Macaque Ganglion Cell Responses to Stimuli That Elicit Hyperacuity in Man: Detection of Small Displacements

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We measured responses of macaque ganglion cells as a function of contrast in a simple hyperacuity task, detection of displacement of an achromatic edge. Responses of ganglion cells of the magnocellular (MC) pathway were much more vigorous than those of cells of the parvocellular (PC) pathway. From the variability in the number of impulses in the response as compared with the distribution of impulses in maintained activity, it was possible to generate receiver operating characteristics for cells of the two pathways, and to predict individual cells' capability to detect a displacement with 75% probability. On comparing cell sensitivities to human psychophysical thresholds (75% probability of correct identification of displacement direction) at an equivalent retinal eccentricity ($\sim 6^\circ$), we found that one or two additional impulses in two MC pathway cells would suffice to support an ideal detector underlying psychophysical performance, at all contrast levels. Many more PC pathway cells would be required, especially at low contrasts. The much higher signal-to-noise ratio in the MC pathway relative to the PC pathway indicates that the MC pathway is likely to support this and other hyperacuity tasks.

[Key words: ganglion cells, macaque, magnocellular pathway, parvocellular pathway, detection thresholds, hyperacuity]

Spatial discriminations much finer than the receptor mosaic can be made by humans. For example, although human foveal cones are about 36 sec of arc apart, Vernier patterns can be discriminated with spatial offsets of as low as 3 sec of arc. The neuronal signals on which such processing is based must already be present in the retina (Shapley and Victor, 1986). We here compare spatial thresholds for human observers with the responses of macaque ganglion cells to the identical visual stimulus. There is good reason to suppose that the visual systems of these two primate species are sufficiently similar (Kaplan et al., 1990) to entrain an analysis based on the assumption that the discharge pattern of the macaque ganglion cell forms the substrate on which primate, including human, visual cortical mechanisms base the processing that leads to hyperacuity.

Physiological and psychophysical data were obtained for a particularly simple hyperacuity task, the minimum just-detect-

able lateral shift of an edge. This task gives thresholds firmly in the hyperacuity range (Basler, 1909). The psychophysical interpretation of the physiological results is more straightforward for this task than for other forms of hyperacuity, such as Vernier thresholds. Psychophysical data were gathered in the parafovea of human observers, at a similar eccentricity to the ganglion cell recordings in the monkey, and both cell and psychophysical data were acquired as a function of contrast across the edge. Their comparison supports the hypothesis that the phasic ganglion cells of the magnocellular (MC) pathway provide the significant retinal signal for the cortical mechanism responsible for detection. The nerve impulses encoding the displacement of an edge are few at threshold, such that the mechanism in the cortex responsible for their detection and analysis must operate in a near-optimal manner.

Preliminary reports of some of these results have appeared elsewhere (Wehrhahn et al., 1991; Lee et al., 1992).

Materials and Methods

Ganglion cell activity was recorded from the retinas of juvenile macaques (*M. fascicularis*). Animals were anesthetized initially with an intramuscular injection of ketamine (~ 15 mg/kg), following premedication with chlorpromazine (~ 10 mg/kg). Anesthesia was then maintained with isoflurane (1–2% during surgical procedures, 0.2–1% during recording) in a 70%/30% N_2O/O_2 mixture. Local anesthetic was applied to areas of surgical intervention. EEG and the electrocardiogram were carefully monitored as a control for depth of anesthesia. Muscular relaxation was achieved by intravenous infusion of gallamine triethiodide (5 mg/kg/hr) together with 5–7 ml/hr of dextrose Ringer's solution. Antibiotic and corticosteroids were administered intramuscularly. End-tidal pCO_2 was kept near 4% by adjusting the rate and depth of ventilation. Rectal temperature was maintained near 37.5°C. Surgical procedures for preparing the eye to record from ganglion cells have been described elsewhere (Lee et al., 1989).

The eyes were carefully focused on a tangent screen 114 cm from the cornea by means of appropriate contact lenses. Artificial pupils of 2 mm diameter were used. The quality of the optic media was frequently checked, and when any deterioration in optical quality became apparent (usually after 20–30 hr), subsequent recordings were used to obtain data for paradigms not related to spatial vision.

Stimuli were generated using a two-channel optical stimulator, each channel having as a light source a tungsten filament lamp to give a white field of CIE chromaticity coordinates $x, y = (0.404, 0.410)$. A razor blade mounted in one channel provided the edge. Beams were combined in a beam splitter, passed through a focusing lens, and reflected off a surface-silvered mirror to focus the edge onto a translucent screen. Microdensitometric examination of the edge showed the luminance transition to be complete well within 20 sec of arc. Neutral density filters were used to adjust edge contrast. Stimuli were presented on a 5° field, the surrounding area being dimly illuminated (~ 10 cd/m²). Luminance of the test area was 250 cd/m², to give a retinal illuminance of around 800 Trolands (Td). Edge position was controlled by rotating the mirror

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Figure 1. Example of a physiological experiment. A vertically oriented edge is placed at different positions in the receptive field, as shown in the drawing to the right. Contrast was 40%. Peristimulus time histograms of the responses of an MC pathway cell to the displacement of the edge by 2 min of arc are shown to the left, as indicated by the double-headed arrows in the drawing. Response was maximal when the edge is displaced over the middle of the receptive field center. For positions to either side, the response falls off. Bin width is 3 msec.

with a galvanometer. A computer moved the mirror and collected responses. The stimulus was abrupt displacement of the edge across the retina. These displacements will be termed “jumps.” Each jump of the edge was complete within 5 msec.

After isolation of a cell's activity, its type was identified using a battery of tests that formerly had proved reliable when distinguishing cells of the MC and parvocellular (PC) layers of the lateral geniculate nucleus. These tests included responses to chromatic stimuli, achromatic contrast sensitivity, and estimation of the time course of responses (Kaiser et al., 1990). The cell's responses to edge displacement were then measured. The edge was first situated just to one side of the receptive field and responses to a given jump size were recorded. The edge was then moved to a new location under computer control, and the test repeated. Fifteen jump locations were usually tested, scanning across the receptive field. The edge movement thus caused a light increment or decrement over a part of a cell's receptive field. The scan across the receptive field was done sequentially, to minimize any interference from eye drift. At the end of a scan, a control observation was inserted to check for such drift. Significant drifts were seldom, and easily detected. The procedure was then repeated with a different jump amplitude. Usually three or four amplitudes (selected from 0.5, 1, 2, 4, or 8 min of arc) were employed. Cell responses were measured at 40%, 20%, 10%, and 5% Michelson contrast, as long as any response was apparent. Stimulus presentation rate was 4/sec. The time of occurrence of each impulse was recorded. The number of jumps varied from 10 to 40, data from a larger number being collected when responses were expected to be weak. In the figures, a bin width of 3 msec is used.

The conditions of the psychophysical experiments were chosen to resemble closely those used physiologically. Stimuli were presented on the screen of a video color monitor (Sony Trinitron). They were generated through an interface (ELSA) by means of a personal computer. Observers were tested using the method of constant stimuli. The stimulus was the horizontal displacement of a vertical achromatic edge at four amplitudes (multiples of 18 sec of arc), which were presented at random with respect to direction and size of the jump. The subjects reported seeing the edge move to right or left and pressed the button accordingly. Error feedback was provided. The values were chosen in preliminary experiments to span the threshold range. The resting edge was visible to the observer for 500 msec before and after the jump. The edge was 100 min of arc in length, and separated areas 50 min of arc in width. The stimulus was presented in the middle of the display, which subtended $5.7^\circ \times 7.4^\circ$. Mean luminance was 25 cd/m². With a natural pupil estimated at 4 mm in diameter, this yields a retinal illuminance

of ~150 Td. This is less than that used in the physiological experiments. However, control observations on three ganglion cells indicated that their sensitivity to jumps differed little between 80 and 800 Td. Also, pilot psychophysical experiments on the stimulator used for the physiology yielded thresholds similar to those obtained using the video display. Subjects fixated monocularly a red light-emitting diode, positioned at eye level, using a head rest. The display was centered at 6.65° eccentricity, at 45° below the horizontal. Data were collected in blocks of 110 responses over several days until 440 responses for each test condition were accumulated. Probit curve fitting of the resulting psychometric function yielded a threshold at which the jump direction was correctly identified in 75% of the cases. The two observers were experienced psychophysical subjects with normal or corrected vision at the distance to the monitor. One of the observers was naive as to the purpose of the experiment.

Results

Neurophysiological measurements

We performed detailed measurement of responses to edge displacements (jumps) on 12 phasic ganglion cells of the MC pathway and 12 tonic cells of the PC pathway. These samples were representative subsets of larger samples (26 phasic cells and 29 tonic cells) also tested with other paradigms designed to mimic hyperacuity tasks. These further experiments will be reported in a subsequent publication. We concentrated our recordings in the parafoveal region, where the psychophysical observations were made. We are confident of our ability to distinguish cells of the MC pathway from those of the PC pathways as discussed in detail elsewhere (Kaiser et al., 1990).

Responses of MC pathway cells to edge displacement

For every cell, the edge was first centered on the receptive field (this corresponds to 0 min of arc in the analyses of Figs. 2 and 3). Responses to abrupt edge displacement were measured at 15 locations in the receptive field, for several jump sizes and at several contrasts. The time of occurrence of each impulse was registered, allowing later construction of response histograms. Some such histograms are shown in Figure 1 for five locations of a jumping edge, for an off-center MC pathway neuron. Jump amplitude was 2 min of arc at 40% contrast. The double-headed arrows on the drawing indicate jump amplitude. When the edge jumped close to the middle of the receptive field center, the response was maximal and was associated with a decrease in illumination of the strip of the receptive field center traversed by the edge. With the edge situated away from the middle of the center, the response became smaller, and when the edge jumped over the on-surround, a small response to the reverse jump direction may be seen in histogram 1. For every cell, responses evoked from the surround were very much weaker than those evoked from the center.

To evaluate responses quantitatively, we measured the peak firing rate in a 40 msec window. Maintained firing rate (defined as the mean firing level in the 40 msec prior to the response) was subtracted, and the resultant rate plotted against the position about which the edge movement took place. Four sets of data are shown in Figure 2A–D, for different contrasts. Each panel shows four jump amplitudes. The relationship between response magnitude and the jump location is obvious. To estimate maximum response amplitude, we fitted the data with the Gaussian function

$$R = R_{\max} \exp[-(x + \delta)^2/2\sigma^2], \quad (1)$$

where R is the response at location x , $R_{\max}$ is the peak response, δ is the locus of the peak response, and σ is the SD of the Gaussian. Values of δ delivered by the fitting routine were close

Figure 2. Response amplitude of the cell of Figure 1 to different displacements of an edge plotted as a function of edge position. Each plot shows the response for one contrast. Responses were measured in a 40 msec window around the peak, and maintained firing rate subtracted. When possible, the responses in each condition were fitted with a Gaussian function.

to zero, but varied slightly due to inaccuracy in the original positioning of the edge. As contrast is decreased, response magnitude diminishes in an approximately proportional manner; halving the contrast approximately halves response amplitude.

The data might be better fitted by considering more carefully the way the receptive field is stimulated by the edge displacement. Then, the relationship between response amplitude and jump location would be described by the difference between the integrals of two Gaussian functions displaced in space by the jump amplitude. In practice, we calculated that the fitted functions should be almost Gaussian in shape, unless jump amplitude was much larger than the Gaussian radius. The parameter σ is then a good estimate of the center radius under the con-

ditions tested. To control for the fact that we used jump amplitudes not much larger than the center radius, we compared σ at different jump sizes, and found no significant differences.

The fitted curves in Figure 2 are seen to describe the data reasonably well. Sets of curves similar to those in Figure 2 were obtained for other phasic cells. Values of σ ranged between 3.5 and 7 min of arc (mean $\pm$ SD, 5.10 ± 1.28 min of arc). Receptive field dimensions in this range are expected of MC pathway cells in the parafovea (Derrington and Lennie, 1984; Crook et al., 1988). In the region of the parafovea from which recordings were obtained (between 4° and 11° ; mean $\pm$ SD, $7.3 \pm 2.1^\circ$), there was no systematic relationship apparent between σ and eccentricity.

Figure 3. A–C, Response amplitude of a PC pathway cell to different displacements of an edge plotted as a function of edge position. Each plot shows the response for one contrast. Responses were measured in a 40 msec window around the peak, and maintained firing rate subtracted. When possible, the responses in each condition were fitted with a Gaussian function. D, Peristimulus time histograms of responses of the cell for 40% contrast at different displacement amplitudes. At a displacement of 8.0 min of arc, a weak response may be seen. Responses at lower contrasts were almost absent. Bin width is 3 msec, and 10, 20 and 40 presentations were averaged for 40%, 20%, and 10% contrast, respectively.

Figure 4. Mean maximum values, $R_{\max}$, and SEs, of the fitted Gaussians for MC pathway cells (*A*; $n = 12$) and PC pathway cells (*B*; $n = 12$), plotted as a function of displacement amplitude at the different contrasts tested. Responses depend linearly on displacement amplitude. Correlation coefficients were greater than 0.99. Slopes are, for MC pathway cells, 36.6, 23.5, 9.0, and 5.1 impulses/sec/min for 40%, 20%, 10%, and 5% contrast and, for PC pathway cells, 6.0 and 2.4 impulses/sec/min for 40% and 20% contrast, respectively.

Maximal response amplitude, $R_{\max}$, could then be plotted as a function of jump size at the different contrasts. Averaged results for the entire cell sample are presented later in Figure 4.

Responses of PC pathway cells to edge displacement

Responses of tonic ganglion cells of the PC pathway were recorded using a set of stimuli similar to those used with phasic

cells. Responses to the achromatic contrast were always much weaker than with phasic cells, and a larger jump size (8 min of arc) was included in the measurements. Figure 3*D* shows typical histograms for a red-on cell. The response to the displacement occurs in the second half of the histogram, and is caused by a segment of the receptive field being incremented in luminance. The response is more sustained than for the MC pathway cell of Figures 1 and 2. A clear response was seen only at 40% contrast with displacements of 8 and 4 min of arc.

We measured the firing rate in the response using the same peak measure as for phasic ganglion cells, and plotted the result against jump location. We fitted the data with Equation 1, as shown in Figure 3*A–C*. Only with larger displacements was such a fit possible. Again, a reasonable fit of the Gaussian to the data may be seen. Values for σ ranged between 3 and 6 min of arc (mean $\pm$ SD, 4.1 ± 0.9 min of arc; $n = 12$). These values are again consistent with estimates in the literature (Derrington and Lennie, 1984; Crook et al., 1988) for the parafovea (mean eccentricity $\pm$ SD, $5.4 \pm 2.1^\circ$). The response amplitudes, $R_{\max}$, were then plotted as a function of jump size at the different contrasts.

Response amplitudes for both MC and PC pathway cells are summarized in Figure 4. For both cell groups, no significant difference between on- and off-center cells was present, and the data have been combined. It can be seen that the MC pathway

Figure 5. Variability in responses of an MC pathway cell to the displacement of an edge with different amplitudes. *A*, Ten consecutive single responses shown for each amplitude. Each dot corresponds to an action potential. *B*, Histograms of number of impulses within the window indicated by the dashed lines in *A*. Between 40 and 160 responses were used to compile each histogram. At the bottom is an equivalent distribution for the maintained activity of the cell. Response variance was found to be independent of response amplitude.

Table 1. Mean number of impulses and response variance of MC pathway cells

Condition	Mean number of impulses	Mean variance (impulses ²)
Maintained activity	0.767	0.556
0.5 min jump	1.607	1.190
1.0 min jump	1.933	1.452
2.0 min jump	3.104	1.424
4.0 min jump	4.121	0.979

Response variance of MC pathway cells (40% contrast; $n = 12$) is independent of response size.

responds much more vigorously to displacement of the achromatic edge than the PC pathway. For any given set of points, the relationship between response amplitude and jump size is approximately linear, and the data have been fitted by linear regression. All correlation coefficients were above 0.99. An approximately inverse relationship between the slope of the regression lines (given in Fig. 4 caption) and contrast for each cell type was seen. For cells of the MC pathway, there was a minor degree of response saturation only to jumps of 4 min of arc at 40% contrast. Response saturation is marked with responses to sinusoidal modulation (Kaplan and Shapley, 1986; Lee et al., 1990), but it appeared that in our results cells were operating largely within a linear range. This result also indicates that jump size was small in comparison to receptive field center size; had this not been the case, some indication of response saturation would be expected.

Reliability of cell responses to displacement

Comparison of cell responses with psychophysical results can be strengthened by estimating the reliability of a cell's response. Response variability is illustrated in Figure 5A, with 40% contrast for an on-center phasic MC-pathway cell. The cell was chosen to be of average sensitivity. Ten sweeps are shown for each condition, and each dot represents an action potential. To a 4 min of arc jump, a burst of four to six impulses occurs. The number of impulses decreases with jump size. We counted the number of impulses in the 40 msec response window around the response peak derived in response histograms such as those in Figure 2 (the bounds are indicated by the dashed lines in Fig. 5A), and histograms of the distributions obtained are shown in Figure 5B. Each histogram was derived from the four edge jump locations around the peak of the fitted Gaussian distribution. Total numbers of responses analyzed were between 40 and 160. For comparison, the numbers of impulses in 40 msec windows from maintained activity periods are also shown.

It was noteworthy that response variance was independent of response magnitude, as may be seen from the distributions of impulses in Figure 5. This was consistently the case in all MC and PC pathway cells studied, at all contrasts. As an example, mean numbers of impulses in the response and their variance averaged for MC pathway cells at 40% contrast are summarized in Table 1. Only in maintained firing distributions was variance sometimes lower than in responses. This was most marked in cells with low levels of maintained firing, when the impulse distributions were truncated at zero impulses. The lack of correlation between variance and response amplitude is in marked contrast to observations on responses of cortical neurons, in which a linear relationship between response amplitude and its

Figure 6. ROC analysis of the MC pathway cell of Figure 5 for the four contrasts used in the experiments. For each choice of a criterion number of impulses, the ordinate plots the probability of attaining a positive response on a trial and the abscissa plots the probability of a false positive. Points along the diagonal indicate chance performance.

variance has been reported, with a slope close to 1 (Tolhurst et al., 1983; Vogels et al., 1989).

Data such as those in Figure 5B allow construction of receiver operating characteristics (ROCs) for individual cells. The application of this analysis to neurophysiological data is discussed by Tolhurst et al. (1983). For the data in Figure 5, one may postulate that an ideal detector uses a certain number of impulses as a criterion for giving a positive response. Using the distributions of the number of impulses in maintained firing, and of the number of impulses in the response for a particular condition, one may plot the probability of correct detection against the probability of a false-positive response. Sets of curves for the neuron in Figure 5 are shown in Figure 6, for the four contrast levels studied. Similar sets of curves for a typical PC pathway cell are shown in Figure 7.

If the impulse distributions in maintained activity and response are completely nonoverlapping, then the ROC curve follows the left and upper bounds of the graph, resulting in 100% correct responses with the appropriate criterion. The jump of 4 min of arc at 40% contrast almost achieves this level. If the impulse distributions for maintained activity and in the response are identical, then the ROC curve follows the diagonal, and 50% correct responses are achieved; even an ideal detector will not be able to distinguish whether a signal was present.

Although in analyzing ROCs, the parameter d' is the usual measure of the discriminability of the "signal" and the "noise" processes underlying detection (Green and Swets, 1966), we analyzed ROCs by taking the area under the curves, as described in Tolhurst et al. (1983). We took as boundaries of the areas a linear interpolation between the points. Averaged data for the entire cell sample is shown in Figure 8. In these neurometric functions (Tolhurst et al., 1983), the probability of detection is plotted against jump size at the different contrasts. Changing

Figure 7. ROC analysis of the PC pathway cell of Figure 3. Details are as in Figure 6.

contrast causes a lateral displacement of the curves for MC pathway cells without any change in slope. For 75% correct, the jump size required can be read off from the x-axis. For PC pathway cells, the 75% level is only reached at 40% contrast.

Psychophysical measurements with human observers

Parafoveal sensitivity to edge displacements as a function of contrast was measured in two observers using the psychophysical method of constant stimuli. Thresholds so defined represent the jump of which the direction could be correctly identified on 75% of occasions. The data shown in Figure 9 (solid circles) represent the mean of the two subjects. At 40% contrast, average threshold was 48 sec of arc. This value increases by a small amount on reducing contrast to 20%. Further reduction in contrast results in greater increases in threshold. These results resemble experiments on detection of displacement of sinusoidal gratings by Nakayama and Silverman (1985), who suggested from their psychophysical data that the MC pathway underlay detection. Thresholds are almost five times higher than foveal displacement thresholds (Westheimer, 1979). The shape of the

curve relating displacement threshold to contrast is very similar to that reported for the dependence of Vernier acuity on contrast (Wehrhahn and Westheimer, 1990). One observer was common to this previous study.

The physiological data in Figure 9 are the 75% values from Figures 7 and 8, and it can be seen that the average sensitivity of MC pathway cells generally resembles the psychophysical results. This implies that ideally only signals from only one or two MC pathway cells would be required by an ideal observer for detection. PC pathway cells are much less sensitive. It is noteworthy that the level of detection by human observers corresponded to approximately one extra impulse in the MC pathway cells stimulated during the 40 msec critical epoch associated with the stimulus displacement.

Discussion

Models of central processing for hyperacuity must be constrained by the signal-to-noise ratio, and the sampling density, of retinal elements. As part of a more general description of retinal signals likely to provide the substrate for the hyperacuties, we compare here physiological and psychophysical results related to detection of small displacements of an edge. We believe this paradigm permits a relatively straightforward interpretation of the physiological basis of the psychophysical performance.

The stimulus situation in this task is sketched in Figure 10. An edge lies across the retina, shown here as mosaics of on- and off-center ganglion cells. The mosaics were derived from those provided by Wässle et al. (1981) for on- and off-center β -cells of the cat retina, and are approximately scaled for MC pathway cell density at 6° eccentricity. Receptive field centers are drawn to represent average diameters (twice σ) derived from the physiological data. If the edge is subjected to an abrupt displacement in one of the two arrowed directions, in one direction a strip of on-center cells is activated and in the other a strip of off-center cells becomes active, in response to a respective increase or decrease in illumination of the segments of the on- or off-center matrices delineated by the dashed lines. If a central decision mechanism has available the static direction of the edge on the retina, then on- or off-center cell activation provides a key to identification of displacement direction. The central mechanism must also be able to distinguish a change in edge contrast from an edge displacement. How this might be done is shown in the lower part of Figure 10. Receptive fields of two hypothetical cells, I and II, are shown. A change in contrast will evoke a response from both cells, but an edge movement will evoke a response only from cell I. We now examine some assumptions

Figure 8. Mean probabilities (with SEM) of attaining a criterion response as a function of jump sizes for MC pathway cells (A; $n = 12$) and PC pathway cells (B; $n = 12$). The jump sizes corresponding to 75% probability of detection can be read off the abscissa and are plotted as the neurometric thresholds in Figure 9.

Figure 9. Psychophysical thresholds (solid circles) for the displacement of an edge in the parafovea of human subjects as a function of contrast. Points are average values from two subjects. Neurometric thresholds (open circles, MC pathway cells; open square, PC pathway cells) were gained from Figure 8. Psychophysical and neurometric thresholds for MC pathway cells are similar as a function of contrast.

of this model and how far our results permit identification of MC or PC pathway cells as the physiological substrate of the task.

Response to displacement and receptive field structure

For both MC and PC pathway cells, responses to edge displacement are dominated by the response of the receptive field center. As shown in Figure 1, surround responses, when the stimulus was just to one side of the center, were weak. In the case of MC pathway cells, the surround mechanism is large in spatial extent (B. B. Lee, J. Kremers, and T. Yeh, unpublished observations), and spatial summation is inadequate to generate a substantial response. For PC pathway cells, recent estimates have indicated much smaller ratios of surround-to-center diameters than for MC pathway cells (Shapley et al., 1991), with many cells of the PC pathway exhibiting almost coextensive opponent mechanisms. Little indication of center/surround structure was visible in response histograms of PC pathway cells. Although it has been proposed that the center-surround structure of PC pathway cells provides the possibility for the multiplexed transmission of an achromatic with the chromatic signal (Ingling and Martinez-Uriegas, 1983; Ingling, 1991), no such multiplexed signal was obvious.

We derived estimates of receptive field center radii from the fitted curves shown in Figures 2 and 3. These estimates are an overestimate due to jump amplitude, but the effect is slight; we calculated that with a jump amplitude of twice the center radius, the fitted curves yield values of σ 16% larger than the radius. Jump amplitudes were usually smaller than values of σ returned by the fitting routine. Our estimates of center radius resemble other estimates in the literature at an equivalent retinal eccentricity (Derrington and Lennie, 1984; Crook et al., 1988). Although center size of MC pathway cells is often assumed to be much larger than that of PC pathway cells, only a small difference (a factor of 1.25) was found in the present experiments. Careful examination of previously published data (Derrington and Lennie, 1984; Crook et al., 1988) suggests a similar result.

Figure 10. Sketch of the stimulus situation relative to the ganglion cell matrix. In the upper part of the figure, two independent ganglion cell matrices are drawn, off-center above and on-center below. Displacement of the edge in the direction toward the reader excites a strip of off-center cells in the top matrix. A shift in the opposite direction excites a corresponding strip of the on-center cells in the bottom matrix. The number of cells activated will depend on the density of the matrix and the length of the edge. The lower part of the figure indicates how edge movement might be discriminated from a change in contrast or light intensity. In the former case, only hypothetical cell I would fire, but in the latter both cells I and II would give some response.

As in earlier work on cat ganglion cells (Shapley and Victor, 1986), responses could be evoked by jumps much smaller than the center radius.

It is well established that ganglion cells of the MC pathway are about 10 times more sensitive to changes in achromatic contrast than those of the PC pathway (Kaplan and Shapley, 1986; Lee et al., 1989), 1–2% contrast typically evoking a response of about 20 impulses/sec in MC pathway cells. We calculated that the present results were quantitatively consistent with these measurements. Assuming linear spatial summation across the center and averaging over the four contrasts tested, we calculated that if the stimulus were to have filled the receptive field center, a contrast of 1.8% would have been required to achieve a response of 20 impulses/sec. A similar calculation was carried out by Shapley and Victor (1986).

Two further features of the physiological data are of note. First, response amplitude bore an approximately linear relation to contrast and jump size (Fig. 4). Responses of PC pathway cells are well described by linear models, with little indication of response saturation with achromatic stimuli (Kaplan and Shapley, 1986; Lee et al., 1990). Response saturation is present in MC pathway cells (Kaplan and Shapley, 1986; Lee et al., 1990), but this effect was not obvious in the present results,

except at 40% contrast with a displacement of 4 min of arc. Second, as shown in Table 1, a striking feature of our data was the lack of any dependence of response variance on response amplitude. This contrasts with the behavior of cells in cat (Tolhurst et al., 1983) and monkey (Vogels et al., 1989) striate cortex.

As part of a more general study of receptive field structure of phasic ganglion cells, responses to displacements of a point source of light were measured by Scobey and Horowitz (1976). With a point source rather than an edge, a biphasic response profile is expected (and was found) as a function of jump location. These authors only measured responses at 80% contrast, but their results appear qualitatively similar to those described here.

Cell responses and psychophysical performance

The model in Figure 10 implies certain assumptions as to the physiological substrate of displacement detection, apart from whether the MC or the PC pathway forms the substrate of the task. One assumption is that the signal available for detection derives solely from on-center cells for one movement direction, and from off-center cells for the other. As an alternative, it is possible to conceive of a "push-pull" mechanism that operates on the difference in on- and off-center cell activity, with a consequent improvement in signal-to-noise ratio. Inspection of response histograms and the dot diagram of Figure 5 shows cessations of maintained firing in the direction of displacement opposite to that generating an excitatory response. We derived ROC curves for such inhibitory responses. Except for cells with high levels of maintained firing, these ROC curves were of abnormal shape, since during maintained activity, many intervals between spikes exceeded the window width of 40 msec. A central decision mechanism would be unable to distinguish between these "spontaneous" pauses in firing and those evoked by a stimulus. It thus seems more plausible that psychophysical detection is primarily based on excitatory responses; this argument was first explicitly formulated by Levick (1973). We have assumed this to be the case, although we cannot rule out minor participation of some kind of "push-pull" effect. We also have assumed that it is the transient response to displacement that provides the relevant signal for psychophysical detection. The 40 msec analysis window was chosen to be close to the critical duration at the retinal illuminance used (e.g., Swanson et al., 1987).

A second assumption is that the activity of neighboring ganglion cells is uncorrelated. Relevant data are not available for macaque ganglion cells. In the cat, neighboring X-cells show little or no correlation whereas correlation between Y-cells is significant (Mastrorade, 1983). If correlation were present in the macaque, this would increase the number of cells required for detection, but it is difficult to pursue this analysis without primate physiological data.

Figure 9 provides a direct comparison between psychophysical thresholds with neural thresholds derived from ROC curves. In the following, we assume that psychophysical thresholds of man and macaque are identical. This is unlikely to be strictly true; foveal visual resolution of the macaque is about two-thirds that of man at photopic levels (Cavonius and Robbins, 1973). For a Vernier-type task, Kiorpes and Kiper (1992) found foveal performance of the macaque to be inferior to that of man, but this difference was not present in the peripheral visual field. In the absence of directly comparable macaque behavioral data, we make here the direct comparison. From Figure 9, an ideal observer would only require the signal of one or two MC path-

way ganglion cells to attain 75% correct discrimination of displacement, the signal corresponding to about one extra impulse in each MC pathway ganglion cell.

Responses of PC pathway ganglion cells to edge displacement were much less vigorous than those of MC pathway cells. From Figure 8, it can be seen that at 40% contrast PC pathway cells are less sensitive than MC pathway cells by about a factor of 8. It is possible to calculate how far probability summation might permit PC pathway cells to participate in detection. The slopes of the neurometric functions in Figure 8 are shallow, and fitting the function

$$P = 1 - (1 - \gamma) \exp[-(m/\alpha)^\beta] \quad (2)$$

gave values of β (a measure of function slope) of between 0.75 and 0.95. P is the probability that the cell response exceeds a criterion value, m is jump size, α is a jump amplitude fixing the position of the curve on the x-axis, and γ is the probability of a criterion response in the absence of a stimulus. Tolhurst et al. (1983) were the first to apply this function to neurophysiological data, and much of the following rests on their analysis. Inspection of data from individual cells also indicated values of β around 0.85, indicating that the slope of the averaged data was not made more shallow due to averaging over cells with different sensitivities but steeper slopes.

With probability summation, threshold, α_n , of a group of n cells is given by

$$\alpha_n = \alpha n^{-1/\beta}, \quad (3)$$

where α is an individual cell's sensitivity. From this, it can be calculated that probability summation of five or six PC pathway cells might give rise to sensitivity comparable to that of an MC pathway cell at 40% contrast. Alternatively, PC pathway cell signals might be enhanced by straightforward averaging, and then the signal-to-noise ratio will improve with the square root of the number of cells summed. This type of analysis is especially applicable at lower contrasts, since then even the largest jumps, covering the entire receptive field center, could not elicit criterion responses from PC pathway cells. The data in Figures 4 and 9 indicate that the average PC pathway signal is about eight times weaker than for the MC pathway, indicating that 64 cells would have to be averaged. About 80% of ganglion cells belong to the PC pathway (Perry et al., 1984; Silveira and Perry, 1991). Some 10–20% of these have S-cone input and thus play little role in spatial vision. If 10% of ganglion cells belong to the MC pathway, then the numerical advantage of PC to MC pathway cells is about 6–7:1. With small edge displacements, the linear rather than the areal density will determine the ratio of cells activated in these pathways, that is, ~2.45–2.65:1. The numerical advantage of PC pathway relative to MC pathway cells is thus inadequate to compensate for their poor signal-to-noise ratio.

The slopes of neurometric functions in Figure 9 are shallower than the usual slopes of psychometric functions. Tolhurst et al. (1983) provide a model by which neurometric functions may be made steeper through probability multiplication, at the expense of a small elevation of threshold. This model implies that more than one neuron must exceed a criterion response level for a signal to be detected. If MC pathway cells indeed support psychophysical performance, it is plausible that an observer might require a significant signal in two or more MC pathway cells before giving a positive response. It is important to note that the foregoing analysis had available to it the precise time

of occurrence of the stimulus, while an observer does not have this information, since during a trial there will be some uncertainty as to exactly when the displacement occurs. Also, the observer may be uncertain as to the particular neurons that will deliver a signal. It may therefore be the case that a reasonable strategy to minimize false positives is to require simultaneous detection by several neurons.

In the cat, Shapley and Victor (1986) noted that cellular hyperacuity thresholds appeared smaller than those demonstrable behaviorally, implying loss of information at a central site. This did not appear to be the case for the comparison in Figure 9, but this could be misleading. The psychophysical data were obtained with edges 100 min of arc in length. We have calculated that this will optimally activate about 10 MC pathway cells, which, as discussed above, could compensate for uncertainty as to where and when a signal occurs. Psychophysical sensitivities to an edge restricted in length so as to activate optimally only one or two cells are thus of interest. This comparison of physiological data, the sampling matrix of MC pathway cells, and psychophysical thresholds with edges of restricted length will be presented elsewhere.

The preceding results analyze only one of the hyperacuities. We have carried out similar experiments designed to measure the sensitivity of responses of MC and PC pathway cells to the locus of flashed or moving edges within their receptive fields, with the intention of extrapolating to Vernier tasks (Lee et al., 1991). The analysis suggested that the MC pathway also forms the substrate of Vernier hyperacuity. However, the central mechanism for extracting a location signal from the ganglion cell matrix is not so readily specified as the scheme proposed in Figure 10 for jump detection. Some possibilities for Vernier tasks are discussed by Parker and Hawken (1985). These authors demonstrated results from macaque cortical cells that closely resemble those for MC pathway cells presented here. Their results demonstrate that the ganglion cell spatial signal is well preserved in a proportion of cortical cells.

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