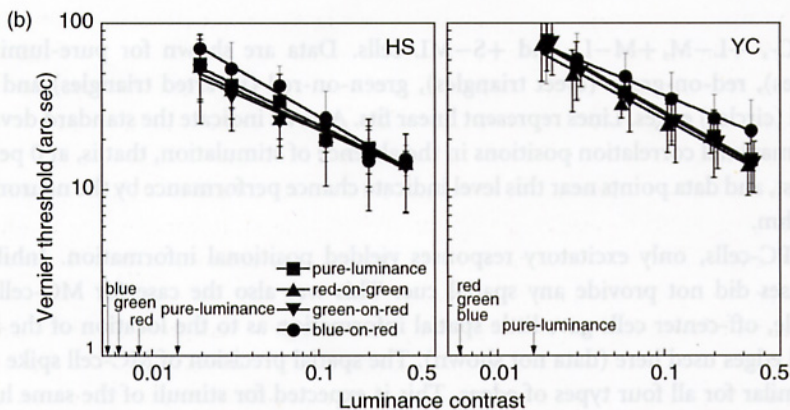
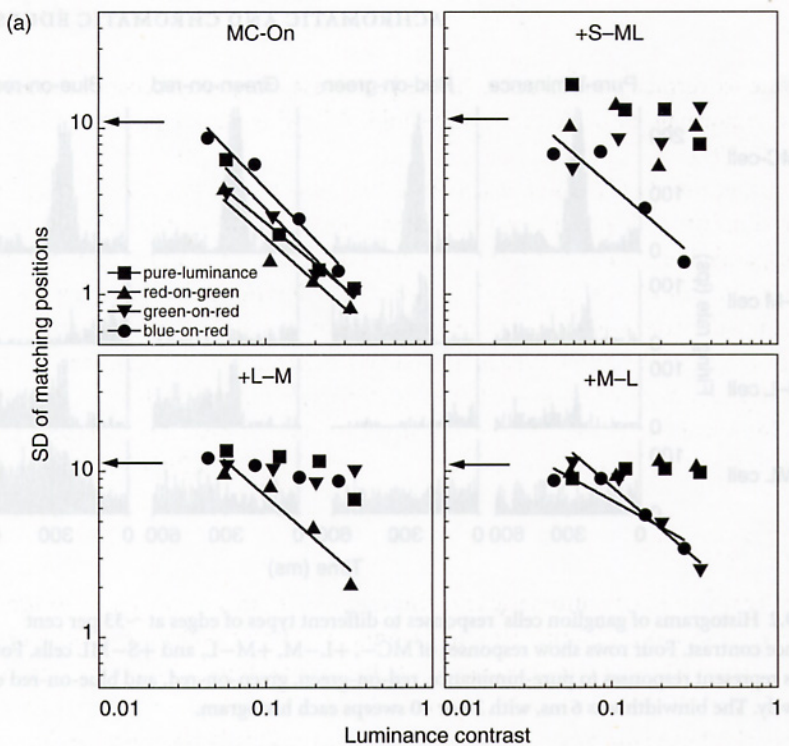


Figure 9.3 Comparison of spatial precision of the cells' responses and human vernier thresholds. (a) SD of the matching positions of ganglion cells at different luminance contrasts. Four plots represent data for MC-, +L-M, +M-L, and +S-ML cells. Data are shown for pure-luminance (squares), red-on-green (erect triangles), green-on-red (inverted triangles) and blue-on-red (circles) edges. Lines represent linear fits where appropriate. Arrows indicate the standard deviation of the maximal correlation positions at 0 per cent contrast. At the maximal luminance contrast, the L- and M-cone contrasts were about (39, 18 per cent) and (28, 52 per cent) for red-on-green and green-on-red edges, respectively, and the L-, M-, and S-cone contrasts were (20, 50, 95 per cent) for the blue-on-red edge. (b) Vernier thresholds from two observers. Data are shown for pure-luminance (squares), red-on-green (erect triangles), green-on-red (inverted triangles) and blue-on-red (circles) edges. Lines represent linear fits. Arrows indicate the detection thresholds for each edge condition.

contribute to vernier performance. In the latter case, they may become similar when contrast is normalized to detection threshold, following the suggestion of Krauskopf and Farell (1991).

The vernier thresholds from human observers are shown in Fig. 9.3b. Data are shown for pure-luminance (squares), red-on-green (erect triangles), green-on-red (inverted triangles) and blue-on-red (circles) edges. Lines represent linear fits. Arrows indicate the detection thresholds for each edge condition. Detection thresholds were highest for the pure-luminance edge and lower in the luminance–chromatic edge conditions.

For all edges, the vernier thresholds decreased steadily as the luminance contrast increased, with a slope of about -0.5 . Vernier threshold curves overlapped when plotted against luminance contrast, but did not overlap when plotted in detection threshold units. This is consistent with a luminance mechanism determining performance.

Discussion

To identify the roles of achromatic and chromatic mechanisms, we chose to use incremental edges with both luminance and chromatic contrast as chromatic stimuli rather than equiluminance edges for two reasons (Morgan and Ingle 1994). One was to avoid the non-linear MC-cell chromatic response which can occur with equiluminance edges (Kaiser *et al.* 1990; Valberg *et al.* 1992). The other was to avoid luminance artifacts arising from chromatic aberration with equiluminance edges. These factors are not expected to play a role with the stimuli used here.

Our result is consistent with earlier psychophysical experiments (Morgan and Aiba 1985*a, b*) which suggested involvement of a luminance mechanism in vernier performance, but inconsistent with Krauskopf and Farell (1991) who showed that, with a Gaussian or Gabor patterns, the luminance and chromatic channels can make equivalent contributions to vernier thresholds. Our data are also consistent with previous results (Lee *et al.* 1995) employing achromatic stimuli which also suggested a dominant role for the MC-pathway in a vernier task.

Detection of targets of different wavelengths on a white background has been attributed to different chromatic and achromatic mechanisms (King-Smith 1975; Sperling and Harwerth 1971), and different cell types of the PC- and MC-pathways are thought to underlie these mechanisms (Crook *et al.* 1987). In these experiments we used different backgrounds to enhance chromatic contrast. We suggest that the differences in detection thresholds between pure-luminance and luminance–chromatic edges result from detection by a luminance mechanism for the pure-luminance edge and by chromatic mechanisms for the luminance–chromatic edges.

The physiological data showed that with pure-luminance moving edges, the spatial information delivered by the MC-cells was more precise than that of PC-cells. PC-cells can only yield accurate spatial information with chromatic contrasts that cause an increase in firing rate. Chromatic contrasts that cause a cessation of maintained activity do not appear to generate a useful spatial signal. It has been proposed that a combination

of +M–L and +L–M cell responses could yield a mechanism with a spectral sensitivity similar to the luminosity function (Ingling and Martinez-Uriegas 1983; Lennie and D’Zmura 1988). However, the responses shown in Fig. 9.2 do not combine to produce such a mechanism due to the rectification associated with zero firing rate for some of the chromatic combinations.

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