Dependence of Center Radius on Temporal Frequency for the Receptive Fields of X Retinal Ganglion Cells of Cat

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ABSTRACT We examined the dependence of the center radius of X cells on temporal frequency and found that at temporal frequencies above 40 Hz the radius increases in a monotonic fashion, reaching a size ~30% larger at 70 Hz. This kind of spatial expansion has been predicted with cable models of receptive fields where inductive elements are included in modeling the neuronal membranes. Hence, the expansion of the center radius is clearly important for modeling X cell receptive fields. On the other hand, we feel that it might be of only minor functional significance, since the responsivity of X cells is attenuated at these high temporal frequencies and the signal-to-noise ratio is considerably worse than at low and mid-range temporal frequencies.

INTRODUCTION

In reporting the spatiotemporal frequency responses of cat retinal ganglion cells, Frishman et al., (1987) noted that the receptive field centers of X cells seem to expand at temporal frequencies above 30 Hz. This conclusion was formed on the basis of estimates of center radius obtained from spatial frequency responses of three on-center X cells at, in each case, four temporal frequencies (one at 2 Hz and three at temporal frequencies of 30 Hz or greater). Our interest in the generality of this observation stems from a desire to develop a precise model of the spatiotemporal frequency response of the X cell. A reasonable first approximation to the spatiotemporal frequency responses of X cells can be obtained by modeling the receptive field under the assumption that center size is invariant with temporal frequency (Enroth-Cugell et al., 1983; Frishman et al., 1987). If this assumption is invalid, these models are incomplete, perhaps in a serious way. To examine this question more closely, we have studied how the center radius of a reasonably large population of X cells varies as a function of temporal frequency.

The work of Koch (1984) provides a reason for believing that the dependence of center radius on temporal frequency might prove to be of critical importance in modeling the spatiotemporal frequency responses of ganglion cells. He developed

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an equivalent circuit model for a quasi-active membrane and found that the space constant of an infinite cable with this kind of membrane would increase with temporal frequency over a substantial range. Applying this cable model (it differs from the classical cable model in that it includes an inductive element) to the case of the dendritic tree of a cat retinal ganglion cell (Boycott and Wässle's [1974] example of the delta cell), Koch (1984) found that the cell should have a larger spatial field for integration of electrical signals at 100 Hz than at 0 Hz. In other words, Koch's (1984) model of the spatiotemporal frequency response of the delta cell predicts that the receptive field center radius would increase over this range. Hence, if the center radius of X cells does increase with temporal frequency, Koch's (1984) model would be a good starting point for modeling the spatiotemporal frequency responses of these cells.

METHODS

Preparation and Recording

The data presented below were collected from 12 on-center and four off-center X cells in eight cats. The receptive field midpoints of all cells were located within the central 20 degrees of visual angle. Other experiments, not relevant to this study, were performed on these and other retinal ganglion cells in the same animals. Hence, the sacrifice of these animals yielded considerably more information than is presented in this paper.

General anesthesia was induced with ketamine hydrochloride (20 $mg \cdot kg^{-1}$) administered intramuscularly. During preparatory surgery thiamylal sodium was given intravenously (as needed), as was a loading dose (100–200 mg) of ethyl carbamate. During recording anesthesia was maintained with intravenous ethyl carbamate and paralysis was maintained with gallamine triethiodide or pancuronium bromide. Heart rate and blood pressure were continuously monitored and if irregularities that could be associated with discomfort occurred, the usual 20–30 $mg \cdot kg^{-1} \cdot h^{-1}$ dose rate was increased. The experimental procedures have been reviewed and approved by the Northwestern University Animal Care and Use Committee. Atropine sulfate and dexamethasone were given intramuscularly to counteract salivation and inflammatory reactions, respectively.

Atropine and phenylephrine hydrochloride were instilled in the conjunctival sacs. Contact lenses with an artificial pupil of 4–5 mm diameter and usually of one to two plus diopters were used. During the experiment the refraction was determined bilaterally with sinusoidal grating stimuli by adding (if necessary) spherical lenses in front of the eyes until a centrally located X cell achieved its best possible spatial resolution.

Tungsten microelectrodes (Levick, 1972) were used to record extracellularly from individual retinal ganglion cell axons in the right optic tract. The cats faced a grey tangent screen (mean luminance, 20 $cd \cdot m^{-2}$) on which the optic disk and other retinal landmarks were projected and drawn (Pettigrew et al., 1979). The locations of the midpoint of the receptive fields were estimated and marked using white and black wands against the tangent screen.

Stimulation

All subsequent visual stimulation was done with patterns generated on the display screen of a cathode ray tube (Joyce Electronics, Cambridge, England) with a P-31 phosphor. The display was viewed by the cat with the aid of a mirror which was adjusted so that the projection of receptive field midpoints were centered on the screen. The stimulus pattern subtended a total of 15.5° × 11° at the cat's eye. Its mean luminance was fixed at 305–315 $cd \cdot m^{-2}$. Sinusoidal grating patterns whose luminance was constant in the vertical direction were used. Contrast is

defined here as the ratio of the difference between maximum and minimum luminances to their sum. The patterns were either stationary with contrast reversing sinusoidally over time, or they drifted across the cell's receptive field. In either case, and regardless of spatial frequency, the space- and time-averaged luminance of the screen remained constant.

Experimental Protocol and Response Measurements

X cells were differentiated from Y cells (Enroth-Cugell and Robson, 1966) by the "modified null test" of Hochstein and Shapley (1976). When a unit had been isolated and identified as an X cell the mirror was rotated to null the fundamental component of the cell's discharge in response to sinusoidal modulation of the contrast of a vertical edge centered on the screen. Next, spatial frequency tuning curves were determined at different temporal frequencies. At each temporal frequency, at a range of spatial frequencies, measurements were made of (*a*) the mean discharge rate of the cell and of (*b*) the amplitude and phase of the component of the cell's discharge rate at the temporal frequency of stimulation (the fundamental Fourier component of the response). Responsivity, defined as the amplitude of the fundamental component in the linear range, divided by the contrast used to generate that fundamental, was plotted (for each temporal frequency) against spatial frequency on double logarithmic axes. The (peak to mean) amplitudes used varied between 5 and 10 impulses per second. The occurrence time of impulses was determined to the nearest 5 ms.

The Gaussian Center-Surround Model and Fitting of Data

The model fitted to the data (amplitude and phase) and the error term minimized during optimization were the same as those used by Frishman et al. (1987). However, we used a different optimization procedure. It was the Broyden-Fletcher-Goldfarb-Shanno positive definite secant update algorithm (Dennis and Schnabel, 1983).

RESULTS

Estimates of center radii were obtained by fitting the Gaussian center-surround model (Enroth-Cugell et al., 1983; Frishman et al., 1987) to spatial frequency responses measured at a range of temporal frequencies. For most cells, spatial frequency responses were measured at 2, 40, 50, 60, and 70 Hz. Fig. 1 illustrates how well this model describes the measurements of spatial frequency response at 2 and 50 Hz in one on-center X cell. The goodness of fit for both cases is typical. Another example (including other temporal frequencies) can be found in Frishman et al. (1987). A systematic mismatch between the Gaussian center-surround model and the spatial frequency responses measured for suboptimal spatial frequencies can be seen in Fig. 1 of this paper and in figures illustrating fits to spatial frequency responses in Frishman et al. (1987) and Enroth-Cugell et al. (1983). This mismatch indicates that a single Gaussian function may not adequately describe the spatial responsivity profile of the surround component of an X cell's receptive field. Since we were interested in studying center radius, and since center radius is characterized by the high spatial frequency responses of the cell (Linsenmeier et al., 1982; Frishman et al., 1987), this mismatch does not concern us in the work presented in this paper.

Given that we were not interested in the surround in this study, for most cells, measurements were restricted at high temporal frequencies to spatial frequencies that define the high spatial frequency limb of the spatial frequency response func-

tion. There is considerably more power in the maintained discharges of X cells at temporal frequencies above 20 Hz than at temporal frequencies below 20 Hz (Robson and Troy, 1987). Consequently, it is harder to measure responses reliably at these higher temporal frequencies. To improve the signal-to-noise ratio, one must collect data for a longer period of time and average the responses. Hence, our strategy was to measure frequency responses at high temporal frequencies from longer samples of data (80 s) than we used at 2 Hz (30 s). We also made frequency response measurements for many high spatial frequencies at each temporal frequency to help define the descending high spatial frequency limb. The trade-off for this greater accuracy in estimating the high spatial frequency limb of the spatial frequency response function was that we made few, if any, measurements at low spatial frequencies at high temporal frequencies. As a result, we can say nothing about the

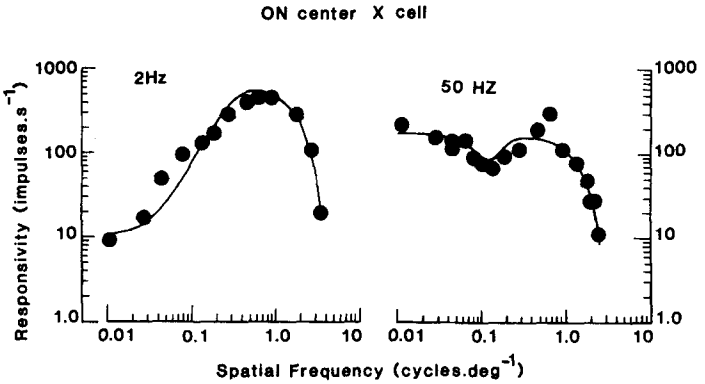

FIGURE 1. Plots of responsivity vs. spatial frequency for an on-center X cell (WS29-1) for two temporal frequencies of stimulation. The smooth curves are the best fits of the Gaussian center-surround model. Values of the parameters returned by the optimization procedure are 2 Hz: center radius, 0.164 degrees; center volume, 627 impulses/s; center phase, 1.3 degrees; surround radius, 1.10 degrees; surround volume, 621 impulses/s; surround phase, −179.4 degrees; RMS error, 0.206; 50 Hz: center radius, 0.210 degrees; center volume, 165 impulses/s; center phase, −75.6 degrees; surround radius, 2.30 degrees; surround volume, 300 impulses/s; surround phase, 75.8 degrees; RMS error, 0.190.

dependence of the spatial properties of the surround on temporal frequency, which is an interesting question in itself.

A typical set of data, as just described, collected from one on-center X cell and fitted with the Gaussian center-surround model is shown in Fig. 2. Please note that, for the 60- and 70-Hz curves, responsivities are extended to one lower order of magnitude. The goodness of fit for each curve is again typical. This can be seen by comparing the RMS errors given in the legend to Fig. 2 with values listed in Table I for the means and standard deviations across cells of the RMS (root mean square) error in fits for the different temporal frequencies used. The errors for the fits to temporal frequencies 40, 50, 60, and 70 Hz are somewhat less than what is found when the Gaussian center-surround model is fitted to spatial frequency responses measured at all spatial frequencies (i.e., including suboptimal spatial frequencies).

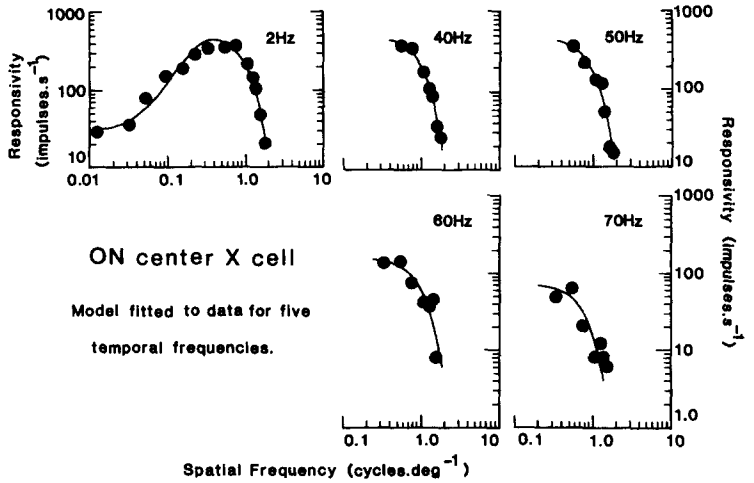

FIGURE 2. Plots of responsivity vs. spatial frequency for an on-center X cell (WS18-10) for five temporal frequencies of stimulation. The smooth curves are the best fits of the Gaussian center-surround model. Values of the parameters returned by the optimization procedure are 2 Hz: center radius, 0.314 degrees; center volume, 554 impulses/s; center phase, −8.2 degrees; surround radius, 1.49 degrees; surround volume, 524 impulses/s; surround phase, 168.2 degrees; RMS error, 0.129; 40 Hz: center radius, 0.319 degrees; center volume, 532 impulses/s; center phase, −50.7 degrees; RMS error, 0.093; 50 Hz: center radius, 0.343 degrees; center volume, 479 impulses/s; center phase, −124.8 degrees; RMS error, 0.188; 60 Hz: center radius, 0.326 degrees; center volume, 159 impulses/s; center phase, 133.4 degrees; RMS error, 0.213; 70 Hz: center radius, 0.400 degrees; center volume, 72 impulses/s; center phase, 50.3 degrees; RMS error, 0.364.

In the case of the data presented, the parameters of the model that characterize the surround component of the receptive field played no role in the fits to the 40, 50, 60, and 70 Hz spatial frequency responses.

It can be seen from the values for the center radius at different temporal frequencies given in the legend to Fig. 2 that the center radius of this cell becomes larger at temporal frequencies above 40 Hz. Since the receptive field center size of X cells varies as a function of position in the visual field and since our sample includes cells with receptive fields in a variety of visual field locations, it was useful to reference

TABLE I

Temporal frequency	RMS error
Hz	
2	0.167 (0.138)
40	0.148 (0.068)
50	0.169 (0.124)
60	0.199 (0.119)
70	0.248 (0.123)

The means and standard deviations (in parentheses) of the RMS errors for fits of the Gaussian center-surround model to the spatial frequency responses measured at different temporal frequencies.

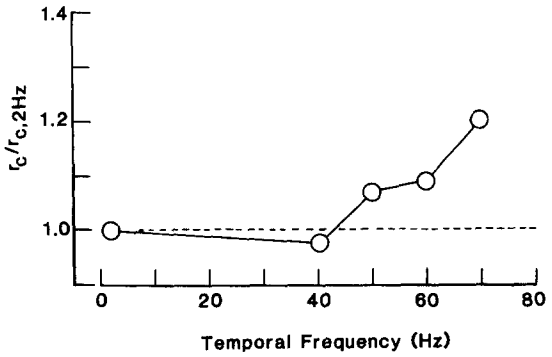

FIGURE 3. The dependence on temporal frequency of the ratio of center radius to the center radius at 2 Hz for one on-center X cell (WS16-7).

center radius at higher temporal frequencies to the center radius at 2 Hz. This is illustrated for another cell in Fig. 3, where the ratio of the center radius at a particular temporal frequency to the center radius at 2 Hz is plotted as a function of temporal frequency. This figure shows clearly that center radius increases with temporal frequency for frequencies >40 Hz. That this picture is found consistently across cells is shown in Fig. 4 where the means of the center radius ratios across cells are plotted as a function of temporal frequency. For one off-center X cell we recorded an unusually large expansion of center radius at 40 Hz. This one measurement accounts for the apparently high value at 40 Hz and for the large error bar around this point. If this one outlier is omitted, the value and its uncertainty at 40 Hz would be as illustrated by the second point (*broken lines*) included in the figure at this temporal frequency. It is likely that the real value lies between these two points, probably closer to the lower point.

There is a potential problem with our procedure of referencing all values of center radius to the center radius at 2 Hz. This is that Robson and Troy (1987) have shown, as noted earlier, that the discharge of X cells has more noise power at higher temporal frequencies than at 2 Hz. If a consequence of this is to increase the uncertainty of the estimate of center radius at these frequencies, then one might believe that center radius increases with increasing temporal frequency in a population of cells, even if it does not. We have mentioned already the steps taken to diminish uncertainty in the estimate of center radius at high temporal frequencies. However,

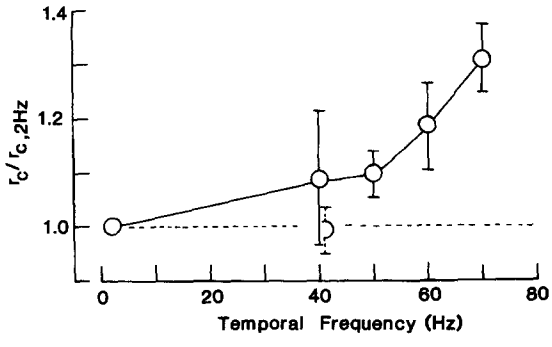

FIGURE 4. The average dependence on temporal frequency of the ratio of center radius to the center radius at 2 Hz for all X cells. The error bars are standard errors of the mean. The lower point at a temporal frequency of 40 Hz is the mean assuming that one outlier is excluded. The mean values were all significantly >1 with the exception of the 40-Hz point.

consider the possibility that in spite of these precautions the variance of our center radius does increase with temporal frequency, but center radius itself does not. By taking ratios in the manner we have done, we might observe a small increase in the "across cells" mean of the ratios with temporal frequency. If an increase in the variance were indeed the cause of our observed increase in center radius, then the expectation is that there would be equal numbers of times that the ratio was above one and below one at each temporal frequency. In addition, the standard error of the mean should increase with temporal frequency. Neither of these occurred. The numbers of cells in which the ratio was below one for each temporal frequency were as follows: 40 Hz (5 of 14 cells), 50 Hz (4 of 12 cells), 60 Hz (3 of 11 cells), and 70 Hz (1 of 9 cells).

The center radius of X cells has been found to be invariant with temporal frequency up to 24 Hz (Dawis et al., 1984) or 32 Hz (Enroth-Cugell et al., 1983). For the sake of completeness and to check that our data were consistent with these earlier studies, we measured spatial frequency responses at 10, 20, and 30 Hz in addition to our five standard temporal frequencies in one on-center and one off-center X cell. Like the earlier studies we found that center radius was unchanged across the range 2–30 Hz.

DISCUSSION

The main result of this study is that the center radius of X cells does indeed increase at temporal frequencies above 40 Hz. This result bears upon both how information is processed within the visual system and on models of the X cell receptive field.

Spatial Representation of Retinal Images

The size of the center radius of the receptive field of a retinal ganglion cell of the center-surround type is a useful metric of the spatial frequency resolution of that cell and, for a particular class of retinal ganglion cells, it serves as a good metric of the resolution for that class of cells. Resolution changes with position on the retina, but it seems that the resolution of a particular class of cells and the density of these cells at a particular retinal location are well matched (Peichl and Wässle, 1979). This is, of course, just what one would expect.

One supposes that the neural image due to a particular class of ganglion cells is represented by the activities of an array of cells with the spatial coordinates of each point in the array being the geometric center of a ganglion cell's receptive field. Under such a scheme the highest spatial frequency to which the cell type responds would be related to the local spacing of receptive field midpoints in such a way that aliasing is minimized, but with maximum efficiency. Our best estimates suggest that this is approximately true at low temporal frequencies (Troy et al., 1986). The expansion of center radius at temporal frequencies of >40 Hz indicates that the sampling density is inefficiently high at these frequencies. One might conclude from this that X cells are designed to operate at lower temporal frequencies.

Support for the idea that X cells are designed to operate at temporal frequencies below 40 Hz comes also from the fact that at temporal frequencies above 40 Hz, the responsivity of X cells begins to decline. If one factors in the greater noise in the

discharge at these temporal frequencies (Robson and Troy, 1987), the decline in signal-to-noise ratio is even more dramatic. Further, it seems that higher stations in the visual pathway produce additional temporal filtering so that the cat's cortical cells probably do not respond at all at temporal frequencies of 40 Hz or higher (Movshon et al., 1978).

Models of the X Cell Receptive Field

It was pointed out in the introduction that Koch (1984) had proposed an equivalent circuit model for the center-surround receptive fields of ganglion cells, which would lead to an increase in center radius with increasing temporal frequency, just as we have observed in the work reported in this paper. One problem with using Koch's (1984) model as a starting point for modeling X cells is that, as presented, the model assumes that the change in summing area occurs within the dendritic field of a ganglion cell. Given that the radius of the dendritic field of an X cell is believed to be smaller than the characteristic radius of the physiologically determined center Gaussian at 1 Hz (Peichl and Wässle, 1979), it is hard to see how the summing area can expand in the way Koch suggests. Refuge from this problem exists in Peichl and Wässle's acknowledgement that the dendritic field sizes of X cells they used in assessing the relationship between dendritic field dimensions and characteristic radius of the center might have been underestimated because of incomplete staining of fine branches at the extremities of the dendritic field. However, we must entertain the possibility that a model based simply on cable properties of the dendritic field may be inappropriate for describing our result. Even so, in a formal mathematical sense, Koch's model is useful. A new correspondence between the elements of the equivalent circuit and the underlying retinal circuitry may be needed, but the mathematical formulation is sound. Detwiler et al. (1978) have shown that a network of turtle rods has the kind of properties needed. We might suppose that there are networks in the cat's cone-driven retina (i.e., the functional circuitry at light levels above rod saturation) with similar properties.

Koch's cable model differs from the classical cable model because it includes an inductive element. He notes that the presence of voltage-sensitive channels in neuronal membranes is a good reason to suppose that precise circuit models of neurons will require the incorporation of active components. The inductive element is suggested as an approximation for these. The use of inductive elements in modeling active membranes dates back at least to Cole and Baker (1941). Hence, the kind of spatiotemporal coupling we observed is probably a common feature of neural networks and may be used functionally in a number of places. As noted above, our suspicion is that the spatial expansion of the center is not of major importance to the X cell's function.

Hence, when attempting to account for the spatiotemporal responses of X cells by the properties of the network of more distal retinal cells, it will be necessary to consider the expansion of X cell center radius reported in this paper. On the other hand, models of the X cell receptive field that are used to develop models of spatial vision probably sacrifice little rigor by ignoring the expansion of center radius we report.

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