Exp Brain Res (1984) 56: 497–501

Experimental Brain Research

The position sensitivity of retinal X- and Y-cells in cats*

M. Sur** and S.M. Sherman

Department of Neurobiology and Behavior, State University of New York at Stony Brook, Stony Brook, NY 11794, USA

Summary. We have devised a measure of a retinal ganglion cell's sensitivity to changes in the spatial position of a grating stimulus. At maximum, this relative position sensitivity is a scaled product of the stimulus spatial frequency and the cell's fundamental component of response to that spatial frequency. We obtained the relative position sensitivity as a function of spatial frequency for 13 X-cells and 14 Y-cells. X-cell functions peak at significantly higher spatial frequencies than do those of Y-cells. At their peaks, X-cells display significantly higher values of relative position sensitivity than do Y-cells. However, Y-cells have higher position sensitivity at lower spatial frequencies, but exhibit less of a range of variation from maximum to minimum than do X-cells. These results are consistent with a hypothesis that Y-cells provide the crucial substrate for form vision at lower spatial frequencies, while X-cells are important for details carried by the higher spatial frequencies.

Key words: Cat retinal ganglion cells – X-cells – Y-cells – Form vision

Introduction

Although response properties of X- and Y-cells in the cat's retina and lateral geniculate nucleus have been thoroughly studied (for recent reviews, see Stone et al. 1979; Lennie 1980; Sherman 1984), the functional roles of these neurons and the parallel pathways they represent remain a matter of speculation. A number of such roles have recently been suggested (e.g., Ikeda and Wright 1972; Stone et al. 1979; Sherman 1979; Lennie 1980), and these derive largely from differences in response properties of X- and Y-cells to spatial and temporal patterns. Many of these neurophysiological data are in the form of spatial contrast sensitivity functions, or analogous spatial tuning functions, for which contrast sensitivity or responsiveness is measured as a function of the spatial frequency of the stimulus.

Such data have generally been used to describe a neuron's response to a wide range of spatial and temporal variables, but such descriptions usually do not address the question of a neuron's sensitivity to changes in spatial position of the stimulus. Since analysis of the visual scene requires information about spatial phase or relative spatial position as well as spatial frequency, it is of some interest to measure such relative position sensitivity for X- and Y-cells. To do so, we devised a simple measure of the relative position sensitivity of these cells that could be derived from their spatial tuning functions. (A similar procedure could be used to derive the analogous temporal parameter from temporal tuning functions.) Our results indicate that X-cells exhibit greater overall relative position sensitivity than do Y-cells, but if stimuli limited to low spatial frequency are considered, Y-cells exhibit the superior relative position sensitivity.

Methods

Our experimental methods have been described in detail elsewhere (Lehmkuhle et al. 1980; Sur and Sherman 1982). Experiments were performed on adult cats anesthetized initially and for all surgical procedures with halothane, then paralyzed with gallamine triethiodide (3.5 mg/kg) and artificially respired with a 70 : 30 mixture of N_2O and O_2. End-tidal CO_2 was maintained close to 4%. Body temperature was kept at 38° C. The eyes were refracted and appropriate contact lenses used to bring them to

* Supported by USPHS grants EY05241 and EY03038

** Present address: Section of Neuroanatomy, Yale University School of Medicine, New Haven, CT 06510, USA

Offprint requests to: S. M. Sherman (address see above)

focus on the visual stimuli 57 or 114 cm distant. Bipolar tungsten stimulating electrodes were inserted to straddle the optic chiasm. Recording micropipettes were lowered through a hydraulically-sealed chamber cemented over a craniotomy made above the lateral geniculate nucleus (A6, L9). The chamber was then filled with a 3% solution of agar and sealed with dental wax to minimize brain pulsations. Retinal axons were recorded in the lateral geniculate nucleus or the optic tract below the C-laminae. Responses and latency to optic chiasm stimulation were used to verify the retinal source of these units.

Each retinal axon was classified as an X- or Y-cell based on a standard battery of tests (Enroth-Cugell and Robson 1966; Cleland et al. 1971; Hoffmann et al. 1972; Hochstein and Shapley 1976a, b), including (1) latency to optic chiasm stimulation, (2) linearity of response to counterphased sine-wave gratings, and (3) size of the receptive field center. For each cell studied, a computer collected responses to sine-wave gratings of 38 cd/m^2 mean brightness, 0.6 contrast, and drifting at a temporal frequency of 2 Hz. A range of spatial frequencies in octave steps was used. These ranged from 0.125 to 4.0 cycle/deg, presented in a random sequence, and each was delivered in 6 blocks of trials for a total of 15 s. Background firing rates were also collected by interleaving a stimulus of 38 cd/m^2 brightness containing no contrast (i.e., a blank screen) with the gratings. The fundamental Fourier or linear component of the response was obtained for each spatial frequency and for the background, and these components were plotted as a function of spatial frequency. The relative position sensitivity of a cell at each spatial frequency was obtained from its spatial tuning function as described below.

The linear component of a cell's response (R) to a drifting sine wave grating can be characterized as

$$R = F \sin \Phi \tag{1}$$

where F is the fundamental Fourier component of the response (in spikes/s) and Φ is a term that describes the spatial or temporal phase of the grating. For such a grating drifting at a constant velocity, V (in deg/s), the spatial and temporal terms are interchangeable. For instance, Equation 1 can be rewritten as

$$R = F \sin 2\pi Sx \tag{2}$$

or

$$R = F \sin 2\pi Tt \tag{3}$$

where S is the grating's spatial frequency (in cycles/deg), x is the distance orthogonal to the grating orientation (in deg), T is the temporal frequency (in cycles/s), and t is time (in s). Equations (2) and (3) are related by

$$T = VS \tag{4}$$

and

$$x = Vt \tag{5}$$

To characterize relative position sensitivity, Eq. (2) can be used, and an analogous operation can be performed by Eq. (3) for the temporal domain. Relative position sensitivity can be defined as the change in response to an incremental change in the grating's spatial position. This change is

$$\frac{dR}{dx} = 2\pi SF \cos 2\pi Sx. \tag{6}$$

The maximum value of dR/dx can be taken as the greatest position sensitivity for the spatial frequency studied. This is maximum when cos 2π Sx equals 1 or Sx is an integer. Thus maximum relative position sensitivity as a function of spatial frequency is simply

$$\max \frac{dR}{DX} = 2\pi SF \tag{7}$$

The physical interpretation of this sensitivity is quite straightforward. Consider two cells that yield linear responses to drifting sine wave gratings (as in Eq. (1)). For a given spatial frequency of the stimulus, the cell with the greater response amplitude will display a larger decrement in response from its peak for a small change in grating position compared to the cell with a lower response amplitude. The more difference there is between the peak and trough response as a grating drifts across the receptive field, the more range of response the neuron has at its disposal for signaling grating position. The relative position sensitivity is thus proportional to response amplitude in this example. Conversely, if response amplitudes are the same but the spatial frequencies of the stimuli evoking these responses differ for two cells, a small change in position will cause a larger response decrement from the peak response for the cell stimulated with the higher spatial frequency. That is, the relative position sensitivity is also directly proportional to spatial frequency, and in general is proportional to the product of the spatial frequency and fundamental response component evoked by that spatial frequency.

Finally, it should be noted that this analysis is based on the fundamental or linear response components, which adequately characterize X-cell responses but ignore the nonlinear responses of Y-cells (Hochstein and Shapley 1976a, b). The term "relative" is used here to describe position sensitivity based on linear responses. This issue is considered further in Discussion.

Results

We obtained spatial tuning data from 13 X- and 14 Y-cells. For each cell, besides the routine determination of receptive field size, eccentricity of the field center, and latency to optic chiasm stimulation, we also obtained a set of histograms to drifting gratings from which we constructed spatial tuning functions. We then derived for each cell the maximum relative position sensitivity at each spatial frequency (Eq. (7)), and termed this function the position sensitivity function.

Spatial tuning and position sensitivity

Figure 1A illustrates spatial tuning functions for an X- and a Y-cell. The X-cell response is maximum at a spatial frequency of 1.0 cycles/deg and decreases at lower and higher spatial frequencies. The spatial resolution of this cell, defined arbitrarily as the spatial frequency at which the cell's response has dropped to the background rate, is roughly 4 cycles/deg. The spatial tuning function for the Y-cell is constructed from its linear response components, and decreases monotonically from 0.125 cycle/deg to its spatial resolution of roughly 2 cycles/deg. Similar data have been documented repeatedly for X- and Y-cells of the retina and lateral geniculate nucleus (Lehmkuhle et al. 1980; So and Shapley 1981; Troy 1983, among many others).

Position sensitivity functions of the X- and Y-cell at stimulus spatial frequencies up to and including the spatial resolution are shown in Fig. 1B. The position

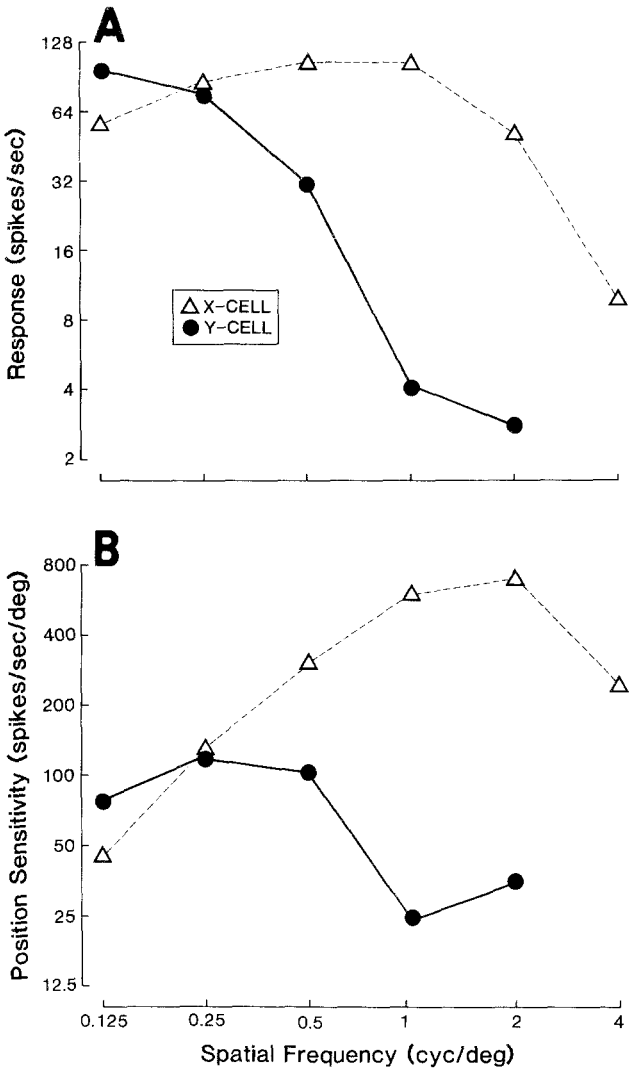

Fig. 1A and B. Responses of a retinal X- and Y-cell to drifting sine wave gratings of different spatial frequency. The gratings had a contrast of 0.6 and were drifted at 2 Hz. **A** Fundamental component of response as a function of spatial frequency. The background levels are 10 spikes/s and 3 spikes/s for the X- and Y-cell, respectively. These were obtained by computing the fundamental component of response during stimulus cycles of zero contrast (i.e., a blank screen of equal average luminance to the gratings). **B** Relative position sensitivity as a function of spatial frequency derived from the data in **A**. Relative position sensitivity was derived from the expression $2\pi SF$, where S is the spatial frequency and F is the fundamental component of response to that spatial frequency (see Eq. (7))

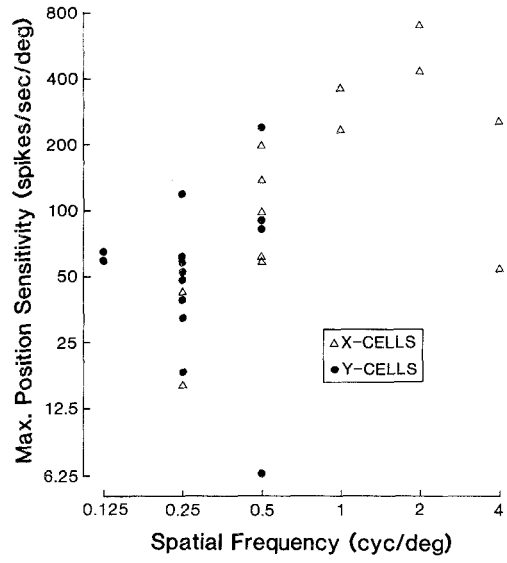

Fig. 2. Scatter plot for retinal X- and Y-cells of the maximum relative position sensitivity versus the spatial frequency at which that maximum sensitivity was evoked. These data were derived from plots similar to those in Fig. 1B

sensitivity of the X-cell increases dramatically from a relatively poor value at 0.125 cycles/deg to a prominent peak near 2 cycles/deg. The Y-cell's position sensitivity function is much flatter than that of the X-cell, and it exhibits a moderately broad peak for lower spatial frequencies.

The shapes of the spatial tuning functions of Fig. 1A are fairly characteristic of the X- and Y-cells in our sample. Each X-cell spatial tuning function displays a peak between 0.25 and 1.0 cycles/deg. The range of receptive field eccentricities from the area centralis of the X-cells is 1°–64°, and their receptive field diameters range from 0.4°–2.2°. In contrast, 9 of the 14 Y-cell spatial tuning functions are maximum at the lowest spatial frequency presented (0.125 cycle/deg). Five Y-cell functions peak at 0.25 cycle/deg. The Y-cell eccentricities are 1°–67°, and receptive field diameters are 0.7°–4.5°. Briefly, X-cell tuning functions differ from Y-cell functions in shape, because the former exhibit a peak response at higher spatial frequencies ($p < 0.001$; here and elsewhere, all statistical statements are based on the Mann-Whitney U-test) and higher spatial resolutions ($p < 0.05$). The maximum fundamental response component varies considerably among our sample, from 18–97 spikes/s for X-cells and from 15–85 spikes/s for Y-cells. These distributions of maximum response for X- and Y-cells are not statistically different ($p > 0.05$).

The shapes of the relative position sensitivity functions of Fig. 1B are also fairly characteristic of the X- and Y-cells in our sample, although considerable variability is also evident among these functions. Every X-cell and 12 of the 14 Y-cell functions for the relative position sensitivity peak at spatial frequencies between 0.25 and 4.0 cycles/deg (see Fig. 2); the other Y-cell functions are maximum at the lowest spatial frequency tested (0.125 cycles/deg). The X-cell functions, however, peak at significantly higher

spatial frequencies than do those of the Y-cells ($p < 0.001$). Although the spatial frequency of maximal relative position sensitivity decreases with eccentricity, particularly for X-cells, the sample of X- and Y-cells are reasonably well-matched for eccentricity, and the greater spatial frequency at which maximum position sensitivity is seen for X-cells is evident at all eccentricities. X-cells also display higher maximal position sensitivities than do Y-cells (Fig. 2; $p < 0.05$), and this, too, is evident at all eccentricities.

Another difference between X-cell and Y-cell relative position sensitivities is the range of values seen in each position sensitivity function (e.g., Fig. 1B). The ratio of highest to lowest position sensitivity at various spatial frequencies is 2.6–23.6 for X-cells and 1.5–5.9 for Y-cells ($p < 0.01$). In other words, Y-cells tend to display roughly similar relative position sensitivity regardless of the spatial configuration of the stimulus, whereas X-cells tend to exhibit much better relative position sensitivity for higher spatial frequencies.

Discussion

In order to analyze the spatial patterns in a visual scene, it is necessary to have information concerning both the spatial frequencies present as well as the relative position or spatial phase of each of these frequency components. Relative sensitivity to spatial position, then, is an important parameter for spatial vision. We have derived this measure for X- and Y-cells from their fundamental components of response to drifting sine wave gratings. This can be done because of the sinusoidal spatial phase dependency of these fundamental response components for X- and Y-cells (Hochstein and Shapley 1976a, b).

Because X-cell responses to stimuli of all spatial frequencies are dominated by the fundamental component, an X-cell can always signal the presence of a stimulus as well as its position within the receptive field. In contrast, Y-cell responses are dominated by the linear component only at lower spatial frequencies. At higher ones, Y-cell responses are dominated by nonlinear components (mostly second harmonic temporal distortions) that are spatially phase-independent (Hochstein and Shapley 1976a, b). Therefore, these nonlinear responses of a Y-cell can clearly signal the presence of a stimulus with considerable resolution, but they cannot accurately signal the relative position of that stimulus within the receptive field. Nonetheless, it is possible at higher spatial frequencies that these nonlinear Y-cell responses are quite sensitive to slight shifts of target position even though they cannot signal relative position.

It is interesting to consider these response parameters in the context of a recent hypothesis for the functional significance of the X- and Y-cell pathways (Lehmkuhle et al. 1980, 1982; reviewed in Sherman 1984). This hypothesis suggests that the Y-cell pathway, with its unique sensitivity to the lower spatial frequencies, is responsible for the basic analysis of visual patterns, whereas the X-cell pathway, with its sensitivity to the higher spatial frequencies, adds spatial detail and raises acuity. (The X-cell pathway may also be crucial to other roles, such as the analysis of stereopsis, and many other quite different models are equally plausible; cf. Ikeda and Wright 1972; Stone et al. 1979; Lennie 1980. All of these are merely working hypotheses.) Y-cells tend to have fairly constant relative position sensitivity for a wide range of spatial frequencies, and such a response pattern seems well-suited to a crude spatial analysis of the visual scene. The nonlinear, phase insensitive responses of Y-cells to higher spatial frequencies could plausibly serve as a sensitive motion alerting system for small targets. Conversely, these responses may be an epiphenomenon of the neural circuitry that subserves the "contrast gain control" of Y-cells (Shapley and Victor, 1978, 1980). X-cells exhibit better relative position sensitivity, but only for the higher spatial frequencies. This response pattern seems suited for extracting the maximum spatial information from the higher frequencies in order to maximize acuity.

References

Cleland BG, Dubin MW, Levick WR (1971) Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. J Physiol (Lond) 217: 473–496

Enroth-Cugell C, Robson JG (1966) The contrast sensitivity of retinal ganglion cells of the cat. J Physiol (Lond) 187: 517–552

Hochstein S, Shapley RM (1976a) Quantitative analysis of retinal ganglion cell classifications. J Physiol (Lond) 262: 237–264

Hochstein S, Shapley RM (1976b) Linear and non-linear subunits in Y cat ganglion cells. J Physiol (Lond) 262: 265–284

Hoffmann K-P, Stone J, Sherman SM (1972) Relay of receptive field properties in dorsal lateral geniculate nucleus of the cat. J Neurophysiol 35: 518–531

Ikeda H, Wright MJ (1972) Receptive field organisation of "sustained" and "transient" retinal ganglion cells which subserve different functional roles. J Physiol (Lond) 227: 769–800

Lehmkuhle S, Kratz KE, Mangel SC, Sherman SM (1980) Spatial and temporal sensitivity of X- and Y-cells in the dorsal lateral geniculate nucleus of the cat. J Neurophysiol 43: 520–541

Lehmkuhle S, Kratz KE, Sherman SM (1982) Spatial and temporal sensitivity of normal and amblyopic cats. J Neurophysiol 48: 372–387

Lennie P (1980) Parallel visual pathways. Vision Res 20: 561–594

Shapley RM, Victor JD (1978) The effect of contrast on the transfer properties of cat retinal ganglion cells. J Physiol (Lond) 285: 275–298

Shapley RM, Victor JD (1980) The effect of contrast on the nonlinear response of the Y-cell. J Physiol (Lond) 302: 535–547

Sherman SM (1979) The functional significance of X- and Y-cells in normal and visually deprived cats. Trends in Neurosci 2: 192–195

Sherman SM (1984) Functional organization of the W-, X-, and Y-cell pathways in the cat: a review and hypothesis. In: Sprague JM, Epstein AN (eds) Progress in Psychobiology and Physiological Psychology. Academic Press, NY (in press)

So Y-T, Shapley R (1981) Spatial tuning of cells in and around lateral geniculate nucleus of the cat: X and Y relay cells and perigeniculate interneurons. J Neurophysiol 45: 107–120

Stone J, Dreher B, Leventhal A (1979) Hierarchical and parallel mechanisms in the organization of visual cortex. Brain Res Rev 1: 345–394

Sur M, Sherman SM (1982) Linear and nonlinear W-cells in the C-laminae of the cat's lateral geniculate nucleus. J Neurophysiol 47: 869–884

Troy JB (1983) Spatial contrast sensitivities of X and Y type neurones in the cat's dorsal lateral geniculate nucleus. J Physiol (Lond) 334: 399–417

Received January 31, 1984 / Accepted May 16, 1984