

Transient cells can be neurometrically sustained: the positional accuracy of retinal signals to moving targets

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The spatial accuracy inherent in retinal ganglion cell responses to moving targets was investigated by measuring trial-to-trial variability in response locus. When moving bars were used as stimuli, analysis of impulse trains showed that parafoveal cells of the magnocellular (MC) pathway provided a consistently accurate spatial signal over a range of target velocities up to ~8 deg/sec. Parvocellular (PC) pathway cells delivered less accurate signals even at low velocities, and their signals became even less accurate at higher target speeds. Human vernier performance in parafovea resembled the physiological MC-cell result, which suggests this feature of MC-cell behavior is functionally utilized. A similar result held with moving gratings; the highest signal-to-noise ratio for MC-cells occurred at low temporal frequencies. Psychophysical vernier thresholds to grating targets resembled phase variability of MC-cell responses as a function of temporal frequency. The analyses of physiological data utilized both the number of impulses a cell generates and their timing; MC-cells' responses may have low peak rates to slow moving stimuli compared to fast stimuli, but a spatially precise signal may be derived because many impulses are evoked at lower speeds. The results show that transient neurons can yield precise information about slowly moving stimuli, provided appropriate central mechanisms for extracting this information are present. Such central mechanisms would require either a long integration time or a suitable spatiotemporal filter that integrates over the ganglion array. Because accurate vernier performance can be achieved with brief presentations, the latter alternative is indicated.

Keywords: magnocellular, parvocellular, ganglion cell, vernier

Introduction

Evidence for transient and sustained channels in the human visual system was first derived from psychophysical observation (Kulikowski & Tolhurst, 1973; Legge, 1978; Tolhurst, 1975). Such channel concepts have since undergone significant modification (Anderson & Burr, 1985; Grossberg, 1991; Lennie, 1980; Stromeyer, Klein, Dawson, & Spillmann, 1982), but there is physiological evidence for pathways with different temporal properties at the subcortical level (Dreher, Fukuda, & Rodieck, 1976; Lee, Martin, & Valberg, 1989b; Lee, Pokorny, Smith, Martin, & Valberg, 1990). Cells of the magnocellular (MC) pathway display transient responses to a step change in luminance whereas responses of cells of the parvocellular (PC) pathway are more sustained. Cells of the MC-pathway exhibit a bandpass temporal modulation transfer function, whereas such functions for cells of the PC-pathway are more lowpass (Lee et al., 1990). It is often assumed that transient channels can yield little information about slowly changing or moving stimuli. Levi (1996) showed that vernier thresholds for drifting gratings remained

constant up to about 8 Hz and then increased. He suggested that PC-pathway contributed to thresholds at lower temporal frequencies and MC-pathway at higher temporal frequencies. In another study, Kontsevich and Tyler (2000) found that stereopsis was superior in a sustained stimulus regime and concluded that the PC-pathway was involved. Here we examine the assumption that the transient MC-pathway does not deliver accurate localization information to slowly moving targets.

The strategy adopted in these experiments was to measure ganglion cell responses to targets moving at different velocities and to compare physiological results with human performance. We analyzed the spatial variability of ganglion cell responses from trial to trial; the analysis revealed an unexpected result. With moving bars, a consistently accurate spatial signal was delivered by MC-cells up to ca. 8 deg/sec in parafovea. With moving gratings, the variability in response phase is least for MC-cells at low temporal frequencies. To compare psychophysical performance on a spatial task with the cellular data, we chose vernier performance as a measure of human spatial localization ability. The pattern of physiological results was similar to psychophysical

vernier performance of human observers with the same targets. Signals from transient neurons can therefore yield more information about slowly changing stimuli than has previously been assumed. Exactly how central cortical mechanisms may extract this positional information remains to be determined. [Mechler and Victor \(2000\)](#) recently showed that some form of spatial comparison by central spatiotemporal filters is necessary for vernier performance; temporal information alone is not sufficient. The current results would be consistent with this suggestion, and we suggest that evidence for transient and sustained channels in human vision reflects an interaction of properties of the retinal output and those of central processing mechanisms, rather than being derived from the properties of peripheral mechanisms per se.

Methods

Physiology

Stimuli

Visual stimuli were generated on a CRT video display (distance 2.26 m, frame rate 195 Hz). The luminance of the background was at 40 cd/m² and chromaticity of the background was (0.45, 0.47) in CIE x, y coordinates. Stimulus chromaticity was always identical to that of the background. In Experiment 1, the stimulus was a rectangular bar (4 × 240 arc min) moving over cells' receptive fields. The luminance contrast of the bar was fixed at 80% Michelson contrast. The velocity of the bar was varied from 0.5 to 32 deg/sec (0.5, 1, 2, 4, 8, 16, and 32 deg/sec). Movement distance was 1 deg visual angle, which is large compared to the size of receptive field centers (15 arc min) at the eccentricities tested. In Experiment 2, the stimulus was a drifting sinusoidal grating. The spatial frequency was 0.4 cycle/deg and luminance contrast 90%. The temporal frequency varied from 0.5 to 26 Hz (0.54, 1.08, 2.17, 4.34, 8.68, 13, 17.4, and 26 Hz).

Procedure

Ganglion cell recordings were obtained from the retinae of five anesthetized macaques ([Lee et al., 1989b](#)). Animal care procedures were approved by the animal care committee of the State of Lower Saxony. Neuronal activity was recorded directly from retinal ganglion cells by an electrode inserted through a cannula entering the eye behind the limbus. Cell identification was achieved through standard tests ([Lee et al., 1989b](#)). These included achromatic contrast sensitivity and responses to lights of different chromaticity. Additional tests (e.g., measuring responses to heterochromatically modulated lights) ([Smith, Lee, Pokorný, Martin, & Valberg, 1992](#)) were employed in rare cases when identification was equivocal. Receptive field eccentricities were between 4 and 8 deg.

The eyes were sutured to a ring during preparation, which minimized eye movement. During each condition of measurement, any residual systematic drifts of response position could be identified through the analysis technique. Occasional systematic drifts of 1 to 2 min of arc were found, and we assume them to be due to residual eye movements. These data were discarded. A 3-mm artificial pupil was routinely used. Gas-permeable contact lenses of the appropriate power were used to bring stimuli into focus on the retina.

Times of spike occurrence were recorded to an accuracy of 0.1 msec, and averaged histograms were simultaneously accumulated. For bar stimuli, numbers of presentations were 20, 20, 40, 40, 40, 40, and 60 cycles (for velocities 0.5, 1, 2, 4, 8, 16, and 32 deg/sec, respectively); binwidths of histograms were 16, 12, 6, 3, 2, 1, and 1 msec, respectively. For grating stimuli, numbers of presentations were 20, 20, 20, 40, 40, 40, 40, and 60 cycles (for temporal frequencies 0.54, 1.08, 2.17, 4.34, 8.68, 13, 17.4, and 26 Hz, respectively). For the bar stimuli, length of histograms recorded was 128 bins (not all bins are shown in Figure 1). Duration of histograms was extended beyond movement duration, to allow estimation of maintained firing and to capture responses at high movement speeds, which are delayed due to response latency. When stimulus presentation time is converted into retinal location, relative retinal positions of the moving bar beyond one arc deg are thus virtual values.

Psychophysics

Stimuli

The same display system as in the physiological experiments was used. The viewing distance was 3.60 m in Experiment 1 and 0.48 m in Experiment 2. In Experiment 1, the vernier stimulus consisted of two vertical bars (4 × 20 arc min) separated vertically by 4 arc min. The two bars were presented 5 deg below a fixation point. During the 185 msec presentation time, the bars were moved randomly from left to right or vice versa. In Experiment 2, the vernier stimulus consisted of two horizontal gratings (6.33 × 20 arc deg) separated horizontally by 11 or 5 arc min. The two gratings were presented 5 deg to the right or left of the fixation point. During the 150 msec presentation time, the gratings were drifted randomly upwards or downwards. Except for the difference in spatial structure due to the presentation of two targets, the luminance, chromaticity, and spatial frequencies of the stimuli and background were the same as in physiological experiments. For bar stimuli, the movement velocities were the same as in physiological experiment, and for grating stimuli, the temporal frequencies were 0.5, 1, 2, 4, 8, 13, 17, and 26 Hz.

To achieve a subpixel resolution in Experiment 1, the intensities of a row of pixels to the left and right of one of the bars were adjusted so as to shift the centroid of the

bar by the required amount (Morgan & Aiba, 1985). To ensure that relative positional information could not be derived from stimuli onset or offset locations, in some set of experiments, 50-msec masking bars were presented at both onset and offset of the bars. Presence or absence of the masks had no effect on thresholds.

Procedure

Observers viewed the visual target monocularly and pressed buttons to indicate the position of the leading bar (Experiment 1) or which grating has a phase shift upward (Experiment 2). A two-alternative forced-choice, random interleaved dual-staircase procedure was used; 71% correct values were estimated from staircase reversals and psychometric functions. For details see Rüttiger and Lee (2000).

Observers

Five observers participated in one or both of the experiments. Observers B.L., L.R., and H.S. are authors, and E.B. and J.K. are naïve observers. E.B., J.K., L.R., and H.S. have normal color vision as assessed with Neitz Anomaloscope, Ishihara pseudoisochromatic plates and Farnsworth-Munsell 100-Hue Test. Observer B.L. is a deuteranope. Observer H.S. is myopic and wore contact lens during experiments.

Results

Experiment 1. Moving bar

We recorded responses to moving targets of macaque retinal ganglion cells in parafovea. For each cell, the locus of the receptive field was determined and the target movement centered around this point. Figure 1a shows responses of a MC-pathway cell to a moving bar at different movement velocities, with time as the abscissa. Increasing target velocity causes the temporal duration of the response to decrease, as does total impulse number, which is represented by the area under the response histogram. Figure 1b shows responses of the MC-cell with the abscissa expressed as retinal locus. As movement speed increases, peak rate initially increases, and the spatial position of the response shifts to the right due to response latency. The width of the response curve remains similar at low target velocities at about 15 arc min, which is the expected size of receptive field center diameters of MC-cells at this retinal eccentricity (Lee, Kremers, & Yeh, 1998). At the highest speeds, the response begins to smear out spatially and decrease in amplitude. This is due to the dwell time over the receptive field center, which is ca. 25 msec at 10 deg/sec, becoming shorter than the duration of the initial peak of cell's impulse response function (ca. 25 msec at the retinal illuminance used [Lee, Pokorny, Smith, & Kremers, 1994]).

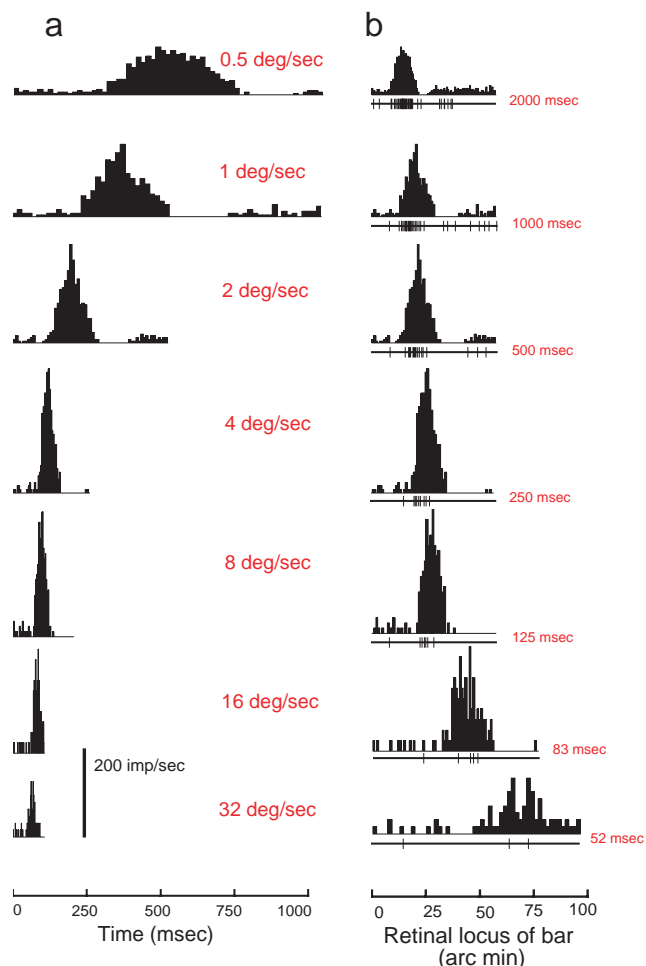


Figure 1. Responses of a MC-cell as a function of velocity. Averaged responses to an elongated bar (80% contrast) moved across the receptive field at different velocities are shown. a. The abscissa is expressed in time. b. The abscissa is expressed in retinal position. Below each histogram is an example of an impulse train from a single sweep. Distance of bar movement was 1 arc deg. At 16 and 32 deg/sec, responses are delayed due to response latency, and the relative retinal position of the moving bar greater than 1 arc deg is a virtual value.

Below each histogram in Figure 1b is shown an example of an impulse train of a single stimulus cycle. There are many impulses (30-40) at low velocity (0.5 deg/sec), but at high velocities, only few impulses are generated.

The relation of stimulus velocity to cells' peak firing rate and to number of impulses per response is illustrated in Figure 2, which includes averaged data from 11 MC- and 11 PC-cells from which complete data sets were obtained (consistent partial data sets were obtained from similar numbers of cells). Details of calculation of these measures are given in the legend. PC-cells generate weaker responses to achromatic stimuli than MC-cells (Kaplan & Shapley, 1986; Lee, Martin, & Valberg, 1989a), and their

responses are more sustained, so that peak rate does not rise as markedly with velocity as with MC-cells. The error bars in Figure 2b represent the standard deviation from cycle to cycle of number of impulses per response.

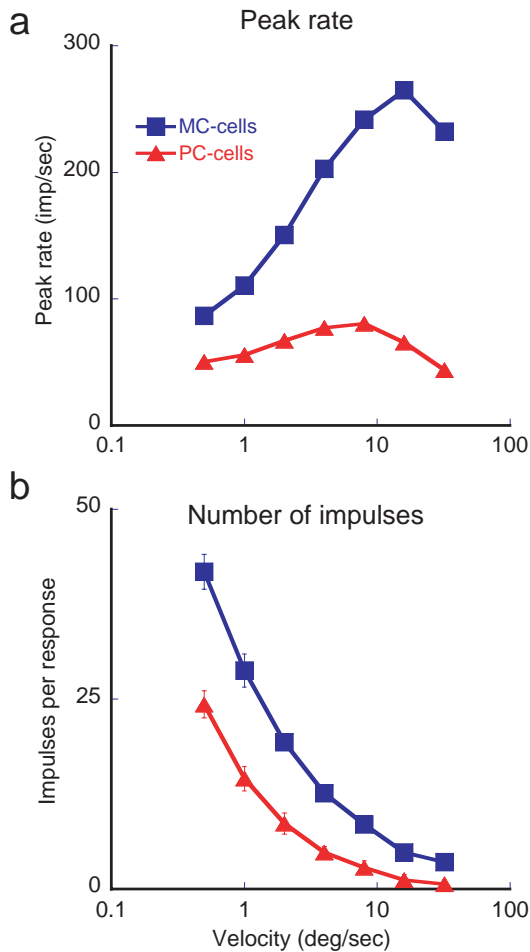


Figure 2. Peak rates (a) and number of impulses per response (b) as a function of velocity. Mean data are shown for 11 MC- and 11 PC-cells. The error bars in "b" indicate the standard deviation of the number of impulses per response from sweep to sweep. Cells' firing rates were found by moving a 5-bin (see "Methods" for binwidth) window to seek the peak response. Numbers of impulses per response were counted within a window defined by the period during which the response was above the maintained activity level. Both of these measures were robust against minor changes in window width.

The accuracy of the spatial signal inherent in the ganglion cell impulse train could be dependent on both number of impulses and their timing. To quantify the spatial reliability of the response, we used a template matching procedure (Sun, Lee, & Rüttiger, 2002). For each velocity, the response histogram was first smoothed with a Gaussian filter to obtain a matching template, as in Figure 3a. Each individual impulse train was shifted over the template until the locus of maximum correlation was found. This is illustrated in Figure 3b, where a number of

impulse trains from a MC-cell are displayed. Arrowheads indicate the best-fit location of each train to the template. The scatter of the best-fit positions is a fraction of the width of the template. We took the standard deviation of these loci as a measure of the accuracy of spatial localization by the cell, and termed it spatial variation. Temporal variation was calculated from the product of spatial variation and stimulus speed. To investigate the robustness of the analysis, we also tested a normal distribution as a template with similar width to the actual response histogram. This did not significantly affect the spatial variation obtained. We then tested the effect of varying the standard deviation of the Gaussian distribution. The pattern of results was robust against this manipulation until the width of the Gaussian was changed by a factor of more than two. We conclude that the results are not an artifact of the template matching procedure.

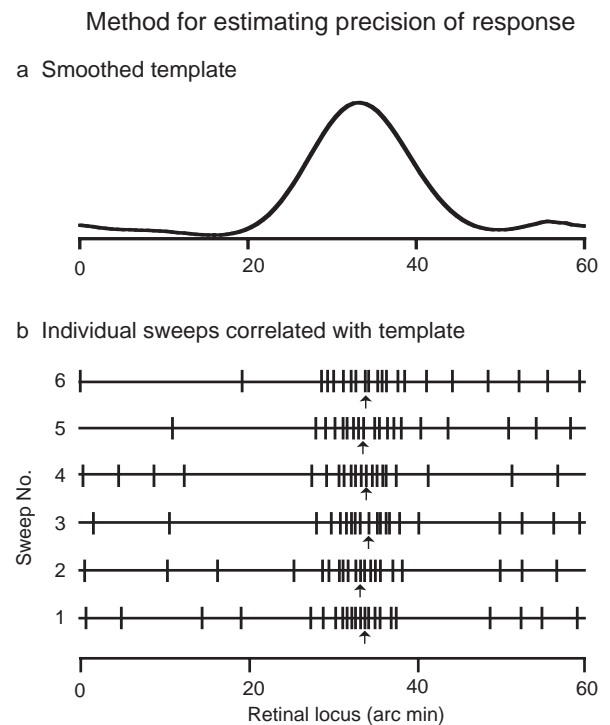


Figure 3. A method of defining precision of the spatial signal. a. A response template was generated by smoothing the response histogram with a Gaussian function (S.D. 4 bins). b. Impulse trains from individual sweeps were shifted over the template until the maximal correlation was found. A subset of individual impulse trains are shown. Arrowheads indicate the locus of maximal correlation. The standard deviation of these loci gives a measure of spatial reliability (termed here spatial variation). Stimulus velocity was 4 deg/sec.

The outcome of the analysis is shown in Figure 4. Spatial variation (Figure 4a) remains similar up to ca. 8 deg/sec for MC-cells and then rises, which implies that cells of the MC-pathway can yield a consistently accurate positional signal over a range of lower velocities. Responses of PC-cells show larger spatial variation than

those of MC-cells even at the lowest target velocity, and spatial variation of PC-cell signals increases rapidly with target velocity. Temporal variation (Figure 4b) decreases as a function of velocity for both MC- and PC-cells, and it reaches a minimum of 1 to 2 msec for MC-cells.

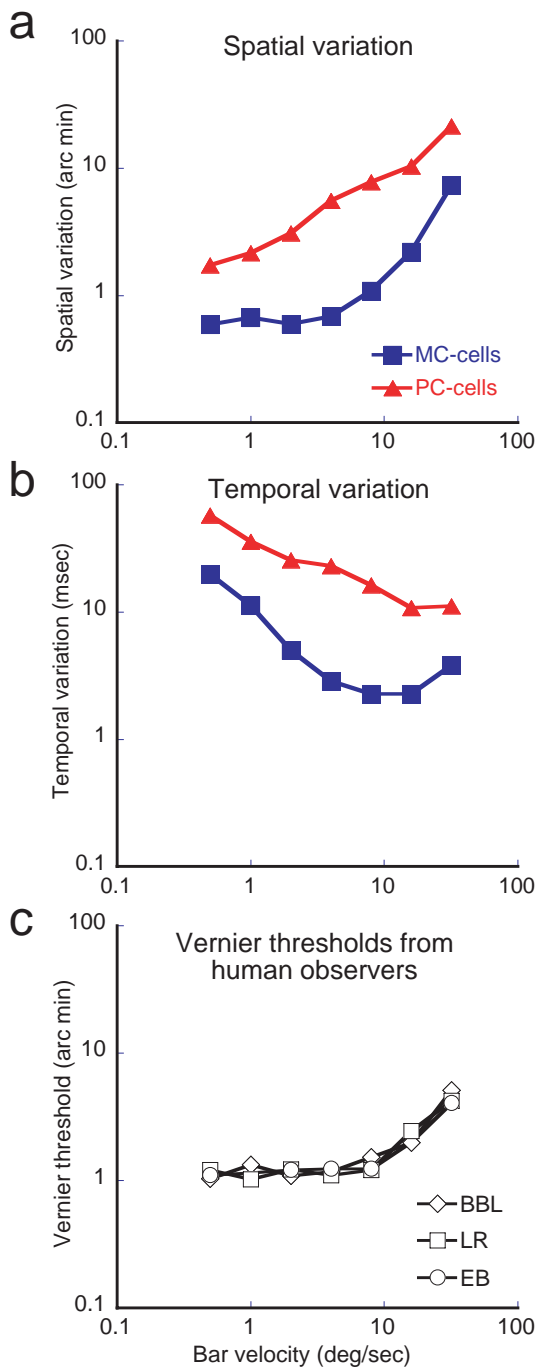


Figure 4. Standard deviations (SD) of response loci as a function of bar velocity in space (a) and time (b). Mean data are shown for 11 MC- and 11 PC-cells; data from on- and off-center cells were similar and have been combined; light bars were used for on-center cells, dark bars for off-center cells. c. Psychophysical vernier thresholds from three human observers as a function of bar velocity.

For comparison with the physiological data, we measured vernier thresholds as a function of velocity for a pair of bars at 5-deg retinal eccentricity, and these are shown in Figure 4c. Vernier thresholds remain constant over a range of velocities, and then increase. The shape of the relationship between vernier threshold and velocity strongly resembles MC-cell data, and furthermore the psychophysical thresholds are similar in absolute magnitude to the response precision of single MC-cells, as in other hyperacuity tasks (Lee, Wehrhahn, Westheimer, & Kremers, 1995; Rüttiger & Lee, 2000). The parafoveal vernier data resemble earlier foveal measurements. In the fovea, Westheimer and McKee (1975) showed that psychophysical thresholds for a vernier task involving pairs of moving targets remained constant with target velocity up to about 4 deg/sec, and subsequent work has confirmed this finding (Levi, 1996; Morgan, Watt, & McKee, 1983). In parafovea, the plateau extends up to 8 deg/sec in both the psychophysical and physiological MC-cell data, presumably due to the coarser retinal grain outside the fovea. The rapid deterioration in PC-cell accuracy with velocity does not match the psychophysical results.

One reason for the deterioration in cellular performance above 8 deg/sec is likely to be the smearing out of the response. At 16 deg/sec, a single cell's receptive field center diameter (15 arc min) will be traversed by the bar in 15 msec, which is shorter than the duration of the excitatory peak impulse response (about 25 msec [Lee et al., 1994]). The statistics of the impulse train making up the response are also likely to be a significant factor.

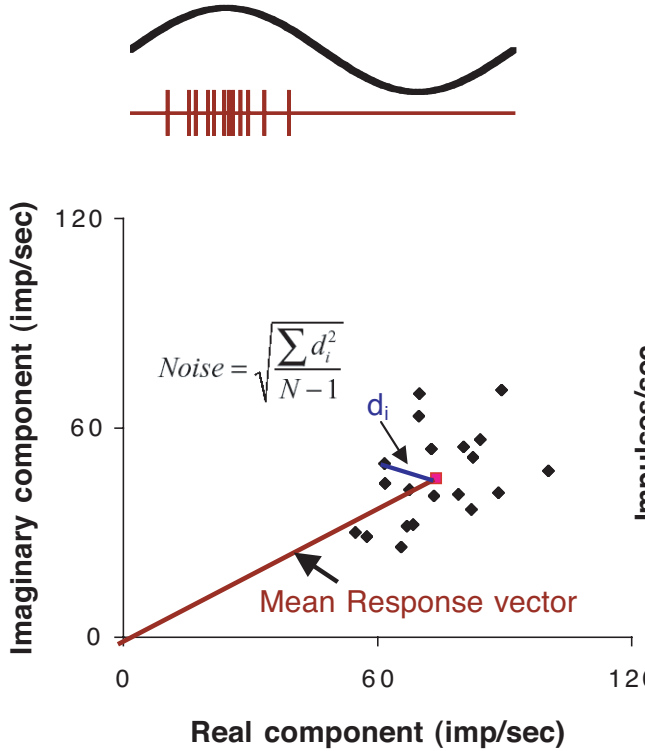
Experiment 2. Moving Grating

The invariant spatial accuracy of MC-cell signals independent of target velocity was unexpected of a transient pathway and led us to consider cell responses to other moving stimuli, such as gratings. Cell responses were recorded to gratings drifted across the receptive field at temporal frequencies from 0.54 to 26 Hz. The impulse train in response to the grating varies from cycle to cycle. To estimate response variability, responses to each cycle were Fourier analyzed, as in a previous study by Croner, Purpura, and Kaplan (1993). In Figure 5a, an example of a response to a single cycle is shown and below are plotted real and imaginary components from the Fourier analysis of a sample of cycles at a temporal frequency of 4.34 Hz. As in Croner et al. (1993), noise was calculated as

$$\text{Noise} = \sqrt{\frac{\sum d_i^2}{N-1}} \quad (1)$$

where d_i is the vector difference between response to cycle i and the mean response, and N is the total number of cycles. Croner et al. showed that at a fixed temporal frequency, the noise of the response was independent of contrast. We confirmed their result, as shown in Figure 5b. Response amplitude saturates as contrast increases and has been fitted by a Naka-Rushton function. Noise is almost independent of contrast.

a A single cycle of response is Fourier analyzed to estimate noise



b Response amplitude & noise vs. contrast

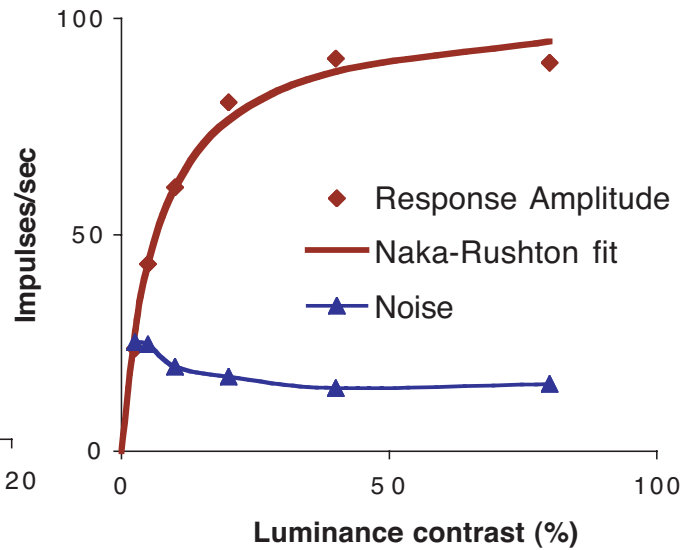


Figure 5. Analysis of noise in grating responses. Each cycle (one example of an impulse train shown) is Fourier analyzed to obtain real and imaginary response components. When plotted on these axes (a), noise can be defined as indicated in the text and in Equation 1. b. For a fixed temporal and spatial frequency, response amplitude increases with contrast following a saturating function, but response noise remains unchanged.

Figure 6 shows single-cycle Fourier analyses for a MC-cell at different temporal frequencies. The line segments indicate mean response vectors of each temporal frequency. As frequency increases, the response vectors rotate clockwise due to response phase delays. Both response amplitude and variability increase with temporal frequency. Averaged data from a set of MC- and PC-cells are shown in Figure 7. Response amplitude (Figure 7a) of MC-cells increases with temporal frequency more rapidly than that of PC-cells. Noise increases steeply as a function of temporal frequency in a similar manner for both cell types (Figure 7b). Figure 7c shows the ratio of response amplitude to noise. For both cell types, the highest ratio occurs at the lowest temporal frequency. Although it is unexpected in view of the transient responses of the MC-cells that the highest signal-to-noise ratio occurs with slowly moving gratings, this result is consistent with the results with moving bars, in that MC-cells potentially can yield precise information about slowly moving stimuli.

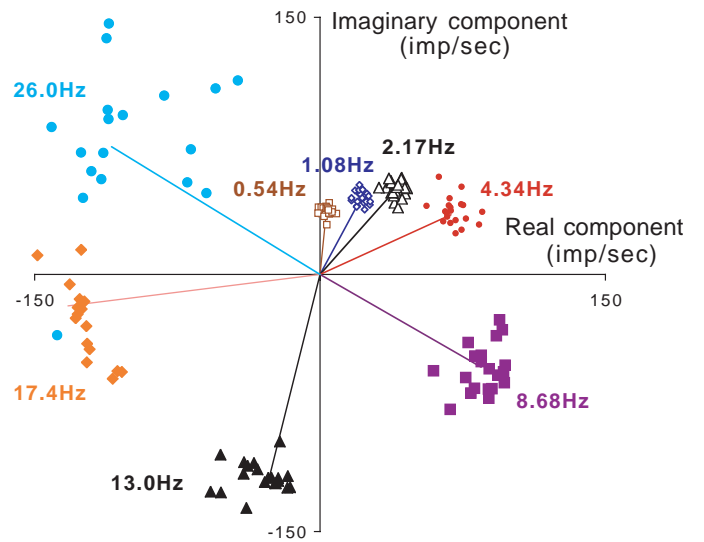


Figure 6. Real and imaginary components of a MC-cell's responses to gratings of different temporal frequencies together with mean response vectors (only 20 cycles per frequency are plotted for clarity). As frequency increases, the mean response vector rotates due to phase delay. Response amplitude and noise both increase.

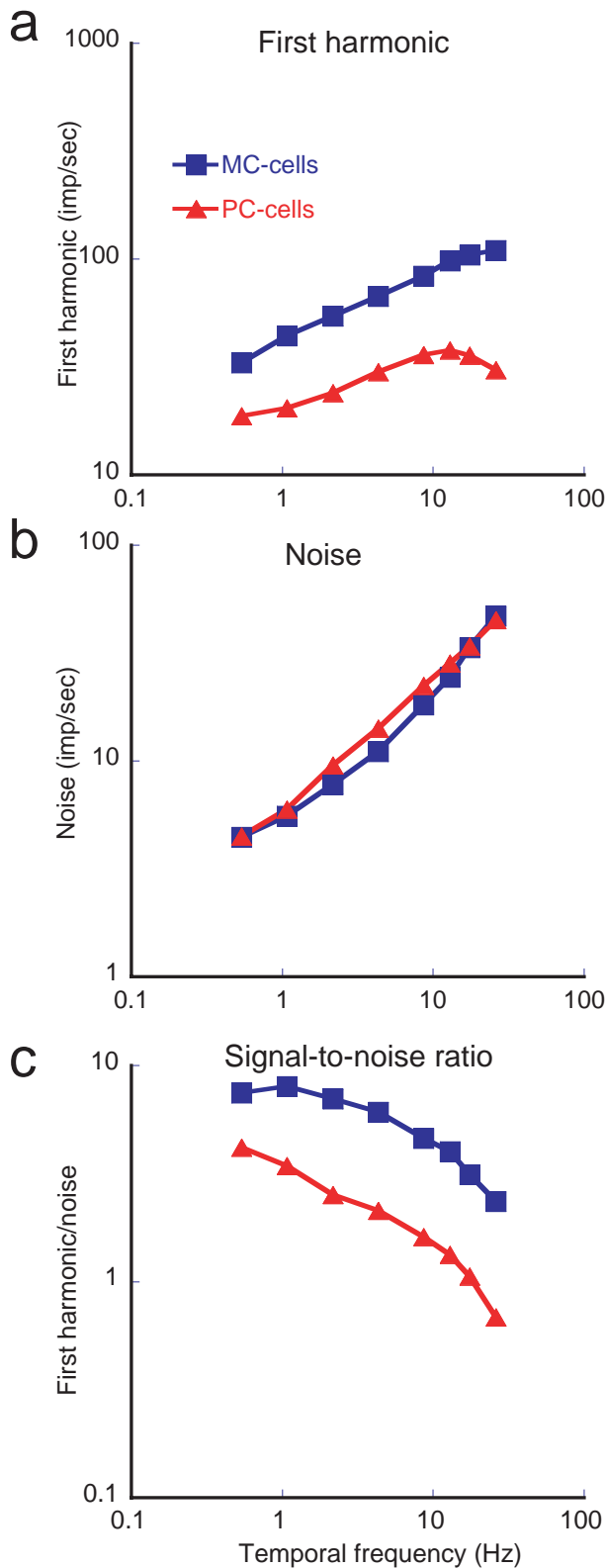


Figure 7. a. Response amplitude as a function of temporal frequency for MC- and PC-cell samples. b. Noise as a function of temporal frequency is seen to increase similarly for the two cell classes. c. The ratio of response amplitude to noise is shown to be maximal at low temporal frequencies for both cell classes.

We tested if the results in Figure 7 could be simulated by a simple description of impulse statistics. Maintained activity of macaque ganglion cells can be described by a low-order gamma process with refractory period (Troy & Lee, 1994). The impulse generation by the drifting grating was assumed to follow a sinusoidally modulated Poisson process with a refractory period. Such a model does not provide a complete description of neuron responsivity to repetitive stimuli (Reich, Victor, & Knight, 1998), but our goal was to test if such a simple model could capture the main features of the data. Probability of impulse generation was modulated around a maintained firing rate of 20 imp/sec with a 3-msec refractory period. The impulse trains so generated were analyzed in the same way as for the actual data. The amplitude of modulation of the probability of impulse generation was adjusted to give Fourier response amplitudes similar to those observed for MC-cells. In the simulation, noise increased steeply as a function of temporal frequency as in the actual data and thus signal-to-noise ratio decreased. We conclude that the results of Figure 7 do not require any special mechanism of impulse generation but are a consequence of impulse statistics.

It remained to be shown if the high signal-to-noise ratio in MC-cell responses at low temporal frequencies is behaviorally utilized by central mechanisms. We again consider this possibility in the context of a vernier task. Response phase is assumed to be the relevant parameter for coding spatial location. We therefore estimated the angular standard deviation of response phase (Figure 8a) from the following equation (Batschelet, 1981).

$$\sigma_{\phi} = \frac{180}{\pi} \sqrt{2 \left(1 - \sqrt{\left(\frac{\sum \cos \phi_i}{N} \right)^2 + \left(\frac{\sum \sin \phi_i}{N} \right)^2} \right)} \quad (2)$$

where ϕ_i is the vector angle between cycle i and the mean response, and N is the total number of cycles.

Mean data for MC- and PC-pathway cells are shown in Figure 8b. For the MC-pathway, standard deviations remain similar up to ca. 3 Hz and then increase, whereas for the PC-pathway standard deviations are higher than the MC-pathway deviations by a factor of 2 (i.e., spatial accuracy of the signal is lower) at the lowest frequency tested and then increase steadily. Psychophysical vernier thresholds for pairs of gratings at 5 deg eccentricity are shown in Figure 8c. Vernier thresholds remained unchanged up to ca. 4 Hz, and then increased with temporal frequency. This result replicates foveal data obtained by other studies (Levi, 1996). The psychophysical data thus showed similar pattern to the MC-pathway cells, which is consistent with the hypothesis that the information delivered by MC-cells is centrally utilized.

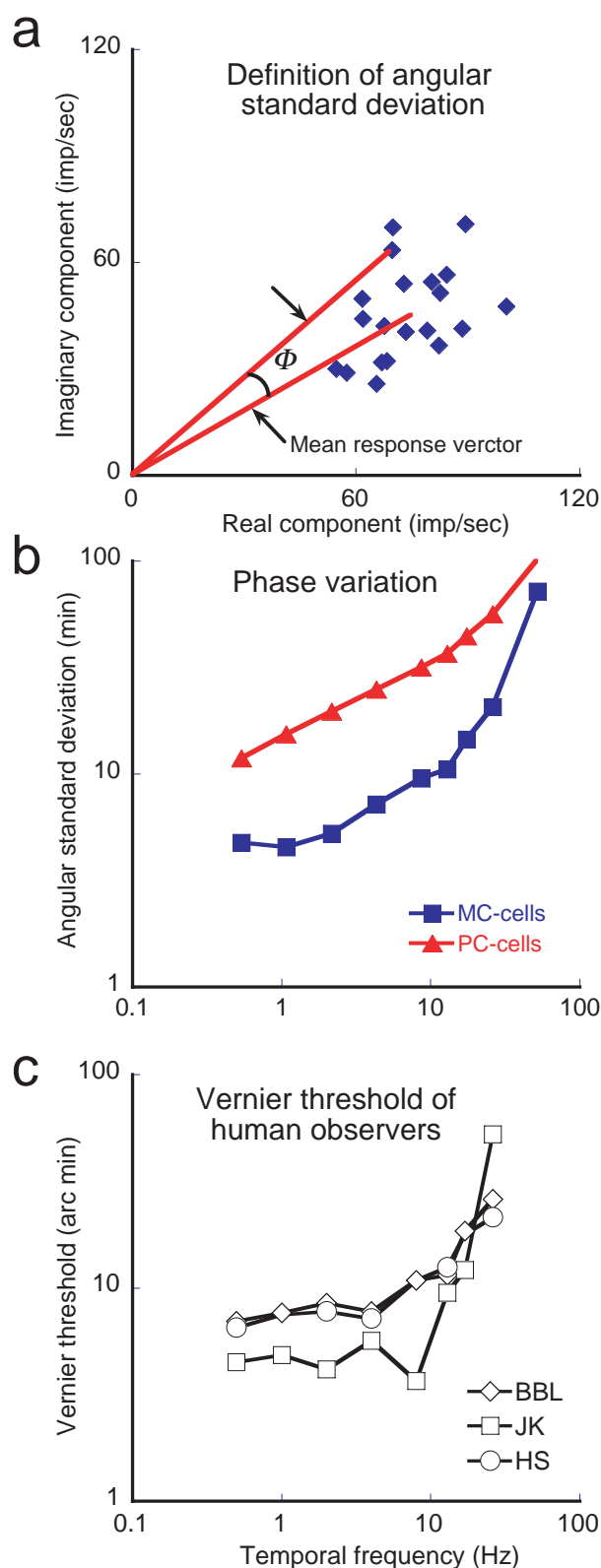


Figure 8. a. Angular standard deviation of response phase is calculated as in Equation 2. b. Angular standard deviation of response phase as a function of temporal frequency for MC- and PC-cells. c. Psychophysical vernier thresholds from three human observers as a function of grating temporal frequency.

Discussion

The goal of the current study was to estimate the spatiotemporal precision inherent in ganglion cells' signals. Vernier tasks, as an unparalleled example of spatial localization, provide a psychophysical benchmark against which cell data may be compared. Central mechanisms responsible for vernier performance may take alternative forms, e.g., independent cortical filters for each vernier target or activation of a single spatial filter by paired targets (Beard, Levi, & Klein, 1997; Burbeck & Yap, 1990; Klein & Levi, 1987; Levi & Klein, 1990; Morgan & Regan, 1987; Watt & Morgan, 1983; Wilson, 1986). Signal-to-noise ratio of the retinal output must provide a limiting factor for performance for both these alternatives. Thus, it is the similarities of curve shape between physiological and psychophysical data in Figures 4 and 8, rather than absolute level, which suggest a link between the cellular and psychophysical performance.

It has been assumed (Kontsevich & Tyler, 2000) that the transient response of the MC-pathway would cause it to yield positional information of low accuracy at slow stimulus speeds, but we show here that this need not be the case. The MC-pathway data in Figures 4 and 8 show that the MC-cells appear well adapted to deliver consistently accurate positional signals over a range of slow target velocities, and this pattern of behavior is consistent with human vernier performance. The MC-pathway provides the main input to the parietal cortical stream responsible for motion and positional processing (Merigan & Maunsell, 1993), and the velocity independence of the positional accuracy of MC-pathway signals is likely to be valuable in other spatial contexts.

In contrast to MC-cells, the spatial information delivered by PC-cells appears to degrade rapidly as target velocity increases (Figure 4). The greater numerosity of cells of the PC-pathway might provide the possibility of integrating over large numbers of cells to compensate for the low positional accuracy of individual neurons. However, it is unlikely that integration over large numbers of cells to improve signal-to-noise ratio is compatible with maintaining high spatial accuracy.

It is thought that visual information in neuronal spike trains may be encoded either in response firing rate (Shadlen & Newsome, 1996) or in response structure, i.e., the timing of individual impulses (McClurkin, Gawne, Optican, & Richmond, 1991). At lower velocities, the MC-cells give extended response with many impulses. Under these conditions, precise timing of individual impulses is not likely to play an important role. At higher velocities, few impulses are delivered and the timing of individual impulses is presumably critical in providing spatial information. At 8 to 10 Hz, MC-cell signals can reach temporal precision of about 1 to 2 msec (Figure 4b). This is consistent with psychophysical studies (Carney, Silverstein, & Klein, 1995; Fahle & Poggio,

1981; Levi, 1996; Mechler & Victor, 2000; Morgan et al., 1983), which suggest that temporal accuracy in the millisecond range is involved in vernier performance at high velocities. Neurophysiologically, a variety of recent studies have shown that in central processing by cortical neurons temporal information can also be signaled with millisecond accuracy (Mainen & Sejnowski, 1995).

The resemblance between the accuracy of MC-cell positional signals and psychophysical vernier performance suggests that this information delivered by MC-cell is utilized by central mechanisms. How can this be achieved at low velocities? The template matching and Fourier analyses use time windows of hundreds of milliseconds or more, but human vernier thresholds with moving targets do not improve much after presentation times exceed 50 to 100 msec (Morgan et al., 1983; Westheimer & McKee, 1977). At least two possible cortical mechanisms may be conceived. One possibility is that a cortical mechanism uses an analysis window of fixed duration independent of target velocity. We tested this possibility on our neurophysiological data and found that, for example, with a Gaussian template of 50-msec standard deviation, position of slow-moving targets was poorly estimated, and the match between physiology and psychophysics became unsatisfactory. The second possibility is that instead of deriving information from a single cell with a long time window, some sophisticated spatiotemporal filter can be used to analyze the differential output from a small group of cells within a brief time window. Recently, Mechler and Victor (2000) reviewed some of the requirements for central mechanisms for vernier tasks and concluded that temporal asynchrony alone does not suffice. They concluded that tuned spatiotemporal integrating mechanisms activated by motion signals are involved, and spatial integration and comparison are essential. The current results would be consistent with this view.

With low bar velocities and brief presentation times, we estimated that only a few MC-cells would be swept during the psychophysical exposure duration in the vernier task. For example, at 0.5 deg/sec, taking into account coverage factor (Grünert, Greferath, Boycott, & Wässle, 1993), receptive fields of 4 to 8 cells would be swept by each (20 arc min) bar. If a limited number of ganglion cells can contribute information, each cell must contribute a signal of precision comparable to psychophysical performance, because improvement by pooling over cells is limited. Our data are consistent with this interpretation. When interaction between cell outputs occurs, a direct relation between retinal physiological data and psychophysical thresholds may break down. For example, psychophysical vernier thresholds tend to plateau at very high contrasts, but Rüttiger and Lee (2000) showed that spatial precision of ganglion cell signals continues to increase with contrast. Detailed comparisons of this sort, including both spatial and contrast parameters, may help define more precisely cortical filters that handle the retinal signal.

Response amplitude curves of MC-cells peak at fast velocities (Figure 2a) and high temporal frequencies (Figure 7a). The MC-pathway is thought to provide the physiological basis of detection of uniform field luminance modulation (Lee et al., 1990). In such detection experiments, psychophysical thresholds are a bandpass function of temporal frequency, and appear to correlate with cellular peak rate per se, rather than signal-to-noise ratio. In comparison, we show here that psychophysical vernier thresholds for bars and gratings are a lowpass function of temporal frequency, and correlate with signal-to-noise ratio (Figure 7c), rather than cellular peak rate. This difference between luminance modulation detection and the spatial vernier judgement presumably arises in the mode of operation of cortical detection mechanisms. Two mechanisms with different spatiotemporal characteristics may be involved in the two types of task. Alternatively, the same mechanism may be involved but in the absence of spatial context it can operate only on the basis of cells' peak firing rates. Introduction of spatial context, e.g., by adding a surround, drastically changes the shape of the luminance detection temporal characteristic (Brown, 1965; Spehar & Zaidi, 1997; Watson, 1986), but this might be consistent with either alternative. Comparison of physiological and psychophysical data in other spatiotemporal contexts may clarify this issue.

Conclusions

Based on neurometric analysis of cell impulse trains, signals from transient neurons, e.g., MC-cells, can yield significant information about slowly changing stimuli. A close parallel between MC-cell data and psychophysical vernier performance suggests that central cortical mechanisms may extract this positional information from transient responses through the use of appropriate spatiotemporal filters. We suggest that evidence for transient and sustained channels in human vision reflects an interaction of properties of the retinal output and those of central processing mechanisms, rather than being derived from the properties of peripheral mechanisms per se.

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Footnote

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