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Luminance and chromatic contributions to a hyperacuity task: Isolation by contrast polarity and target separation

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ABSTRACT

Vernier thresholds are known to be elevated when a target pair has opposite contrast polarity. Polarity reversal is used to assess the role of luminance and chromatic pathways in hyperacuity performance. Psychophysical hyperacuity thresholds were measured for pairs of gratings of various combinations of luminance (Lum) and chromatic (Chr) contrast polarities, at different ratios of luminance to chromatic contrast. With two red–green gratings of matched luminance and chromatic polarity (+Lum+Chr), there was an elevation of threshold at isoluminance. When both luminance and chromatic polarity were mismatched (−Lum−Chr), thresholds were substantially elevated under all conditions. With the same luminance contrast polarity and opposite chromatic polarity (+Lum−Chr) thresholds were only elevated close to isoluminance; in the reverse condition (−Lum+Chr), thresholds were elevated as in the −Lum−Chr condition except close to equiluminance. Similar data were obtained for gratings isolating the short-wavelength cone mechanism. Further psychophysical measurements assessed the role of target separation with matched or mismatched contrast polarity; similar results were found for luminance and chromatic gratings. Comparison physiological data were collected from parafoveal ganglion cells of the macaque retina. Positional precision of ganglion cell signals was assessed under conditions related to the psychophysical measurements. On the basis of these combined observations, it is argued that both magnocellular, parvocellular, and koniocellular pathways have access to cortical positional mechanisms associated with vernier acuity.

1. Introduction

In a series of studies designed to specify the retinal signals responsible for the hyperacuities (Lee, Rüttiger, & Sun, 2005; Lee et al., 1993, 1995; Rüttiger, Lee, & Sun, 2002; Sun, Ruttiger, & Lee, 2004), the parasol ganglion cells of the magnocellular (MC) pathway were shown to respond with the necessary spatial precision and with suitable properties (e.g., as a function of drift velocity (Rüttiger, Lee, & Sun, 2002)) to support psychophysical performance with achromatic targets. The situation with chromatic patterns is less clear. Morgan and Aiba (1985) first demonstrated that vernier acuity is degraded with equiluminant patterns. In an attempt to unify data over a large parameter space (including chromaticity), Krauskopf and Farell (1991) proposed that all vernier thresholds with chromatic and luminance patterns became comparable when stimulus contrast was normalized to detection threshold, although careful examination of their data reveal some deviations from this rule. In combined physiological and psychophysical studies (Rüttiger & Lee, 2000; Sun, Lee, & Rüttiger, 2003), it was shown that with chromatic targets superimposed on chromatic backgrounds, hyperacuity thresholds were closely related to luminance contrast, rather than to detection threshold, which varied widely (in luminance contrast) with the different colored targets on different colored backgrounds. It was hypothesized that although detection may take place through chromatic channels, a luminance mechanism dominated psychophysical vernier performance under these conditions. However, the data of Krauskopf and Farell (1991; Krauskopf & Forte, 2002) certainly suggest chromatic mechanisms can support vernier judgements. Lastly, the critical duration for vernier with both achromatic and chromatic targets is ca. 50–100 ms (Sun & Lee, 2004), which is similar to the critical duration for detection of luminance but much shorter than that for chromatic targets (e.g., Swanson et al., 1987).

Vernier thresholds increase if members of the target pair have opposite contrast polarity (Levi & Waugh, 1996; Levi & Westheimer, 1987; Mather & Morgan, 1986; O'Shea & Mitchell, 1990). For example, the vernier threshold for aligning a bright bar with a dark bar is much higher than for aligning either two bright bars or two dark bars. However, if separation of the targets is increased, thresholds become similar (Levi & Klein, 1990; Levi &

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Waugh, 1996; Waugh & Levi, 1993). It was suggested that with targets of opposite contrast polarity and/or large separation, 'local sign' was used as a vernier cue (i.e., some feature of each stimulus is used as a position cue independent of the features' properties), while with targets of the same polarity close together a local filter operation was involved (i.e., some linear filter, such as an orientation detector, is involved, and then stimulus properties will affect the filter's response).

We have used contrast polarity as a tool to isolate the contribution of luminance and chromatic signals to vernier performance. Most contrast polarity experiments have used edge or bar targets, but here we use gratings; there is a considerable literature using gratings on hyperacuity tasks (e.g., Levi, 1996). With chromatic patterns, use of gratings (rather than edged patterns) avoids possible problems with chromatic aberration, as long as the spatial frequency is not too high.

Hyperacuity judgements were made with gratings with luminance and/or chromatic contrast. Examples of the stimuli used are shown in Fig. 1. In each of four conditions, the relative modulations of the red and green guns were changed so that the stimuli had only achromatic contrast (top panels), only chromatic contrast (isoluminance; lower panels) or both (middle panels). In Fig. 1A, both achromatic and chromatic contrast are matched in polarity. In Fig. 1B, both achromatic and chromatic contrast are of opposite polarity. Finally (Fig. 1C and D), mixed conditions are shown. The mismatch of achromatic and chromatic polarities is seen in the middle panels; when the red/green gun ratios were such that only luminance or chromatic contrast was present, then the conditions in the upper and lower panels revert to those seen in Fig. 1A and B. Observers were instructed to align the pairs of gratings either in or out-of-phase, or based on the luminance or chromatic cue.

If luminance contrast was present, its polarity was found to be a strong determinant of hyperacuity thresholds, even if chromatic contrast was present; however, at and near equiluminance, chromatic contrast polarity became a determining factor. For both luminance and chromatic gratings, contrast polarity became unimportant at large target separations. The psychophysical observations were also related to physiological measurements. The results are consistent with both luminance and chromatic mechanisms having access to the spatial mechanisms responsible for vernier acuity (rather than, for example, chromatic judgements being dependent on local sign), although the latter deliver less positional precision, as might be suggested by the lower psychophysical acuity for chromatic gratings (Mullen, 1985).

2. Methods

2.1. Psychophysics: stimuli

Visual stimuli were generated via a VSG series 2/5 graphic controller (Cambridge Research Systems, UK) controlled by a PC computer (Gateway E6500) and presented on a CRT monitor (SONY CPG520, frame rate 100 Hz) 0.48 m from the eye. There was a small cross in the center of the display for fixation. The hyperacuity stimulus consisted of a pair of horizontal gratings (usually 0.4 cycles per degree), each $5 \times 25°$, separated horizontally by a gap. Fig. 1 shows some examples of the pairs of gratings used; the fixation point has not been included. The grating pair was randomly drifted upward or downward at 2 Hz for 120 ms, with a 10-ms raised cosine onset and offset contrast envelope to reduce transients at the beginning or end of the presentation. Mean luminance was 25 cd/m^2 and between trials the gratings were replaced by a background of the same mean luminance and chromaticity.

2.2. Psychophysics: observers

Five observers participated in the experiments, the three authors, and ZXY and MJ as naive observers. All observers except for BBL have normal color vision as assessed with the Neitz Anomaloscope, Ishihara pseudoisochromatic plates and Farnsworth-Munsell 100-Hue Test. Observers HS and BC wore

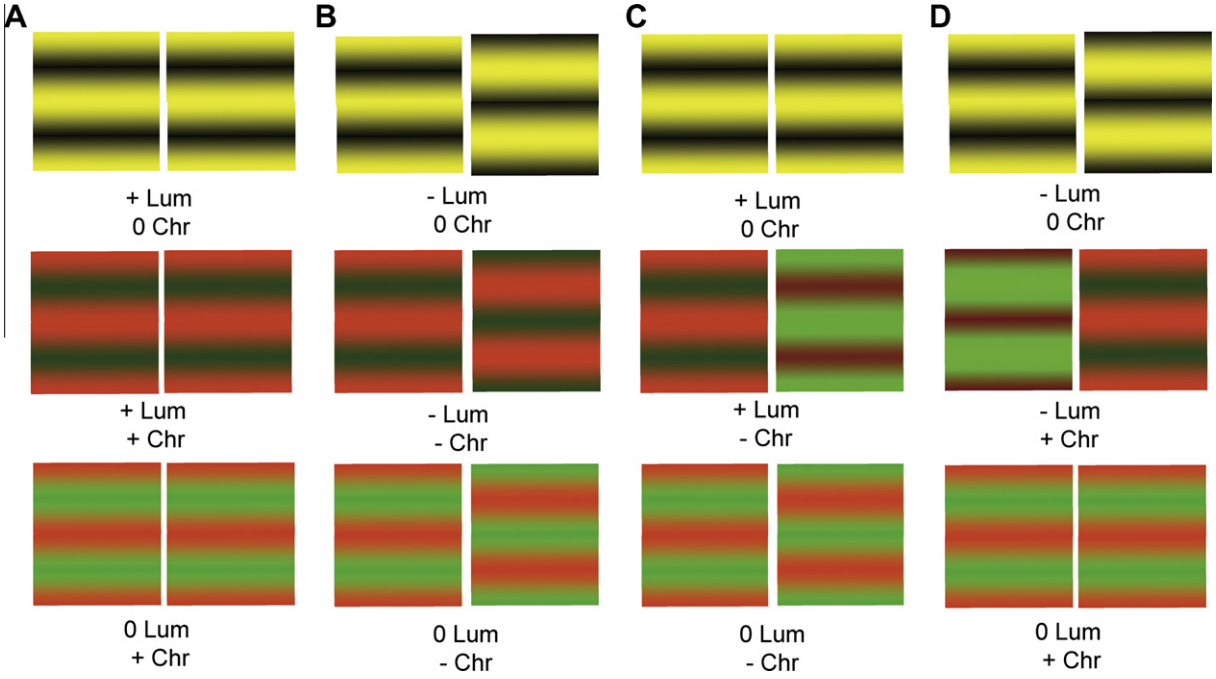

Fig. 1. A selection of stimulus configurations. (A) Pairs of gratings aligned in both luminance and chromatic contrast, which are manipulated in each panel by changing the relative modulation of the red and green guns. The upper panel shows maximum luminance contrast, the lower panel the equal luminance condition, and the middle panel an intermediate modulation of the red and green guns. (B) Pairs of gratings of mismatched achromatic and chromatic contrast, again with different gun modulations. (C and D) Grating pairs in which either luminance or chromatic contrast is matched, and the other mismatched.

correction as required. Observer BBL is a single gene deuteranope and was used to isolate chromatic mechanisms based on the S-cone pathway. Observers ZXY and MJ 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. Partial sets of data from three other observers were consistent with those presented here.

2.3. Psychophysics: procedure

Each observer first set an equiluminance point between the red and green (or between the red and blue for observer BBL) guns using the minimal motion technique (Anstis & Cavanagh, 1983). A horizontal grating of the same dimensions as the hyperacuity targets was used. Observers minimized the motion of the grating by changing the modulation depth of the green gun, and repeated this estimate 10 times. The mean value was used to define equiluminant red–green (or blue–yellow) gratings for each observer.

Observers viewed the screen monocularly and pressed buttons to initiate each trial. The task was to indicate with a button press which grating was presented with a vertically higher shift in phase in comparison to the other (irrespective of movement direction). Observers were instructed to make the judgement based on the luminance cue or the chromatic cue, or to use an in- or out-of-phase criterion, as appropriate. Observers rapidly learned to attend to the appropriate cue; the first experimental session for each observer was used to accustom them to attend to the relevant cues and data were discarded. In the contrast polarity experiment, the grating separation was fixed at 0.1° (foveal viewing). Because physiological recordings were obtained in the parafovea, psychophysical performance for some observers was obtained for viewing conditions in the parafovea. For these conditions, the pairs of gratings were presented centered at random either 5° left or right of the fixation cross. In the separation experiment, the grating separation was varied from 0° to 2° symmetric about the fixation cross, i.e., foveal measurements were obtained.

Hyperacuity thresholds were measured using a randomly interleaved dual-staircase procedure. As mentioned above, she/he had to indicate whether the left or right grating was shifted upward in phase relative to the other based on the cue instruction given (i.e., whether luminance and/or chromatic components were to be aligned in or out of phase). Staircases began well above threshold so that observers could accustom themselves to align the appropriate cues. A two-down, one-up procedure was used, with a step size of 0.3 log unit, reduced to 0.15 log unit. Staircases were terminated after 12 reversals (usually achieved in from 35 to 50 trials) and the mean of the last seven reversals used as a threshold estimate. With a dual staircase, this gave two thresholds, and the data shown represent means of 2–3 repetitions of the dual staircase.

2.4. Physiology: stimulus

Visual stimuli were generated via a VSG series 3 graphic controller (Cambridge Research Systems, UK) controlled by a Mac computer (Quadra 950) and presented on a CRT monitor 2.26 m from the eye. Mean luminance of the background was 40 cd/m^2 and mean chromaticity was (0.45, 0.47) in CIE x, y coordinates. The stimuli were 0.4 cpd horizontal sinusoidal gratings drifting vertically across a cell's receptive field at a speed of 2 Hz. The stimulus was a single grating ($4 \times 4°$) centered on the cell's receptive field, and the luminance and chromatic contrasts of the grating was varied by varying the relative modulation of the red and green guns of the CRT monitor. In separation experiments, two gratings of various phase offsets and various separations were presented centered on the cell's receptive field center. In positional offset experiments, two abutting gratings of various phase offsets (0°, 90°, or 180°) were presented at various locations relative to the cell's receptive field center.

2.5. Physiology: procedure

Ganglion cell responses were recorded in vivo from the retinas of five macaque monkeys (*Macaca fascicularis*). The animals were initially sedated with an intramuscular injection of ketamine (10 mg/kg). Anesthesia was induced with sodium thiopental (10 mg/kg) and maintained with inhaled isoflurane (0.2–2%) in a 70:30 N_2O–O_2 mixture. Local anesthetic was applied to points of surgical intervention. Elecroencephalogram and electrocorticogram were monitored continuously to ensure animal health and adequate depth of anesthesia. Muscle relaxation was maintained by a constant infusion of gallamine triethiodide (5 mg/kg/h i.v.) with accompanying dextrose Ringer solution (5 ml/kg/h). Body temperature was kept close to 37.5°. End tidal CO_2 was adjusted to close to 4% by adjusting the rate of respiration. Procedures conformed to the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research and were approved by the SUNY State College of Optometry Institutional Animal Care and Use Committee.

Neuronal activity was recorded directly from retinal ganglion cells by an electrode inserted through a cannula entering the eye behind the limbus. The eye was sutured to a ring, which minimized eye movements. During each condition of measurement, any residual systematic drifts of response position could be identified through the analysis technique. Occasional systematic drifts of 1–2 arc min were found, and we assumed them to be due to residual eye movements. These data were discarded. Gas-permeable contact lens of the appropriate power was used to bring stimuli into focus on the retina.

Responses of macaque retinal ganglion cells were recorded between 4° and 8° eccentricity. Cell identification was achieved through standard tests (Lee, Martin, & Valberg, 1989a). These included achromatic contrast sensitivity and responses to lights of different chromaticity. Additional tests (e.g., measuring responses to heterochromatically modulated lights (Smith et al., 1992) were employed in cases when identification was uncertain. For each cell, the locus of the receptive field center was determined and the stimulus movement was centered around this point. Cell responses were recorded to stimuli as described in the previous section. Times of spike occurrence were recorded to an accuracy of 0.1 ms and averaged histograms were simultaneously accumulated. Cycle-by-cycle Fourier analysis of the histograms were carried out and 1st and 2nd harmonic response amplitude and phase were calculated.

3. Results

3.1. Psychophysics – contrast polarity

Hyperacuity thresholds were measured for grating pairs of various luminance and chromatic contrasts and different combinations of contrast polarities as was sketched in Fig. 1. Data from three observers are shown in Fig. 2. For each condition, the relative modulation depths of the guns was varied so as to give pure luminance gratings (luminance contrasts +1 and −1, at either end of the x axes), isoluminant chromatic gratings (midpoint on x axis) and intermediate grating conditions in which both luminance and chromatic content were present. In the top row of plots, luminance and chromatic contrasts were both matched in polarity. The instruction was either to match the relative positions of the gratings for in phase (+Lum+Chr) or out of phase (−Lum−Chr) conditions, as sketched in Fig. 1A and B. In the lower row of plots,

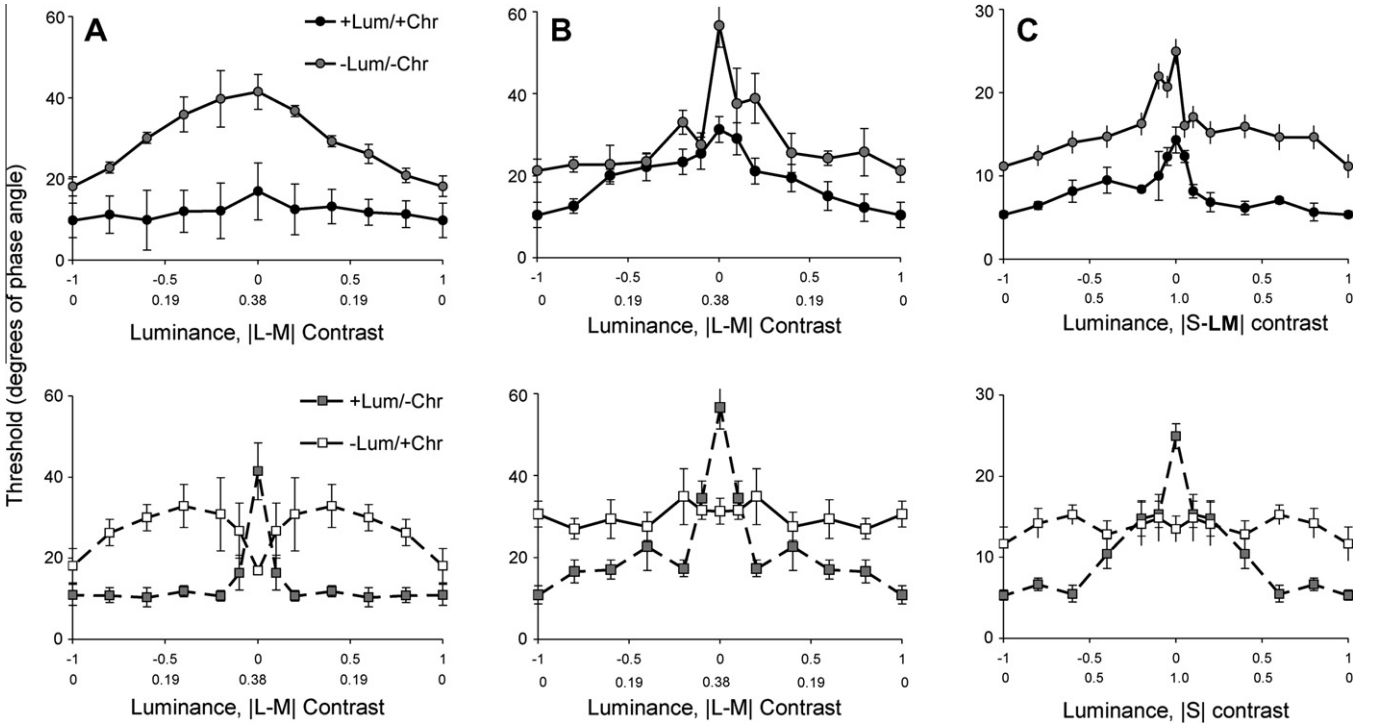

Fig. 2. Hyperacuity thresholds for gratings of the same luminance and chromatic contrast polarities (+Lum/+Chr), opposite luminance and chromatic contrast polarities (−Lum/−Chr) are shown in the top row of plots. For the lower plots, the luminance and chromatic contrast polarities were reversed and the observers were instructed to align either the luminance or chromatic component. (A) Red–green gratings, parafoveal viewing (observer HS). (B) Red–green grating, foveal viewing (observer BC). (C) Blue–red grating, foveal viewing, deuteranopic observer, foveal viewing (observer BBL). Both luminance and chromatic contrast are labeled on the *x*-axis.

the luminance and chromatic contrasts were of opposite polarity and the instruction was to either align the luminance or chromatic components of the gratings (Fig. 1C; +Lum−Chr and −Lum+Chr). Again, the relative modulation depths of the guns were changed. Some of the points are identical in different conditions; for example, for −Lum+Chr at isoluminance the grating is identical to the +Lum+Chr condition at isoluminance, as was sketched in Fig. 1.

In Fig. 2, the luminance and chromatic contrast for the different conditions are indicated along the abscissa. Chromatic contrast is expressed in terms of |L–M| or |S| cone contrast. Hyperacuity thresholds are expressed in degrees of grating phase. The results are within the range found in the literature (Levi, 1996). It should be stressed that these thresholds are expressed in terms of degrees of grating phase rather than visual angle. In Levi (1996), both metrics are given; in the current report we use degrees of grating phase since this metric makes thresholds less dependent on retinal eccentricity (Sun, Ruttiger, & Lee, 2004).

Fig. 2A shows results from observer HS with 5° viewing eccentricity, close to the eccentricity of the physiological measurements described in the next section; Fig. 2B shows results from observer BC with foveal viewing. Fig. 2C shows foveal measurements for the deuteranopic observer (BBL) with blue–red gratings; these were aimed at stimulating S-cone spatial mechanisms for reasons described below.

Hyperacuity thresholds for pairs of gratings of the same luminance and chromatic contrast (+Lum/+Chr) polarities are shown by the black solid symbols in the upper row of plots. For all observers, there is an increase in threshold as luminance contrast decreases towards equiluminance. These data resemble Morgan and Aiba's original observation (Morgan & Aiba, 1985). Hyperacuity thresholds when observers matched gratings of opposite luminance and chromatic contrast polarities (−Lum/−Chr) are shown in the upper row of plots by the gray shaded symbols. When compared to the conditions with matched luminance and chromatic contrast polarity, the thresholds for opposite luminance and chromatic contrast polarity trials increased under all conditions for all observers. There is again an increase in threshold at and near equiluminance for all observers. The magnitude of the threshold increase is consistent with previous measurements with stimuli consisting of bars and dots of mixed polarity (Levi & Westheimer, 1987; O'Shea & Mitchell, 1990).

In the lower row of plots, the results for conditions with mixed luminance and chromatic contrast polarity are shown. When observers were asked to align the luminance component of the gratings (+Lum−Chr), in the presence of luminance contrast (gray shaded squares), thresholds are similar to the luminance/chromatic in-phase condition in the upper plots. As the equiluminant point is approached (luminance contrast 0%), hyperacuity thresholds increased toward the −Lum−Chr thresholds in the upper plots.

When luminance contrast polarity is reversed and chromatic polarity remained the same (unfilled square symbols), the hyperacuity thresholds followed the −Lum/+Chr curve at high luminance contrasts. At and near equiluminance, grating thresholds become similar to the +Lum/+Chr condition, and there was a gradual transition of the hyperacuity threshold from the one curve to the other as luminance of the gratings was reduced.

It should be stressed that there is no chromatic contrast when luminance contrast is 1, as was shown in Fig. 1 (upper panels). We also measured thresholds when the members of the pair of luminance gratings consisted of red–black and green–black modulation, that is when luminance contrast is 1 but chromatic contrast is nevertheless inverted (or red–black and blue black for BBL). Thresholds were very similar to the 100% luminance condition.

Results for foveal viewing for observers DW and ZXY were similar to those in Fig. 2A and B. There is some variability between observers. For observer HS in the +Lum/−Chr condition, thresholds are only elevated above the +Lum/+Chr curve very close to

equiluminance. For the other observers, the effect of chromatic contrast reversal caused a broader increase in threshold around the isoluminance point; the +Lum/−Chr thresholds fell above the +Lum/+Chr curve over a comparatively broader range of luminance contrast. Data from the deuteranopic observer (BBL) are included for reasons described below, and show a similar pattern to the other observers with red–green gratings. The pattern of results in a set of data obtained at 5° eccentricity from this observer (BBL) resembled the foveal data. Observer HS also obtained a set of parafoveal thresholds with gratings modulated along the tritanopic confusion line, and the results showed similar pattern as those of observer BBL.

These results suggest that when luminance contrast is present, it is important for determining hyperacuity; chromatic contrast polarity has little effect except close to equiluminance. On the other hand, at equal luminance, chromatic contrast polarity affects hyperacuity judgements. We now consider the physiological signals associated with these positional judgements.

3.2. Physiology – positional accuracy of cell responses at and near equal luminance

Previous studies have shown that signals from the MC pathway play an important role in vernier tasks with achromatic moving bars or gratings (Rüttiger, Lee, & Sun, 2002; Sun, Ruttiger, & Lee, 2004). The results in Fig. 2 suggest that a luminance signal, presumably deriving from the MC pathway, defines vernier performance when enough luminance contrast is present. Close to equiluminance, chromatic mechanisms may play a role, or alternatively the frequency-doubled response in the MC pathway (Lee, Martin, & Valberg, 1989b; Lee & Sun, 2009) may provide positional information. To examine these possibilities we first illustrate the frequency-doubled response. It should be stressed that in these physiological measurements we use only a single grating; the goal is to determine the positional precision inherent in the ganglion cell signal, in order to constrain the mechanisms responsible for psychophysical performance.

We recorded responses from ganglion cells using drifting gratings of mixed luminance and chromatic contrasts as was carried out in our previously described psychophysical experiments. Fig. 3 shows histograms of typical MC (Fig. 3A; on-center cell) and PC cell (Fig. 3B; +L–M cell) responses to gratings (two cycles) of various luminance and chromatic cone contrasts, as indicated by the numbers alongside each pair of histograms. The MC cell responded vigorously to luminance gratings, and the fundamental response amplitude decreased with luminance contrast to reach a minimum near equiluminance. However, there is a frequency-doubled response near and strongest at the equiluminant condition. The PC cells' response amplitude is vigorous when there is chromatic contrast in the grating, with a weak response to a pure luminance grating. Fig. 3C and D shows amplitudes of 1st and 2nd harmonic components of the responses for the MC cell and the PC cell respectively; the 2nd harmonic response of the MC cell near equiluminance represents the frequency-doubled response; otherwise when there is a large 1st harmonic response, the 2nd harmonic response represents response shaping due to response rectification or distortions from a sinusoidal shape. These data are consistent with previous reports (Lee, Martin, & Valberg, 1989b; Lee & Sun, 2009).

Ganglion cell's impulse trains in response to a drifting grating vary in phase from cycle to cycle. This variability is a measure of the reliability of a cell's spatial signal, and is relevant in the context of vernier performance. This spatiotemporal variation inherent in a cell's signal can be estimated using a cycle-to-cycle Fourier analysis and the variability in response phase can be calculated using angular standard deviation (Sun, Ruttiger, & Lee, 2004). Fig. 4 shows the averaged angular standard deviation of 1st harmonic response phases for MC and PC cells to gratings with different luminance and chromatic contrasts, using a similar convention to earlier figures. The *x*-axis represents the luminance or chromatic contrast of each grating. The angular standard deviation of the MC cells' 1st harmonic responses increases steeply close to equiluminance, i.e. the positional accuracy of the signal decreases. The angular standard deviation for P cells is low at and around equiluminance, with little variation, but is high for luminance gratings. This suggests that response of MC cells can provide precise spatiotemporal information to gratings of luminance contrast, but the 1st harmonic does not deliver reliable spatial information for the equiluminant conditions. The positional variability of the PC cell response near and at equiluminance shows considerably lower angular standard deviation than the MC 1st harmonic response, and therefore the responses of PC cells can provide precise information for chromatic gratings, but not for luminance gratings.

However, this analysis of angular standard deviation only utilizes spatiotemporal information contained in the 1st harmonic, but does not utilize information contained in the 2nd or higher harmonic responses. To analyze the spatiotemporal information delivered by MC cells' frequency-doubled responses, we reanalyzed the data using a template-matching method, as described in Rüttiger, Lee, and Sun (2002). Briefly, a response template is generated by smoothing the response histogram, which is an averaged response over many cycles, and then each individual spike train (i.e. response to a single stimulus cycle) is cross-correlated with the template to find a best matching locus. Variation of the best matching loci across all response cycles gives an indication of the cycle-to-cycle spatiotemporal response variation; one might hypothesize that central mechanisms make use of such information.

Results of analysis using the template-matching method are also shown in Fig. 4. The standard deviation of the matching loci remains lower for MC cells around equiluminance compared to the 1st harmonic analysis, with only a minor peak. For PC cells data the two analysis methods are similar, as might be expected if the 1st harmonic component dominates the response. This suggests that if the frequency-doubled response is taken into account, MC cells can provide psychophysically useful spatiotemporal information for hyperacuity around equiluminance with red–green gratings.

However, the following arguments are against the hypothesis that this information can be used for hyperacuity. The frequency-doubled response of MC cells is thought to require chromatic input from the red–green opponent channel (Lee & Sun, 2009). This is not present for stimuli isolating the S-cone mechanism, which is missing in the deuteranopic observer; this observer showed a similar pattern of psychophysical results as the color normal observer (Fig. 2C), as did another observer tested with stimuli aimed at isolating the S-cone at equiluminance. This argues against the frequency-doubled response hypothesis. Also, psychophysical performance based on a frequency-doubled response should not be affected by polarity reversal, since there are two response peaks per cycle. These considerations argue against the frequency-doubled response hypothesis and further suggest that chromatic mechanisms have direct access to vernier mechanisms (see Section 4).

3.3. Effect of target separation: psychophysics

Others have shown that for targets of the same luminance contrast polarity, vernier thresholds increase steadily with target separation. If luminance contrast polarity is mismatched, vernier thresholds are higher at low target separation. As target separation is increased, vernier thresholds for the matched and mismatched polarity conditions converge (Levi & Waugh, 1996; Levi & Westheimer, 1987; O'Shea & Mitchell, 1990). If operation of local

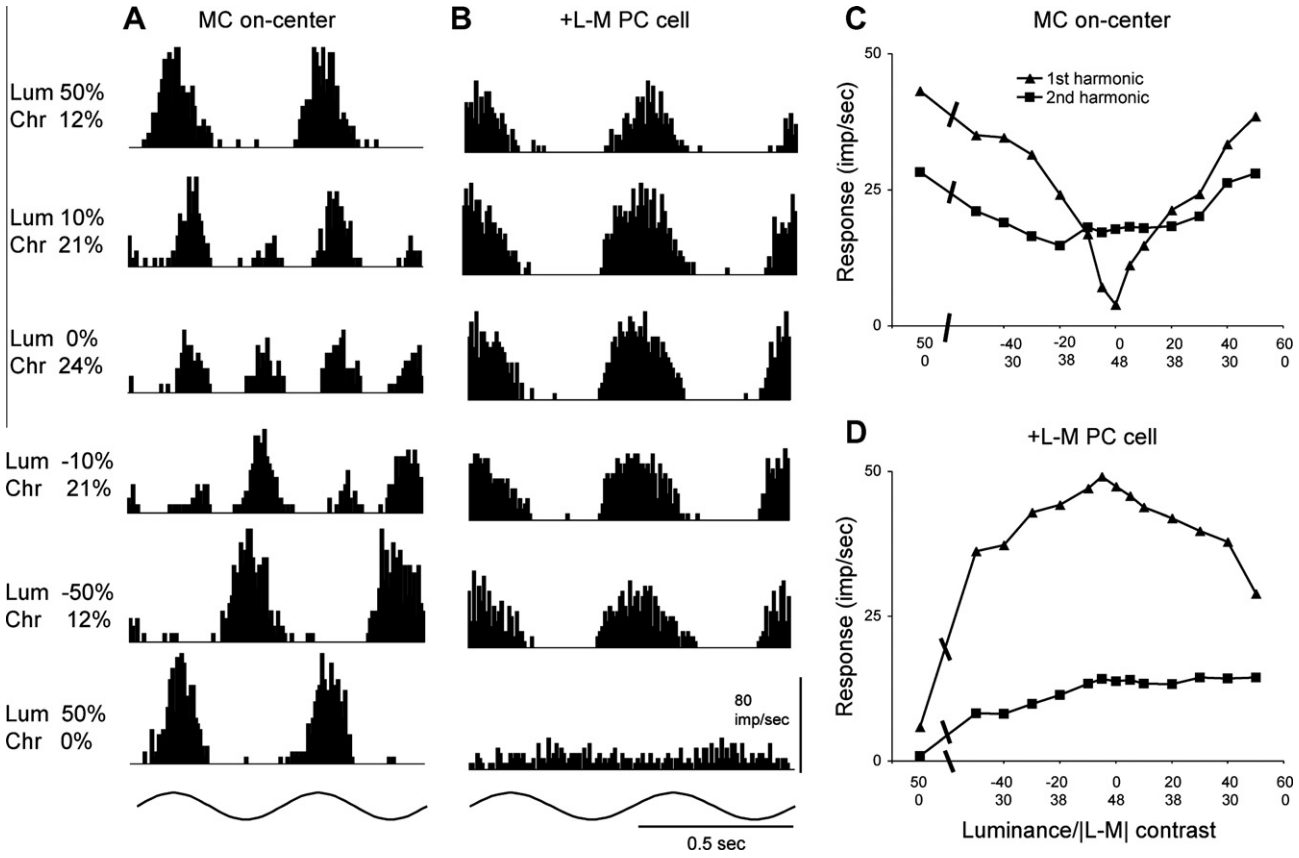

Fig. 3. Response histograms of a typical on-center MC (A) and a +L–M PC cell (B) and their 1st and 2nd Fourier harmonic amplitudes (C and D) to gratings of various luminance and chromatic contrasts. Mean cone contrasts are indicated alongside each pair of histograms. A marked 2nd harmonic response is present in the MC cell near equal luminance. Two cycles of 2 Hz stimulation, 64 bins/cycle. (C and D) First- and second-harmonic amplitudes of the responses of cells in (A and B) as a function of luminance ratio of the red and green grating components.

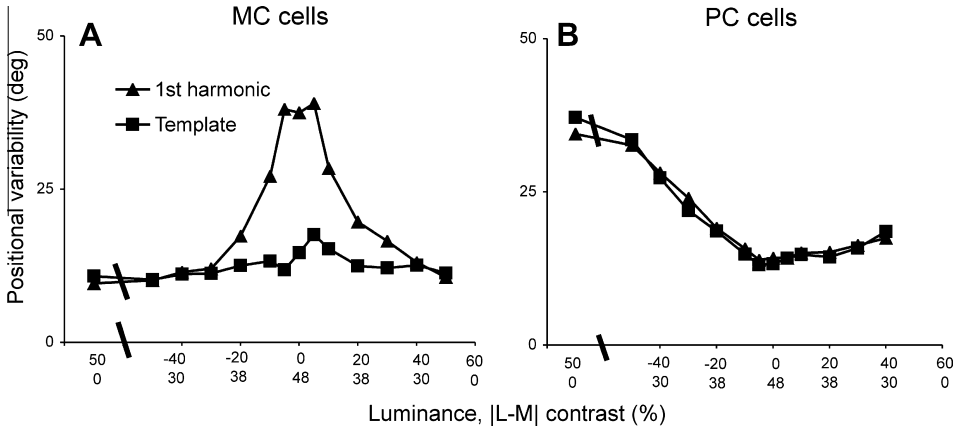

Fig. 4. Averaged angular standard deviation of response phases for 18 MC cells and 16 PC cells to gratings of various luminance or chromatic contrasts. The *x*-axis represents the luminance or chromatic contrast of each grating. Standard deviations have been calculated in two ways as described in the text.

filters (rather than 'local signs') underlies performance with both luminance and chromatic gratings, then the effect of separation should be similar in both cases, and we now test this hypothesis.

Fig. 5 shows the effect of a gap between the luminance and equiluminance chromatic gratings for two observers. Both observers viewed the hyperacuity stimuli foveally. The deuteranopic observer BBL used blue–yellow chromatic gratings that activate the S-cone mechanism. In both of the matched polarity cases, as target separation increases, so does hyperacuity threshold, although thresholds for chromatic gratings tend to be higher. For opposite polarity, thresholds are higher and stimulus separation has less effect over the range tested. Results from another trichromatic observer were similar (BC). These similarities suggest both luminance and chromatic mechanisms may access hyperacuity mechanisms in a similar way, consistent with some kind of local filter at low separation and a local sign mechanism at larger separation.

3.4. Effect of target separation: physiological analysis

Levi (1996) and others have suggested models for vernier hyperacuity; one aspect of these models is that linear filters of

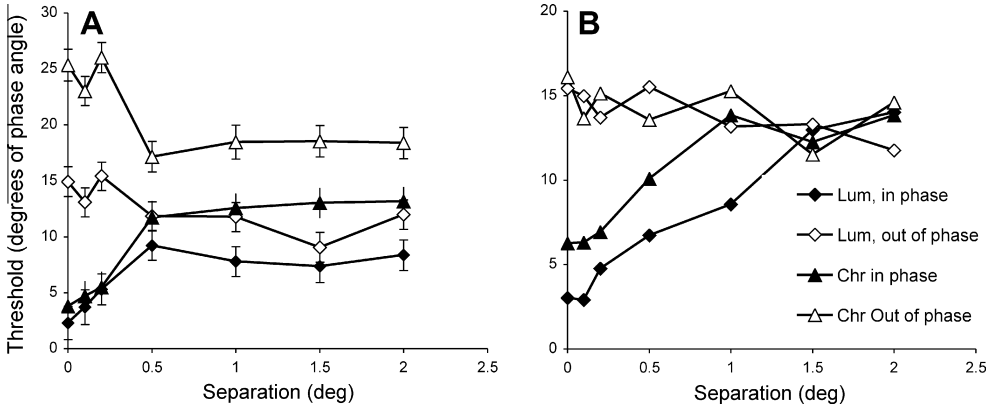

Fig. 5. Hyperacuity thresholds as a function of stimulus separation. Luminance and chromatic in- and out-of-phase conditions are shown. (A) Thresholds of a trichromatic observer to red–green targets. (B) Thresholds of a deuteranopic observer to blue–yellow targets.

limited spatial extent are responsible, and this may partially explain threshold increase with stimulus separation with same-polarity targets (Wilson, 1986). Vernier thresholds for opposite polarity conditions may depend on a local sign model, and performance based on this cue are not so sensitive to stimulus separation. In either case, a cortical mechanism must extract positional information from ganglion cell responses. The physiological context of this situation has yet to been addressed. Here we briefly consider the effect of target separation on ganglion cell responses, and some of the constraints imposed by noise in neuronal responses on vernier detection. Our goal is not to provide a comprehensive model, but to draw into focus some physiological properties that vernier models might incorporate.

We recorded responses from MC and PC ganglion cells to a pair of drifting gratings with various separations. The stimulus was always centered on the cell's receptive field, and the separation between the grating pair was varied from 0 to 120 arc min of visual angle for each of four phase offset conditions. Fig. 6A shows sketches of stimulus conditions as well as the response amplitude and phase of a typical off-center MC ganglion cell recorded in the parafovea. The *x*-axis represents separation between the grating pair in arc min visual angle. Different symbols represent grating pairs of different phase offset. For grating pairs of small phase offsets (0° and 22.5°), the ganglion cell gave vigorous responses at small stimulus separation, and the response amplitude decreased rapidly when separation increased, and the grating no longer covered the receptive field center. When separation exceeded the cell's receptive center but still stimulated the receptive field surround (~20–40 arc min), there is a 180° phase reversal of response and the response amplitudes are plotted as negative values. When the grating phase offset increased from 0° to 90°, the ganglion cell response amplitude decreased and response phase shifted. When the grating phase offset was 180° out-of-phase, the ganglion cell showed little response because responses to each half of the stimulus were out-of-phase and hence cancelled one another. The solid curves represent the fit of a difference-of-Gaussians receptive field model. Parameters are given in the figure legend; they are in the range found in the literature for this eccentricity. Similar responses were obtained from 8 other MC cells, both on and off center. Responses of PC cells were weak to luminance gratings, but were vigorous to red–green chromatic gratings, to which a similar pattern of responses were observed as in Fig. 6.

In terms of the psychophysical separation experiments of Fig. 5, inputs from a ganglion cell array to a central filter receiving inputs will decrease from those cells with receptive fields within the gap; it should be noted that although response amplitude may decrease, noise from these sources will remain similar (Sun, Lee, & Rüttiger, 2003). In addition, the phase reversed responses generated by the surround might be expected to affect the operation of such a central filter. The cells studied were from parafoveal retina, and receptive field sizes in the fovea would be smaller. How far the effects shown in Fig. 6A contribute to psychophysical separation effects remains to be determined.

With an array of ganglion cells, some receptive fields are centered on the stimulus pair, while other receptive fields are offset away from this point. We recorded responses from ganglion cells to a pair of abutting drifting gratings presented at various retinal locations offset relative to the receptive field center. The phase offsets between the two gratings was either 0°, 90°, or 180°. This latter case corresponds to the out-of-phase condition in the psychophysical experiments. Fig. 6B shows the response amplitude of the off-center MC ganglion cell to grating pairs presented at various locations relative to the cell's receptive field center. For 0° aligned grating pairs, the ganglion cell response amplitude or phase did not vary with stimulus location; the stimuli are identical for the ganglion cell. When the phase offset increased to 90°, the curve for ganglion cell response versus displacement from the receptive field center showed a decrease in amplitude and a gradual phase transition. Since the response to each half of the stimulus partially cancel each other, the response to the other grating segment is phase shifted. The cancellation was complete for 180° grating pairs. Similar data were obtained for seven other MC cells and for six PC cells with chromatic gratings. All showed similar behavior describable with a linear model. These results suggest that MC cell behavior to be consistent with a linear difference-of-Gaussians model and the model again fits the data satisfactorily. This argues against any Y-like non-linearities influencing the spatial position signal (Crook et al., 2008).

Under most in-phase conditions, psychophysical vernier thresholds are just a few degrees of grating phase. Fig. 6 shows that with such small phase offset, variation in ganglion cell's response amplitude is small, and information contained in response phase must be critical in a vernier context. We have previously reported positional precision of MC ganglion cell responses estimated from cell's response phase variation in such vernier contexts (Sun, Lee, and Rüttiger (2003) and Fig. 5). In Fig. 6, it is apparent that when there is a gap between a pair of gratings, and when the gratings are in counterphase (Fig. 6B, 180° condition), that the responses of ganglion cells over a region of retina around the grating boundary are decreased or abolished so that the similarity in the psychophysical results in not unexpected. However, to use this data as a direct basis for a vernier model involves further considerations, and some of these are taken up in Section 4.

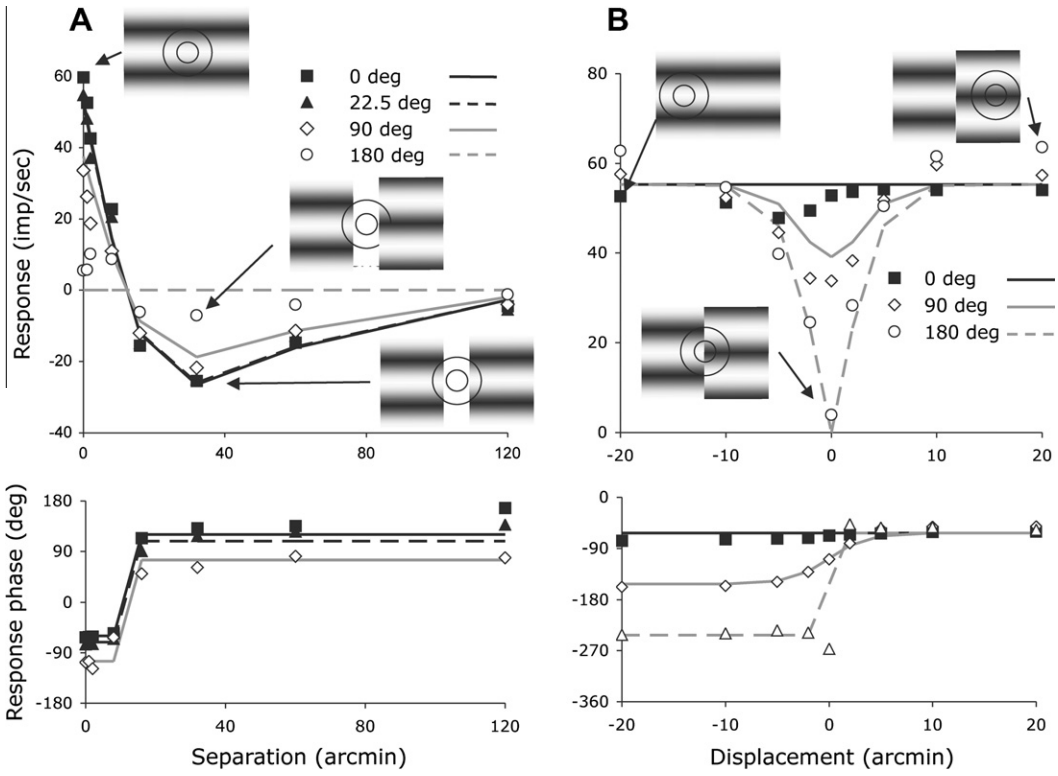

Fig. 6. Response amplitudes (top panels) and phases (bottom panels) of an off-center MC ganglion cell to grating pairs of various separation (left panels) or various location (right panels). Different symbols represent grating pairs of different phase. The two grating pair was always centered on the cell's receptive field in (A) and they are always abutting in (B). Lines represent the fit of a difference-of-Gaussians receptive field model, with center radius 6.8 arc min, surround radius 45 arc min, and surround weighting factor 0.075. The negative response amplitude represent the shift of response phase.

4. Discussion

Recently there has been considerable emphasis on spatial mechanisms that utilize chromatic information (see Shevell and Kingdom (2008) for review), but vernier performance with chromatic mechanisms has received less attention. One obvious hazard in such experiments is that small, sharp-edged equiluminant targets are likely to be subject to luminance artifacts due to chromatic aberration. Such artifacts with red–green targets are obvious to dichromatic observers (Rüttiger & Lee, 2000). The use of Gaussian or Gabor profiles (Krauskopf & Farell, 1991) or sinewave gratings, as here, tends to minimize this problem. Nevertheless, the first report of vernier thresholds with equiluminance targets (Morgan & Aiba, 1985) did note an increase in vernier threshold at equiluminance.

Krauskopf and Farell (1991) stressed that the cone contrast available with equiluminant patterns is less than with luminance patterns, and showed that after contrast was normalized to detection threshold, hyperacuity thresholds with Gaussian or Gabor targets were similar along all three cardinal directions in color space. However, examination of their data indicate that hyperacuity thresholds for luminance targets are lower than for chromatic targets at high spatial frequencies, especially for Gaussian profiles. These authors stressed the role of cone contrast and discounted a differential role for post-receptoral retinal mechanisms in this and a subsequent study (Krauskopf & Forte, 2002).

Evidence against the cone-contrast hypothesis was obtained when hyperacuity targets were presented on chromatic backgrounds (Rüttiger & Lee, 2000; Sun, Lee, & Rüttiger, 2003). For example, detection thresholds for blue targets superimposed over red backgrounds are very low in terms of luminance contrast (<0.5%), but under all chromatic and achromatic conditions hyperacuity thresholds were primarily luminance-contrast related. This was interpreted as the detection of the blue-on-red target being mediated by a chromatic mechanism (e.g., based on S cones), but hyperacuity by a luminance mechanism. Similar results were found with, for example, red targets on green backgrounds. Observers reported that low-contrast chromatic targets (e.g., red edges on a blue background) were detectable but their edges indistinct. This does not establish that chromatic channels do not have access to hyperacuity mechanisms; it only indicates that post-receptoral processing cannot be neglected.

The data presented here suggest a more nuanced interpretation. The results in Fig. 2 indicate an elevation of hyperacuity thresholds at equiluminance for the in-phase condition. Normalization to detection threshold (not shown) did not resolve this discrepancy. The out-of-phase condition results in a general elevation of threshold. When luminance contrast is present, the polarity of chromatic contrast does not influence thresholds except close to equiluminance, when it does become an important determinant of threshold. The simplest explanation of these results is that both luminance and chromatic channels have access to hyperacuity mechanisms, and the most responsive of them governs performance.

We have used grating targets rather than the bars and edges conventional in vernier experiments. Grating targets avoid chromatic aberration artifacts with equiluminant bars or edges. It remains to be shown if similar results may be obtained with more conventional vernier targets.

The presence of the frequency-doubled response to red–green modulation in MC cells complicates this interpretation. It has been suggested that this response may contribute to residual distinctness of equiluminant borders in the minimally distinct border task (Kaiser et al., 1990; Valberg et al., 1992) and the perception of movement of equiluminant patterns (Lee & Sun, 2009). The results in Fig. 5 suggest that spatial information could be derived from

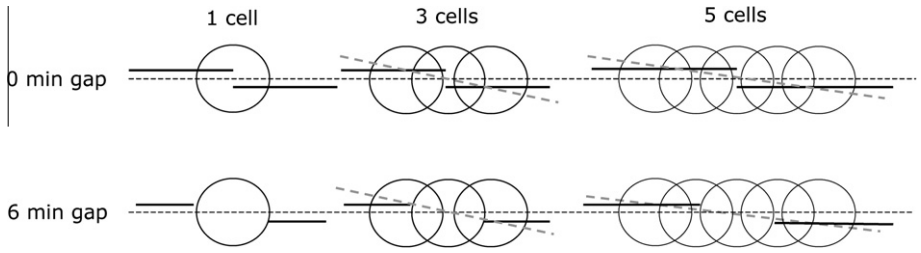

Fig. 7. Central filters that receive input from different numbers of ganglion cells. The solid black lines represent a pair of vernier stimuli with a small offset. The circles represent ganglion cells' receptive field centers. The gray, dashed lines indicate orientations of cortical filters that give the best response. Top panels show abutting vernier stimuli, and the bottom panels show vernier stimuli with 6-arc min separation.

such signals. However, one would expect that the frequency-doubled response might not be affected by polarity reversal of a red–green grating, since this non-linear response is an unsigned chromatic signal (Dobkins & Albright, 1993, 1994). Also, insofar as hyperacuity mechanisms involve linear filters derived from both on- and off-center cells, their function might be disrupted by such a non-linear response. It should be noted that, in the frequency-doubled response, on- and off-center MC cells respond in phase with each other to a chromatic grating, but at twice the grating spatial frequency. However, they respond out-of-phase with each other to a luminance grating with double the spatial frequency. Lastly, the pattern of psychophysical results was similar with gratings isolating S-cone mechanisms. There is no frequency-doubled response to such stimuli. Taken together, these arguments suggest that chromatic mechanisms do access spatial mechanisms responsible for vernier acuity, although they may deliver a less precise signal compared to that conveyed by achromatic mechanisms.

Further support for this hypothesis derives from the effect of target separation. Target separation is known to influence vernier thresholds for targets of matched and opposite contrasts in different ways. This was originally interpreted as indicating that, with targets of matched contrast, some linear filter operation determines vernier thresholds, while with opposite-contrast targets, 'local sign' is used as a cue (Waugh & Levi, 1993). However, masking experiments (Levi, Klein, & Carney, 2000; Waugh, Levi, & Carney, 1993) have not been entirely consistent with this interpretation. In any event, in our data the interaction between contrast polarity and target separation appears similar for both luminance and chromatic targets, which would suggest a commonality in the underlying mechanism. This is in keeping with the fact that the critical duration for vernier both with luminance and chromatic targets is similar (Sun & Lee, 2004). Observers reported that, for both luminance and chromatic gratings, when these were in phase alignment judgements were made based on the transitions of light to dark or red to green. When they were out of phase, judgements were made based on estimation of 'global' location of the grating bars.

Target separation will alter the ganglion cell inputs to central filters that might be responsible for vernier tasks; those ganglion cells with receptive field centers within the separation gap can no longer provide a positional signal, as sketched in Fig. 7. We measured responses of ganglion cells to pairs of drifting gratings separated by small gaps, with the receptive field situated at different loci relative to the gap, and with different phase offsets of the gratings (not shown). Response amplitude and phase changed as would be expected of a linear receptive field model. However, it proved difficult to relate these data to the psychophysical separation data in Fig. 6. Psychophysical separation effects occur over a distance (up to 0.5–1.0°) much larger than foveal receptive field centers. The receptive field centers of foveal MC cells have a Gaussian radius of ca. 0.02–0.04° in the macaque (reviewed in Lee, Martin, and Grünert (2010)), corresponding to a center diameter of 6–12 min, which is smaller than dimensions over which psychophysical separation effects occur.

A central filter receiving information from 2 or more ganglion cells has intrinsic orientation specificity, as in cells in striate cortex. Ganglion cell response phases show intrinsic variation or noise, so averaging over more ganglion cells along a contour will produce a more reliable orientation cue which might be used in hyperacuity judgements. However, averaging over more cells decreases the orientation cue which might be used as a basis for hyperacuity, as sketched in Fig. 7. This suggests there may be compromise between the optimal filter length and the maximal signal-to-noise ratio. However, pursuing this approach further is beyond the scope of this report. The difficulties of modeling filters that might account for vernier performance led to the suggestion that such filters adapt to stimulus conditions (Levi, McGraw, & Klein, 2000), which seems to avoid the issue of defining a unitary spatial mechanism for vernier.

As mentioned above, the role of chromatic mechanisms in spatial vision, for example in depth perception and texture segmentation, has been well documented (Shevell & Kingdom, 2008). How far such spatial chromatic mechanisms share a common substrate with channels thought to be involved in detection of chromatic differences remains unresolved. The critical duration for chromatic detection tasks is several hundred milliseconds (Swanson et al., 1987), but for chromatic vernier tasks is much shorter, of the order of 50–100 ms, similar to luminance vernier tasks (Sun & Lee, 2004). This might point to a more differentiated set of post-retinal chromatic mechanisms than usually supposed.

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