

A single mechanism for both luminance and chromatic grating vernier tasks: Evidence from temporal summation

HAO SUN¹ AND BARRY B. LEE^{1,2}

¹SUNY State College of Optometry, New York

²Max Planck Institute for Biophysical Chemistry, D37077 Göttingen, Germany

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Abstract

Vernier thresholds are determined by luminance rather than chromatic contrast when both are present in vernier targets. The role of luminance and chromatic mechanisms in vernier performance under equiluminant conditions remains uncertain. Temporal summation functions for vernier thresholds with luminance and red–green equiluminant gratings were compared to those for detection thresholds with similar stimuli. Vernier thresholds showed similar temporal summation for luminance and chromatic gratings, which is consistent with a single mechanism underlying vernier performance in the two conditions. However, detection thresholds showed a shorter temporal summation duration for luminance gratings than for chromatic gratings, which suggests that two different mechanisms underlie detection thresholds. Analysis of physiological data supports the hypothesis that the frequency-doubled response of ganglion cells in the magnocellular pathway can provide accurate spatiotemporal information for vernier performance at equiluminance.

Keywords: Vernier, Temporal summation, Luminance, Chromatic

Introduction

Luminance signals may play a more important role in vernier tasks than chromatic signals when both are present. Sun et al. (2003) measured vernier thresholds for edges consisting of incremental chromatic targets superimposed upon steady chromatic backgrounds. They found vernier thresholds were determined by luminance contrast rather than chromatic contrast of the edge, although detection thresholds were dependent on both luminance and chromatic content. Sun and Lee (ARVO, 2003) recently showed vernier thresholds remained unchanged when the chromatic contrast polarity of sinusoidal grating targets was reversed (i.e. bright red stripes of one grating must be aligned to bright green stripes of the other) but increased dramatically when luminance contrast polarity was reversed (i.e. bright red stripes of one grating must be aligned to dark red stripes of the other grating). This suggests that the sign of luminance contrast rather than of chromatic contrast determines vernier thresholds. The mechanism underlying vernier threshold with equiluminant targets (zero-luminance contrast) remains uncertain. Residual responses of a luminance mechanism with equiluminant chromatic stimuli could provide information for vernier performance at equiluminance. Morgan and Aiba (1985*a*; *b*) found

vernier thresholds deteriorated when bar targets were equiluminant to a surround, and interpreted their data in terms of vernier threshold relying on a luminance channel. Their data might be consistent with contributions of residual luminance signals to vernier performance at equiluminance. However, when Krauskopf and Farell (1991) measured vernier thresholds for either luminance or equiluminant chromatic patterns, they claimed that chromatic signals can be as effective as luminance signals in vernier performance when normalized to detection threshold. They argued that cone contrast, rather than postreceptoral mechanisms, is the critical determinant of vernier performance.

In this paper, we examine the mechanism underlying vernier tasks with luminance and equiluminant chromatic gratings by measuring the temporal summation functions for vernier thresholds in comparison with those for detection thresholds. Extensive psychophysical data suggest that at detection threshold chromatic mechanisms have longer temporal integration and poorer temporal resolution than luminance mechanisms (de Lange, 1958; Regan & Tyler, 1971; Bowen et al., 1977; Kelly & Norren, 1977; Smith et al., 1984; Swanson et al., 1987). If vernier thresholds should show similar temporal summation functions for the two conditions, this would argue for a common vernier mechanism with luminance and chromatic stimuli. Different temporal summation functions for the two conditions would indicate different mechanisms.

We found vernier thresholds showed similar temporal summation functions for luminance and chromatic gratings. This is con-

Address correspondence and reprint requests to: Hao Sun, SUNY State College of Optometry, 33 W. 42nd Street, New York, NY 10036. E-mail: hsun@sunyopt.edu

sistent with a single mechanism underlying vernier performance in the two conditions. We then considered the possibility that residual signals in a luminance pathway provide information for vernier performance at equiluminance and sought physiological data which might support this hypothesis. There is substantial evidence that cells of the magnocellular (MC) pathway form the physiological substrate of a psychophysical luminance channel (Lee et al., 1988; Kaiser et al., 1990). MC cells show a vigorous response to luminance modulation, but they also show frequency-doubled responses to chromatic modulation (Lee et al., 1989a). This MC-cell residual response may underlie residual border distinctness at equiluminance in the minimally distinct border task (Kaiser et al., 1990; Valberg et al., 1992). To analyze if this response of MC cells is accurate enough to provide spatial information at equiluminance, we recorded MC cells' responses to luminance and chromatic gratings. Analysis of the cell spike trains showed that the frequency-doubled responses of MC cells can provide precise spatiotemporal information at equiluminance.

Materials and methods

Psychophysics

Stimuli

Visual stimuli were generated via a VSG series 5 system (Cambridge Research Systems, UK) and presented on a CRT monitor (SONY CPG520, frame rate 100 Hz) 0.48 m from the eye. The vernier stimulus consisted of a pair of 0.4-cycles/deg (cpd) horizontal sinusoidal gratings (5×15 arcdeg) drifting randomly upward or downward at 2 Hz. The grating pair was separated horizontally by a 30-arcmin gap. The detection stimulus was similar to the vernier stimulus except that a single rather than a pair of gratings was presented. The center of the grating (detection stimuli) or the center of the gap between the grating pairs (vernier stimuli) was at 5-arcdeg eccentricity randomly to the right or left of the fixation point. The gratings were either luminance gratings of 100% luminance contrast or equiluminance chromatic gratings of 15% L-cone and 34% M-cone contrast (the maximal contrast that obtainable on our CRT monitor). The luminance and chromatic gratings were obtained by modulating the red and green guns either in-phase of out-of-phase of each other. The equiluminant point between the red and green guns were estimated with the minimum motion technique (Anstis & Cavanagh, 1983). Mean chromaticity of the stimulus and the background (30×25 arcdeg) was about (0.45, 0.47) in CIE x, y coordinates (varying slightly according to individuals' equiluminance settings); mean luminance of the stimulus and background was 40 cd/m^2 . Exposure duration of the vernier and detection stimuli was varied from 30 ms to 1200 ms. The contrast of the stimulus was ramped on and off with 10-ms raised cosine to reduce any transient artifact.

Procedure

In the vernier experiment, a grating pair with a spatial phase shift was presented, and the observer indicated which grating was shifted upward. In the detection experiment, a single grating was presented randomly to the right or left side of the fixation point and the observer indicated which side contained the stimuli. For both experiments, the observer viewed the targets monocularly. Thresholds were measured with two randomly interleaved staircases. The threshold of each staircase was the average of the last six reversals. Overall, threshold for each stimulus condition was an average

of four to six staircases. Error bars represent one standard error of four to six staircases.

Observers

Two observers (HS & YZ) participated in the experiments. HS was an author and YZ a practiced psychophysical observer who was naïve to the purpose of the experiments. Both have normal color vision as assessed with the Neitz Anomaloscope, Ishihara pseudoisochromatic plates, and Farnsworth-Munsell 100-Hue Test. Observer HS is myopic and wore contact lens during experiments. Observer YZ is emmetropic. Observer YZ provided informed written consent according to a protocol conforming to the Declaration of Helsinki and approved by the SUNY State College of Optometry Institutional Review Board.

Physiology

Procedure

Ganglion cells were recorded from the retinas of anesthetized macaques (*Macaca fascicularis*). The details of the preparation and cell-identification techniques can be found elsewhere (Lee et al., 1989b). All procedures were approved by the SUNY Animal Care Committee and conform to American Physiological Society and the Society of Neuroscience guidelines for ethical care of animals. Receptive-field eccentricities were between 4 and 8 deg. Times of spike occurrence were recorded to an accuracy of $100 \mu\text{s}$. Binwidth was 6 ms, with 20 or 40 sweeps for each histogram.

Stimuli

Visual stimuli were generated with a VSG series 3 system (Cambridge Research Systems, UK) controlled by a Macintosh 950 computer, and presented on a CRT monitor (SONY CPG520, frame rate: 160 Hz) 2.6 m away from the animal. The stimulus was a 0.4-cpd horizontal grating moving downward at a frequency of 2 Hz. The averaged luminance of the gratings and background was 40 cd/m^2 , and the averaged chromaticity was (0.45, 0.47) in CIE x, y coordinates. The relative modulations of the red and green guns were varied to obtain gratings of pure luminance contrast, pure chromatic contrast, or mixed luminance and chromatic contrasts.

Data analysis

The spatial precision of a cell's impulse trains was estimated using two procedures: a cycle-by-cycle Fourier analysis and a template-matching procedure. For cycle-by-cycle Fourier analysis (Rüttiger et al., 2002), the cell's response to each cycle is Fourier analyzed, and the angular standard deviation of the response phase is calculated (Batschelet, 1981; Zar, 1999). Angular standard deviation, σ_ϕ , so defined ranges from 0 deg to 81 deg. For the template-matching method (Rüttiger & Lee, 1998; Sun et al., 2003), the response histogram is smoothed and used as a template. Each impulse train is shifted over the template to find the best-matching location that gives maximal correlation between the impulse train and the template. This procedure is repeated for impulse trains of all cycles, and the standard deviation of the best-matching locations is a measure of the reliability of spatial localization by the cell.

The Fourier analysis method assesses spatiotemporal information carried by the first harmonic. The template-matching method uses information contained in first, second, and higher harmonics.

Comparison of these two methods can reveal spatial information carried by the frequency-doubled responses.

Results

Psychophysical temporal summation

Vernier thresholds as a function of stimulus exposure duration are shown in Figs. 1a and 1b. Detection thresholds are shown in Figs. 1c and 1d. Data are shown for luminance (●) and equilumi-

nant chromatic (■) gratings. Vernier thresholds are expressed in units of spatial phase shift (i.e. grating phase), and detection thresholds are expressed in units of luminance contrast for luminance gratings and units of L-cone contrast for chromatic gratings. To compare the temporal summation functions of luminance and chromatic stimuli, both vernier and detection thresholds for chromatic gratings were scaled vertically to overlap with the thresholds for luminance gratings at long exposure durations. The scaling factors are shown in the figure. Vernier thresholds for luminance and chromatic gratings show a similar temporal course; data

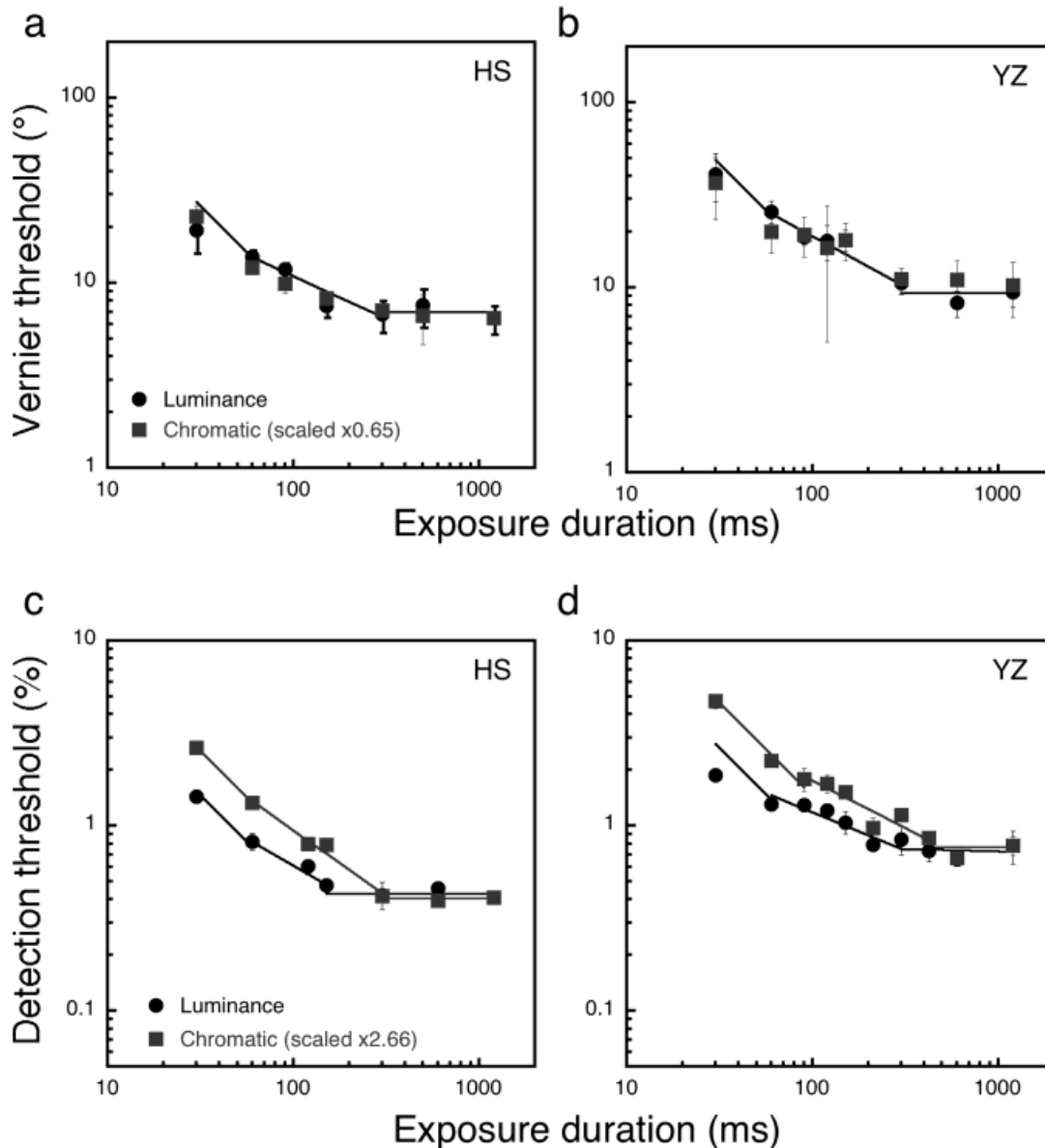


Fig. 1. Vernier thresholds and detection thresholds as a function of exposure duration for observers HS (a & c) and YZ (b & d). Data are shown for luminance (●) and equiluminant chromatic (■) gratings. Vernier thresholds are in units of degrees of spatial phase shift, and detection thresholds are in units of luminance contrast for luminance gratings and L-cone contrast for equiluminant chromatic gratings. Solid lines represent linear fit of slope of -1 , a variable slope, and slope of 0 . Temporal summation data for equiluminant chromatic gratings were scaled vertically to overlap with those for luminance gratings at long exposure durations. The scaling factor for chromatic vernier thresholds was ~ 0.65 and for chromatic detection thresholds was ~ 2.7 for both observers. Vernier thresholds for luminance and chromatic gratings show similar temporal summation functions. Detection thresholds for luminance and chromatic gratings show different temporal summation functions.

superimpose at all exposure durations. However, detection thresholds showed longer temporal summation durations for chromatic gratings than for luminance gratings. The results are consistent with two different mechanisms for detection in the chromatic and luminance conditions but a single mechanism for the vernier task under the two conditions.

The temporal summation function was fitted with three lines; a line of slope -1 , which represents Bloch's law, a line of variable slope, and a line of slope of 0 which represents no temporal summation (Legge, 1978; Waugh & Levi, 1993). For vernier thresholds, the first two lines intercept at ~ 60 ms for both observers, and the second and third lines intercept at 270 and 360 ms for the observers HS and YZ, respectively. These values are comparable to those obtained by Waugh and Levi (1993) with 1 cpd gratings (80% luminance contrast) presented foveally. For detection thresholds, the first two lines intercept at ~ 50 ms to ~ 60 ms for both stimuli and both observers; the second and third lines intercept at ~ 200 ms and ~ 300 ms, respectively, for luminance and chromatic gratings for observer HS, and at ~ 400 ms and ~ 500 ms for observer YZ. This is shorter than the 100-ms and 1000-ms intercepts obtained by Legge (1978) using a fovea 1.5-cpd sinusoidal gratings, which would be comparable to the 0.4-cpd gratings we used after M-scaling for 4–8 deg eccentricity. The difference may be due to the different stimulus temporal profiles used; Legge used a 20-ms mask preceding and following the stimuli, while we used a 10-ms cosine ramp preceding and following the stimuli.

In a statistical analysis, we fitted the temporal summation curves with a variation of Watson–Nachmias model (Watson, 1986) which incorporates a difference of two five-stage linear filters, with a latency difference between the two filters. This model is a widely used working model for temporal sensitivity (Smith et al., 1984; Swanson et al., 1987), and previous studies have shown that the five-stage filter is representative of the slope of the amplitude-sensitivity data for chromatic and luminance modulations. The temporal summation function was resampled by randomly choosing each threshold from one of the four to six staircase thresholds at that temporal duration. We then fitted the resampled curve with the Watson–Nachmias model and found the corner frequency. We calculated the mean and standard deviation of corner frequency for all possible random resamples.

The corner frequency was about 8–10 Hz for luminance detection and 4–5 Hz for chromatic detection for both observers. This is very similar to the results from Smith et al. (Smith et al., 1984). A z-score test showed that the probability of luminance and chromatic detection temporal summation functions having similar corner frequency was less than 0.0001, and the probability of luminance and chromatic vernier temporal summation functions having different corner frequency was less than 0.01.

For one observer (HS), vernier temporal summation functions were also obtained for luminance and chromatic gratings with contrast equated in units of detection threshold. This changed the relative ordinate position of the luminance and chromatic curves but the course of temporal summation remained the same.

Physiological measurements of positional accuracy

The similar temporal summation function for vernier performance with luminance and chromatic patterns has two alternative explanations. Both luminance and chromatic afferent signals could provide input to a single cortical spatiotemporal mechanism, and the temporal summation functions for vernier thresholds may be

determined by this mechanism. Alternatively, a cortical spatiotemporal mechanism may receive signals only from the luminance pathway, residual signals in which might provide information for vernier performance at equiluminance. We now analyze physiologically if residual responses in the MC pathway are adequate to support psychophysical vernier performance at equiluminance.

Responses were collected from 18 MC and 15 L/M cone-opponent PC ganglion cells. Fig. 2 shows response histograms of a MC (Fig. 2a) and two PC cells (Fig. 2b) to gratings of various combinations of luminance and chromatic contrast; the right-hand column shows histograms to gratings of luminance contrast alone. The sinusoidal curves above each histogram represent the relative red- (solid line) and green-gun (dashed line) modulations that generate the grating. The MC cell gave first-harmonic responses to luminance gratings and gave frequency-doubled responses to equiluminant chromatic gratings. The PC cells responded vigorously to gratings with chromatic contrast, but only gave weak responses to pure luminance gratings.

The estimated spatiotemporal information inherent in ganglion cell's spike trains is shown in Fig. 3. Data are shown for cycle-by-cycle Fourier analysis (■) and template-matching method (●) averaged for all MC and PC cells. The X-axis represents grating luminance contrast, and the Y-axis represents either angular standard deviation of first-harmonic phase (■) or angular standard deviation of template-matching loci (●). A larger deviation indicates poorer spatiotemporal precision. For MC cells, the standard deviations of first-harmonic response phases show a substantial increase at equiluminance while those of template-matching loci, which utilize information in both first- and second-harmonic responses, show only a minor increase. This suggests the frequency-doubled responses can provide precise spatiotemporal information at equiluminance. Cellular responses of PC cells can provide precise spatiotemporal information in the chromatic but not in the luminance condition.

Discussion

Vernier thresholds show similar temporal summation for luminance and chromatic gratings. This suggests a single mechanism underlies vernier performance in the two conditions. On the other hand, detection thresholds of luminance and chromatic gratings show different temporal summation durations, implying different underlying mechanisms. Krauskopf and Farell (1991) suggested that vernier thresholds should be acquired with stimuli normalized, in contrast, to detection threshold. This would be inappropriate if different underlying mechanisms are responsible for detection and vernier tasks.

We propose that the frequency-doubled response of MC cells at equiluminance could provide a residual signal which supports vernier performance under these conditions; an analysis of MC-cell's responses to chromatic stimuli was consistent with this hypothesis. Another possible source for MC-cells' residual signals at equiluminance could be a first-harmonic chromatic response at low temporal frequencies; this was first identified through analysis of MC-cell's responses as a function of the relative phase of a pair of sinusoidally modulated lights (Smith et al., 1992). This signal has been proposed as a basis for some psychophysical results with moving patterns (Mullen et al., 2003). However, MC-cells' responses in Fig. 2 showed little indication of a first-harmonic component at equiluminance; the most prominent response was the frequency-doubled response in all cells tested. In the earlier measurements of Smith et al. (1992), uniform field stimuli were used

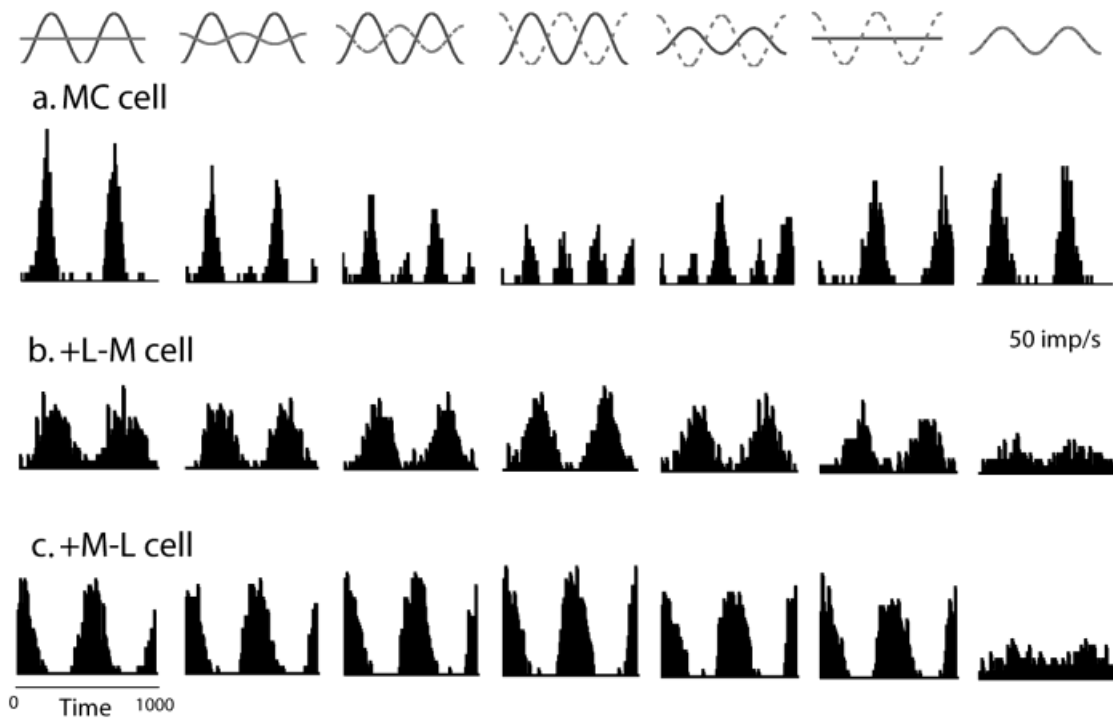


Fig. 2. Histograms of ganglion cells' responses to gratings of mixed luminance and chromatic contrast. Three rows show responses of a MC and two PC (a +L-M and a +M-L) cells. The sinusoidal curves illustrate the red- (solid line) and green-gun (dashed line) modulations that generate the grating. The MC cell gives vigorous first-harmonic responses to gratings with luminance contrast and frequency-doubled responses to chromatic gratings. PC cells respond well to chromatic gratings but only give weak responses to luminance gratings.

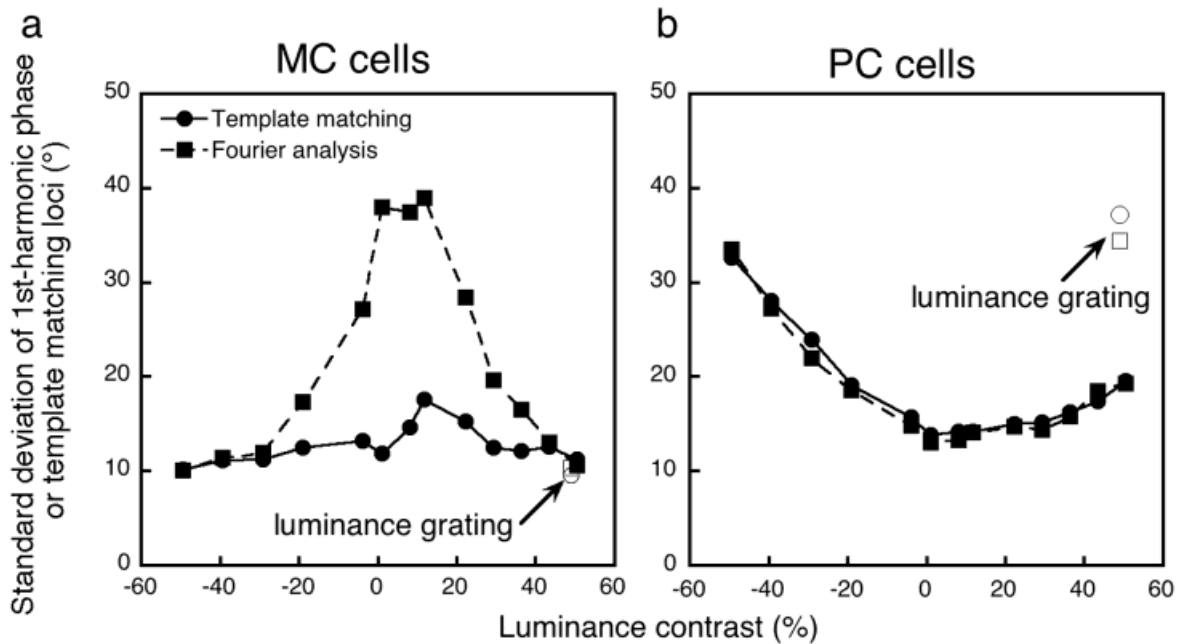


Fig. 3. Spatiotemporal precision inherent in MC- and PC-cell's responses. Data are shown for cycle-by-cycle Fourier analysis (■) and template-matching method (●) averaged for 18 MC and 15 PC cells. For MC cells, the mean standard deviations of first-harmonic response phases show a substantial increase at equiluminance while those of template-matching loci increase only to a minor degree. Frequency-doubled responses of MC cells can provide precise spatial information with chromatic gratings, while their first-harmonic response cannot.

rather than gratings. It is uncertain why grating stimuli should make the frequency-doubled response more prominent than the first-harmonic response.

In the minimally distinct border task, the distinctness of equiluminant borders is closely related to the tritanopic purity difference across the border, that is, the $|M-L|$ cone signal (Kaiser et al., 1971; Valberg & Tansley, 1977; Tansley & Boynton, 1978). The residual MC-cell's nonlinear response to equiluminant borders closely matches the psychophysical border distinctness in relative and absolute amplitude (Kaiser et al., 1990; Valberg et al., 1992). It appears plausible that the distinctness of a border may be related to accuracy of its localization in a vernier task. We used here gratings rather than borders but a similar argument would apply.

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