
Comparison of ganglion cell signals and psychophysical localization of moving targets can help define central motion mechanisms

Barry B Lee§, Lukas Rüttiger¶, Hao Sun

SUNY College of Optometry, 33 West 42nd Street, NY 10036, USA; e-mail: blee@sunyopt.edu;

§ also at Department of Neurobiology, Max Planck Institute for Biophysical Chemistry, am Faßberg 11, D 37070 Göttingen, Germany

Received 5 January 2004, in revised form 13 August 2004; published online 15 June 2005

Abstract. Vernier acuity thresholds can be related to visibility of targets. This is considered in relation to retinal signals. Spatial precision of macaque ganglion cell responses to moving targets was assessed by neurometric analysis and compared with psychophysical performance. Under some conditions the amplitude of ganglion cell signals per se may relate target visibility to spatial precision of psychophysical performance. Other conditions are more complex; we suggest central mechanisms may adapt their properties, eg their dimensions, depending on the stochastic properties of ganglion cell signals. Thus, the relation of Vernier acuity to the visibility of targets is a rule of thumb which has a complex relation to physiological substrates.

1 Introduction

One of the determinants of Vernier acuity is the precision inherent in the retinal signal. We have recently compared the precision of ganglion cell signals to moving targets with Vernier performance by using a form of neurometric analysis (Rüttiger et al 2002; Sun et al 2004). The transient, magnocellular (MC) pathway was found to give accurate positional signals even with slow target movement. At low velocities, peak impulse rates are low but the number of impulses is high, and both the number and timing of impulses are important in determining the signaling precision of a cell. MC cell spatial precision closely resembled psychophysical performance, implying that cortical mechanisms must be able to make use of these signals. We consider here other aspects by which the structure of the impulse trains leaving the retina might constrain how cortical mechanisms handle retinal signals. It should be noted that we do not suggest that we have identified Vernier mechanisms per se; Vernier is a convenient metric to gauge human spatial performance.

A number of authors have pointed out that Vernier thresholds are related to the visibility of a target, eg when target contrast is normalized to detection threshold, Vernier thresholds become similar (Waugh and Levi 1993). One reason for this may lie in the retinal output; if different targets evoke neural responses of different size, then detection thresholds may differ. Normalizing contrast to detection threshold will make the neural response similar in amplitude, and yield responses of similar precision. We show that it is possible to find examples where this is the case. However, we also show more complex examples which indicate that the ways central mechanisms handle retinal signals are flexible and sophisticated, and likely to be modified to make best use of the stochastic properties of the retinal output.

2 Methods

A detailed description of methods may be found in Rüttiger et al (2002). In brief, neuronal activity was recorded from retinal ganglions of the anesthetized macaque.

¶ Present address: University of Tübingen, D72076 Tübingen, Germany.

Procedures were approved by the Animal Care and Use Committee of SUNY Optometry and conformed to the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research. Psychophysical thresholds were obtained from human observers by staircase methods. Informed consent was obtained from observers according to a protocol conforming to the Declaration of Helsinki and approved by SUNY Optometry Institutional Review Board. The identical visual display and the same stimuli were used in physiological and psychophysical experiments. Stimuli were pairs of Vernier targets varying in dimensions, velocity, and contrast. They were usually presented 5 deg ventral to a foveal fixation point. Observers were practiced in fixation, and some controls were made in which the trial was presented randomly above or below the fixation point. Details are given in text and figure legends.

The spatial precision of ganglion-cell signals was estimated by a template matching method (Rüttiger et al 2002). A response template was generated by smoothing the average response. The impulse train of a single response was correlated with the template at a given locus, the impulse train shifted by 100 μ s and the correlation repeated. The point of maximum correlation was taken as a 'best estimate' of the response locus. The standard deviation of these response loci was estimated; we term this the spatial precision of cell signals. About 30 sweeps were required to obtain reliable estimates of spatial precision, and at least this number of stimulus repetitions was done for each condition.

We consider here three target configurations. These are the effect of target width on cell precision and psychophysical thresholds, the effect of Vernier target contrast, and the effect of Vernier target contrast polarity.

3 Results and discussion

We have previously reported on the precision of ganglion cell signals to moving targets and gratings (Rüttiger et al 2002; Sun et al 2004). We consider here stimulus conditions in which psychophysical data appear directly related to the ganglion cell signal, and instances in which the relation is less obvious.

3.1 *Effect of target width on precision of responses*

We recorded from ganglion cells using bar and edge targets moving at different velocities. Figure 1a shows the precision of the response of cells as a function of velocity for a 4 deg edge and a 4 deg \times 10 min of arc high-contrast bar. Precision of response is defined as the sweep-to-sweep standard deviation of the response locus, as outlined in section 2. For both targets, MC cell precision is independent of target velocity up to ~ 8 deg s^{-1} , but then deteriorates more rapidly for the bar target than for the edge. PC cell precision decreases steadily with velocity. Figures 1c and 1d show Vernier performance for pairs of parafoveally presented targets for two observers; a third observer (not shown) yielded similar results. As in the original study of Westheimer and McKee (1975), threshold is initially independent of target velocity but then increases, to a greater extent for the bar than for the edge. We have argued (Rüttiger et al 2002) that the similarity in shape between the Vernier threshold and MC cell curves indicates that this cell class forms the physiological substrate of the task.

The difference in MC cell precision above 8 deg s^{-1} is due to a difference in response amplitude to bars and edges. Figure 1b shows peak rates for the two conditions. These are similar at low velocities but diverge at higher speeds. This is due to the short dwell time of the bar over the field center at high velocity. For a speed of 32 deg s^{-1} and a center of 20 min of arc diameter, dwell time is ~ 10 ms, which is comparable in duration to the MC cell impulse response function at the luminance level used (Lee et al 1994). We suggest that this example illustrates that, under some circumstances, change in cell responsivity may directly be related to performance.

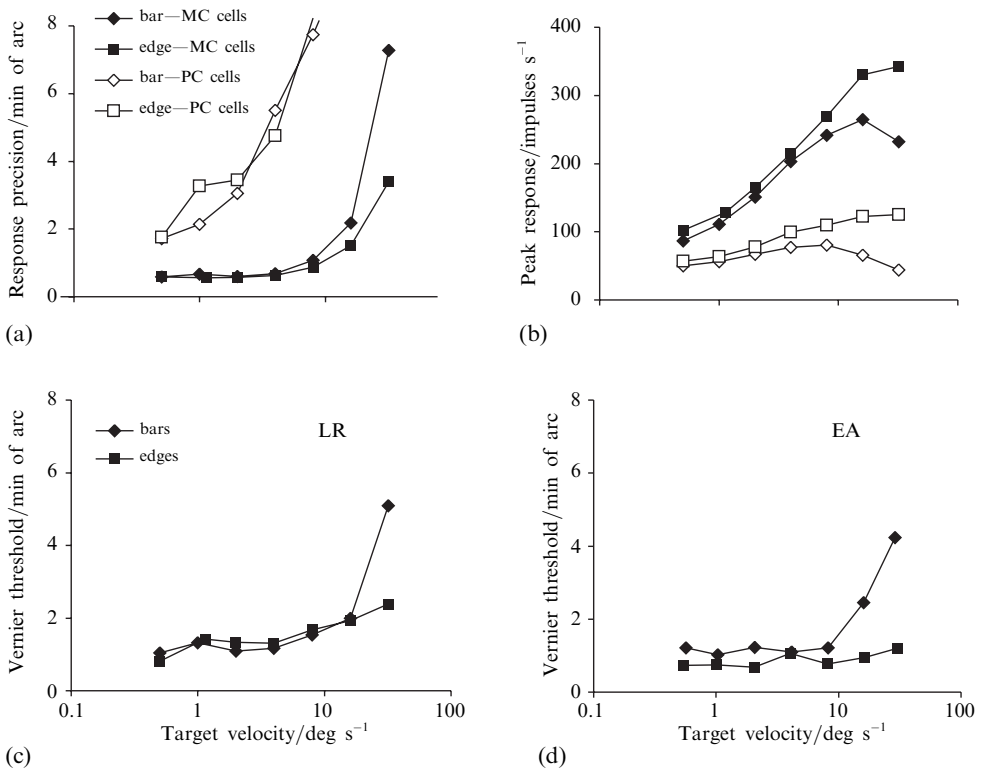


Figure 1. (a) Spatial precision measure as a function of target velocity for a 4 deg edge and for a 4 deg \times 10 min of arc bar (80%) contrast. Spatial precision measure derived through template matching method. Mean data shown are for 11 PC and 11 MC cells. Data combined for on-center and off-center cells, for targets of appropriate polarity. (b) Mean peak rates (50 ms window) for same-cell samples. (c) and (d) Psychophysical Vernier thresholds for pairs of the same targets for two observers (LR, EA). Targets presented at 5° eccentricity in ventral visual field. Thresholds determined by staircase procedure.

3.2 Effect of target contrast

Changes in response precision are also dependent on target contrast. Figures 2a and 2b show spatial precision of MC and PC cells for moving bar targets at 1 and 4 deg s⁻¹, and the associated peak response rate. Spatial precision improves with contrast, since response amplitude increases with contrast. The regression line shown has a slope of -0.96 , with little indication of saturation. For PC cells, a spatial signal only became apparent at high contrast. In figure 2c equivalent parafoveal psychophysical data are presented for two observers. Vernier thresholds decrease with contrast, with some indication of a high-contrast plateau. The regression line shown has a slope of -0.62 , which is typical of Vernier contrast relations (McKee 1991). There is thus a discrepancy between the neurophysiological and psychophysical results.

Analysis of neurophysiological data required a modification of the standard procedure which might account for this discrepancy. It was found that at low contrast some stimulus sweeps failed to evoke a detectable response, so that the template-matching procedure delivered a random result, ie on some sweeps the movement of the bar was localized close to the receptive field but on others insufficient impulses occurred for detection of the target by the algorithm. These sweeps were discarded. This is illustrated in figure 2d, in which sample responses are shown for 50% and 15% contrast. At the higher contrast every sweep elicits a clear response. At low contrast some sweeps (arrowed) fail to elicit a response. The percentage of sweeps eliciting

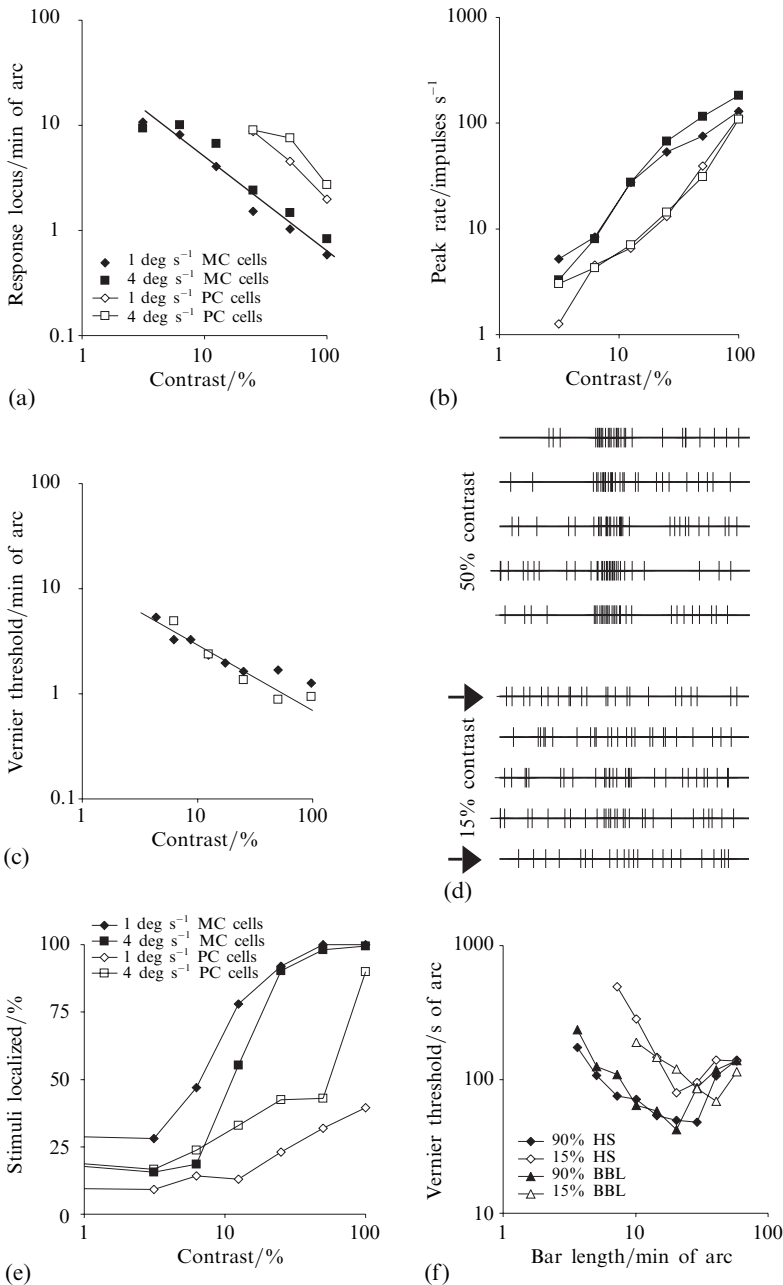


Figure 2. (a) Relation of precision of cell signals to contrast at two velocities. Bar target, 8 min in width, 4 deg in length. Mean of 8 MC, 6 PC cells. Data not plotted when <25% of targets 'detected' by cells. Regression line slope: -0.76 . (b) Relation between response amplitude and contrast, 50 ms peak window. MC cells responses do not saturate on log/log coordinates. (c) Psychophysical thresholds as a function of contrast for pairs of the same-edge targets, 5° eccentricity for two subjects (LR, EB). (d) Examples of MC cell spike trains to 1 deg s⁻¹ edge at high and low contrast. At high contrast every sweep evokes a response, at low contrast some sweeps (arrowed) fail to evoke enough extra impulses to be detected by the algorithm. (e) Percentage of 'detected' targets for MC ($n = 8$) and PC ($n = 6$) cells as a function of contrast. Criterion for detection was correct estimation by the algorithm of the target location within the firing rate increase of the template. (f) Psychophysical thresholds as a function of contour length at two contrasts. Edge targets, 4 deg s⁻¹, 1 min of arc separation.

a localizable response is plotted as a function of contrast for the two target speeds in figure 2e. For MC cells, even at moderate contrasts (20%), not all sweeps are localized; for PC cells, even at high contrast, not all sweeps are localized.

The result in figure 2d, from many sweeps and a single cell, is presumably transferable to the cell array, with many cells and a single sweep. At low contrast, presumably not all cells deliver a useful spatial signal. Cortical analysis mechanisms must handle such properties deriving from the stochastic properties of cell firing. One obvious way this might occur would be to extend spatial summation along a contour at low contrast, and we investigated this possibility psychophysically. We measured Vernier thresholds as a function of line length for pairs of bar targets. For foveal viewing of high-contrast targets, Vernier thresholds plateau at 5–10 min of arc bar length (Westheimer and McKee 1977). With high-contrast parafoveal targets (figure 2f), thresholds plateau at ~ 20 min of arc bar length. At low contrast, thresholds decrease up to much longer bar length; with short bars the target cannot be seen reliably, ie is below threshold. We interpret this result in terms of cortical filters which adjust their spatial parameters—in this case, length—to make best use of the retinal signal. When retinal signals are large, cortical filters are of restricted size to permit accurate localization of the position of small targets. When retinal signals are weak, cortical mechanisms must adapt their properties to make best use of a signal sparsely distributed through the cell array. Greater length summation for the psychophysical task would lead to a shallower contrast relation than for single cells.

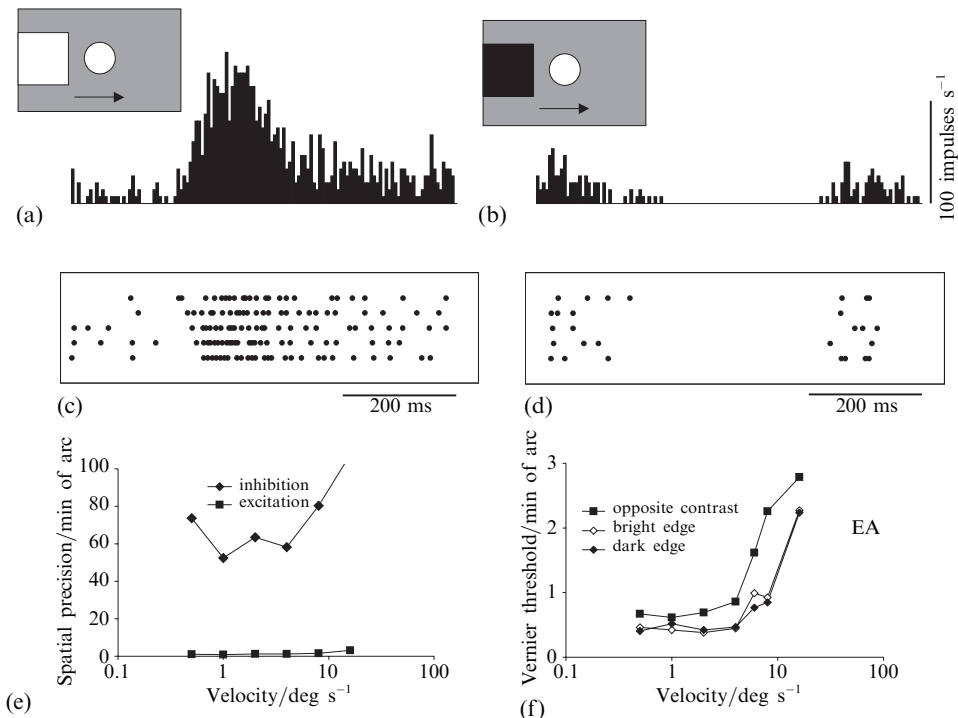


Figure 3. (a) and (b) Response histograms of an on-center MC cell to moving light and dark edges, 2 deg s^{-1} , average of 40 sweeps, 4 ms bin width. (c) and (d) Examples of individual sweeps displayed in dot raster format. The excitatory response yields a burst of impulse with greater spatial information than a cessation of firing. (e) Results of neurometric analysis as a function of movement speed; note expanded abscissa. The excitatory response yields accurate positional information, the inhibitory response does not. Mean data of 9 MC cells. (f) Psychophysical thresholds as a function of velocity for target pairs of the same or opposite contrast.

3.3 *The effect of contrast polarity*

The example in figure 2 represents an instance in which changes in Vernier threshold are not only related to the size of the signal of an individual ganglion cell but may reflect cortical integration over the cell ensemble. A further example is shown in figure 3. Vernier thresholds to target pairs of opposite contrast (eg a dark and a light edge or bar) are typically elevated compared to thresholds for target pairs of the same contrast (Levi and Waugh 1996; Levi and Westheimer 1987), provided target separation is small. With an edge target, an on-center ganglion cell will increase its firing rate to a light edge and decrease its firing rate to a dark edge as shown in figures 3a and 3b for an MC on-center cell. Figure 3c shows responses to individual stimuli in a dot raster format. The burst of impulses caused by the light edge potentially gives much more accurate spatial information than the cessation of firing caused by the dark edge. A quantitative analysis employing the neurometric template matching method is shown in figure 3d. Data from on-center and off-center MC cells, with contrast directions as appropriate, have been combined to provide the averaged data shown. The spatial precision delivered by the inhibitory response is over 1 log unit less accurate than that delivered by the excitatory response. Figure 3f shows Vernier threshold of an observer to edge targets of the same or mixed polarity. A moderate threshold elevation (mean factor of 1.8) was observed. We conclude from this analysis that, in order to achieve the psychophysical task, a comparison of on-center and off-center cell activities is required of central mechanisms.

4 General discussion

In earlier reports we have shown that ganglion cell activity may be closely related to spatial performance on Vernier tasks. We show here that Vernier performance is not always directly related to ganglion cell responses per se but may be conditioned by the way cortical mechanisms handle their signals. The goal of this approach is to constrain the possible mode of operation of these cortical mechanisms. The comparison of neurophysiological and psychophysical data here permits certain conclusions of this sort.

The neurometric analysis matched each individual response spike train with a template generated by smoothing the averaged response at the different target speeds. A Gaussian template also gave similar results, provided it was of similar width to the actual response. A template of fixed width, as would occur with a simple central mechanism with a single time constant, yielded results which did not match the psychophysical data. In control experiments, we showed that, as a function of presentation time, Vernier thresholds stabilized after 100 ms independently of target speed. To account for these two results, it may be necessary to postulate a central spatiotemporal filter which differentiates the activity of the local ganglion cell array to obtain a motion signal. It is unclear whether it is appropriate to consider a single filter able to adapt its temporal properties with target speed, or to consider an array of filters tuned to different target speeds.

Contrast affects the amplitude of ganglion cell responses. However, as shown in figure 2, our analysis procedure indicates that at low contrast not all cells may deliver a spatial signal. The length of a target at which Vernier thresholds stabilize is also contrast-dependent. It is plausible that cortical mechanisms adopt a flexible processing strategy, changing their spatial characteristics to make optimal use of the retinal signal. There are reports that length summation in area 17 neurons, ie the relation between response and target length, is strongly contrast-dependent (Sceniak et al 1999): at high contrast, summation plateaus at much shorter lengths than at low contrast. This suggests that this mechanism is implemented at an early level of cortical processing.

Contrast polarity influences Vernier thresholds when targets are close together but, for foveal viewing, has no effect when they are separated by more than 20 min of arc. This has been modeled in terms of thresholds being dependent on local linear filters or 'local signs' depending on separation (Levi and Waugh 1996). The current analysis shows that edges of the inappropriate polarity for the center of a cell yield a very weak spatial signal. Psychophysical performance could be achieved by a rectifying model, or by direct comparison of on-center and off-center signal arrays. In view of the dependence of length summation on contrast, the separation effects on polarity should also be contrast-dependent, and preliminary data indicate this may be the case. In any event, the interaction of ON and OFF channels must be considered in modeling the effects of contrast polarity on spatial processing.

Acknowledgment. This work was partially supported by NEI EY13112.

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ISSN 0301-0066 (print)

ISSN 1468-4233 (electronic)

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VOLUME 34 2005

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