Spatial and Temporal Properties of Luminosity Horizontal Cells in the Turtle Retina

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ABSTRACT Luminosity horizontal cells in the turtle retina respond approximately linearly to visual stimuli with contrast levels spanning a large part of the physiological range. We characterized the response properties of these cells under conditions of low photopic background illumination by measuring their spatial and temporal frequency transfer functions. Our experimental results indicate in two ways that, under these conditions, feedback from luminosity horizontal cells to cones does not play a major role in the mechanisms underlying the spatial and temporal tuning of horizontal cell responses. First, the shape of the spatial transfer function depended only weakly on the temporal frequency with which it was measured. Second, the shape of the temporal transfer function depended only weakly on the spatial frequency with which it was measured.

INTRODUCTION

In this paper we examine both spatial and temporal aspects of the response properties of luminosity horizontal cells in the turtle retina. By studying horizontal cells one can learn a great deal about visual information processing at the level of the outer plexiform layer. An understanding of the response properties of these cells provides a foundation for understanding the response properties of more proximal neurons.

We were concerned with characterizing the response properties of these cells under physiological stimulus conditions, and so the visual stimuli we used consisted of spatial and temporal perturbations of retinal illuminance around a mean level well above threshold. Recent studies have shown that under these conditions, horizontal cells in the retinas of the catfish (Davis and Naka, 1980) and the turtle (Tranchina et al., 1981; Naka et al., 1983) respond approximately linearly over a wide range of stimulus contrasts. In the linear regime the response properties of horizontal cells can be characterized by their spatial and temporal frequency transfer functions.

Our measurements of temporal transfer functions showed that these cells act as band-pass temporal frequency filters. The fact that the extent of the

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decline in temporal frequency sensitivity at low temporal frequencies was the same under conditions of both high and low spatial frequency indicates that this feature reflects a property of the feed-forward pathway from cones to horizontal cells and cannot be ascribed to "slow" inhibitory feedback from horizontal cells to cones. The low-frequency filtering might occur in the cone itself or in the feed-forward synapse between the cone and the horizontal cell.

A cable model for the network of horizontal cells was used to characterize our experimentally measured spatial transfer functions quantitatively. In this model the network of electrically coupled red-sensitive cones (Baylor et al., 1971; Baylor and Hodgkin, 1973; Detwiler and Hodgkin, 1979) interacts, through feed-forward and feedback synapses (Baylor et al., 1971; O'Bryan, 1973; Piccolino and Gerschenfeld, 1980; Piccolino et al., 1981), with a network of electrically coupled luminosity horizontal cells (Simon, 1973; Lamb, 1976). This model gives a receptive field with an exponential "line-spread" spatial sensitivity profile. We will show that the exponential space constant depended only weakly on temporal frequency. This result implies that there is little dynamic filtering of signals as they propagate within the network of electrically coupled horizontal cells. We conclude that feedback from horizontal cells to red-sensitive cones is either weak or weakly dependent on temporal frequency.

METHODS

Biological Preparation

All experiments were done on eyecups excised from the turtle *Pseudemys scripta elegans*. After the turtles were decapitated and pithed, the eyes were excised and hemisected in dim orange light. A substantial amount of the vitreous was removed from the eyecup and the eye was put into the recording chamber. The temperature of the eye was maintained at 18°C using a thermoelectric heat pump (MELCOR, Trenton, NJ) to heat or cool the chamber and a thermistor to monitor the temperature. The thermistor output controlled a feedback network that maintained the temperature within 0.1°C. Moist oxygen was blown on the retina. We usually used 100% O₂ but have also used 95% O₂-5% CO₂ with no apparent difference. The retina was stable for up to 4 h.

Recordings

Intracellular recordings were obtained from cells located in the area dorsal to the visual streak. We used fine micropipettes made with either a Brown-Flaming (Sutter Instrument Co., San Francisco, CA) puller or a modified Livingston puller. The tip diameters measured with a scanning electron microscope were $\leq 0.1 \mu\text{m}$, and the resistances, when filled with 4 M potassium acetate, were $>100 \text{ M}\Omega$. Electrodes were advanced with a hydraulic microdrive (David Kopf Instruments, Tujunga, CA) or a piezoelectric micropositioner (Burleigh Inchworm; Burleigh Instruments Inc., Fishers, NY). Signals were amplified with a negative-capacitance bridge amplifier (designed and built in the Rockefeller University Electronics Shop). A sometimes neglected consequence of high-impedance electrodes is the distortion of the high-frequency components of neural responses caused by significant electrode capaci-

tance. We adjusted the amplifier to neutralize this capacitance in order to obtain an accurate measurement of these high-frequency responses. To facilitate cell penetration, an excess amount of capacitance was used for a brief period, causing the circuit to oscillate. The amplifier was modified so that the duration and amplitude of this "buzzing" could be controlled. Neural responses were displayed on an oscilloscope and recorded and averaged using a microprocessor (see below). To aid in stability, the preparation and optical system were mounted on a pneumatic vibration isolation table (Newport Research Corp., Fountain Valley, CA).

Visual Stimulator

The visual stimulus was provided by a three-channel projection system in which two beams are from a conventional optical system and the third is from an intensity-modulated raster of lines on an oscilloscope screen (model 5103 [Tektronix Inc., Beaverton, OR], P31 phosphor, without internal graticule). All three beams were superimposed with beam splitters and imaged in the plane of the retina with a projection lens that provided an object/image ratio of 10:1. The position of this lens could be adjusted with a manual hydraulic manipulator (Narishige, Tokyo, Japan). We focused the stimulus by using the response of a cell as an indicator. A fine pattern was modulated and the position of the lens was changed to optimize the neural response.

The electronic instrument used to control the oscilloscope pattern and to average the neural responses was designed and built in the Rockefeller University Electronics Shop. A more refined instrument of the same type is described by Milkman et al. (1978). The basic idea behind the visual stimulator-averager is the use of a microprocessor as an organizer that can coordinate and control logical and analog circuits responsible for the production of the electronic visual stimulus. Some of the signals under the microprocessor's control include the spatial waveform, the temporal modulation, spatial offset, and the orientation angle of the pattern. The pattern, composed of 512 raster lines, is presented repetitively at a frame rate of 256 Hz and a line rate of 192 kHz. The circuitry for the spatial waveform was designed so that spatial frequency (cycles per millimeter) and temporal rate of drift (hertz) are independent variables. This allows one to measure, for example, the spatial frequency response of a cell to drifting gratings, all presented at a constant drift rate in hertz.

The contrast of a sinusoidal grating on the retina may be defined as $(I_{\max} - I_{\min}) / (I_{\max} + I_{\min})$, where $I_{\max}$ is the peak retinal illuminance of the grating and $I_{\min}$ is the illuminance at the trough of the grating. The contrast on the oscilloscope screen was linear, with modulation depths up to 0.9 contrast, and all our measurements were made in this range.

White Light and Monochromatic Light Stimuli

The two channels of the conventional optical system use 45-W tungsten filament, quartz iodide lamps (GE T2 1/2 Q). In one channel, a high-intensity monochromator (half-amplitude bandwidth set at 15 nm) (Bausch & Lomb, Inc., Rochester, NY) is interposed. Retinal illuminance and irradiance were measured by means of a model 40A photometer (United Detector Technology Inc., Santa Monica, CA) with its photocell placed in the plane of the retina. The intensity of each beam was varied by the use of Inconel neutral density filters (Bausch & Lomb, Inc.). Stimulus onset and offset were controlled by electromagnetic shutters (Uniblitz; Vincent Associates, Rochester, NY) with rise and fall times of <1.5 ms and were timed with digital timers built in the Rockefeller University Electronics Shop.

The maximum irradiance of the monochromatic lights in the retinal plane varied between 1.2×10^{-7} and 5.0×10^{-7} W/cm² for wavelengths between 450 and 700 nm. The maximum illuminance of the oscilloscope in the retinal plane was 2 lm/m². By adjusting the intensity of a 630-nm monochromatic light to produce the same amplitude of response from a luminosity horizontal cell as a step of light from the oscilloscope, and by measuring the power of the monochromatic light, we calculated that the mean retinal illuminance produced by the oscilloscope corresponds to $\sim 2.0 \times 10^{11}$ quanta/s·cm² (6.3×10^{-8} W/cm²) at 630 nm. A measurement made on one luminosity horizontal cell indicated that this background light hyperpolarized the cell by 15 mV, which was $\sim 25\%$ of the amplitude of the response to a saturating flash of light.

Luminosity Horizontal Cell Identification

Luminosity horizontal cells were identified by several characteristic features. The cells were located at a depth of 110–140 μ m from the surface of the retina, as measured by the microdrive unit used to advance the microelectrode. These cells hyperpolarized to all wavelengths of light. The size and waveform of the response to a flash of light were characteristic of luminosity horizontal cells. These cells lacked an antagonistic center-surround receptive field organization. All luminosity horizontal cells in the present study had large receptive fields. The spatial sensitivity profiles were characterized by exponential space constants that were all $>343 \mu$ m. These cells probably correspond to the L1-type (Simon, 1973) of luminosity horizontal cell.

Grating Stimuli

A drifted sinusoidal grating stimulus is defined by

$$I(x, t) = I_0[1 + m\cos(2\pi kx - 2\pi ft)],$$

where I_0 is the mean retinal illuminance, m is the contrast (consistent with the definition above), f is the temporal frequency and also the number of spatial cycles per second that pass a point on the retina (the drift rate), and k is the spatial frequency in cycles per millimeter. In this paper the quantity $2\pi f$ is called ω , and the quantity $2\pi k$ is called ξ . Horizontal cells, in the linear range of operation, respond to a drifting sinusoidal grating with a sinusoidal voltage fluctuation at a temporal frequency equal to the drift rate f (Tranchina et al., 1981).

Spatial and Temporal Transfer Functions

The spatiotemporal transfer function gives the amplitude per unit contrast and phase of the response (or, to be more exact, the fundamental Fourier component of the response) at each spatiotemporal frequency pair (ξ, ω) . The spatial frequency transfer function is a cross section of the spatiotemporal transfer function at a fixed temporal frequency. It measures the amplitude and phase of the response as a function of spatial frequency when each grating is drifted across the retina at the same rate in hertz.

The temporal frequency transfer function is a cross section of the spatiotemporal transfer function at a fixed spatial frequency. It measures the amplitude and phase of the response to a drifting sinusoidal grating of fixed spatial frequency, as a function of drift rate in hertz. The special case of a grating with zero spatial frequency corresponds to sinusoidal modulation of spatially homogeneous retinal illuminance.

Response Averaging

The graded-potential responses were measured with an analog-to-digital converter by sampling at a rate of 256 Hz and storing the sums in N bins phased to the stimulus cycle, where N is given by the following rule. The number of data bins N per stimulus cycle at frequencies <8 Hz was 64. For frequencies of ≥ 8 Hz, the number of data bins per stimulus cycle was equal to 256 divided by the stimulus frequency in hertz; for example, 32 bins for 8 Hz, 16 bins for 16 Hz, and 8 bins for 32 Hz. This dependence of bin number on stimulus frequency is a consequence of the fixed data sampling rate of 256 Hz (the frame rate of the raster display). The averaged signals were then read out and stored on floppy disks for later harmonic analysis with a PDP 11/45 computer (Digital Equipment Corp., Marlboro, MA).

Data Analysis

Harmonic analysis of neural response to periodic stimuli was performed by taking the discrete Fourier transform (Cooley and Tukey, 1965) of the array, which is composed of signal-averaged responses contained in the N bins. In this way we determined the linear component of the response and the nonlinear frequency components at integer multiples of the input frequency.

A least-squares method of curve fitting on the complex plane was used to fit experimentally measured spatial and temporal transfer functions to various mathematical models. Spatial and temporal transfer functions are complex-valued functions. Therefore, in this method, a distance function is defined that is equal to the sum of the squares of the distances (on the complex plane) between each data point and the corresponding value of a theoretical transfer function derived from a model. This distance function was minimized with respect to the model parameters by means of a minimization routine called FMFP, which is contained in the IBM Scientific Subroutine Package. If we define the complex number d_i as the amplitude and phase of the transfer function measured at the i th frequency and t_i as the corresponding value given by the model, the function to be minimized, F , is given by $F = \sum_{i=1}^N |t_i - d_i|^2$. The relative error is given by $(F/N)^{1/2}/\bar{d}$, where $\bar{d}$ is the average amplitude for the N points.

RESULTS

Spatial Properties of Luminosity Horizontal Cells

We characterized spatial aspects of the response properties of luminosity horizontal cells by measuring their spatial frequency transfer functions. Fig. 1 shows the responses of one horizontal cell from which a spatial transfer function was computed. These are the responses to sinusoidal gratings of various spatial frequencies, all of which were drifted across the retina at a rate of 4 Hz. For each spatial frequency, the filled circles plot the signal-averaged response and the continuous line plots the best-fit sinusoid. The spatial transfer function at 4 Hz is defined by the amplitude (per unit contrast) and phase of the best-fit sinusoid (or, equivalently, the fundamental Fourier component of the response) at each spatial frequency.

Fig. 2 shows spatial transfer functions of one cell (the same cell as in Fig. 1) measured at 0.25, 1, 4, 8, and 16 Hz. The amplitude of the spatial transfer

function scaled simply with temporal frequency in the 0.25–8 Hz range. This is reflected in Fig. 2 by the fact that the amplitude curves for the spatial transfer functions measured at 0.25, 1, 4, and 8 Hz are parallel; they nearly superimpose with appropriate vertical shifts on the log-amplitude axis. The

FIGURE 1. Responses of a luminosity horizontal cell to sinusoidal gratings of various spatial frequencies that were drifted across the retina at a rate of 4 Hz. Beside each response is the spatial frequency and contrast of the grating and a calibration marker. Filled circles plot the signal-averaged response. The response was sampled at 64 times per stimulus cycle and averaged over 64 repetitions. (Every other point is plotted for sake of clarity.) The continuous line plots the best-fit sinusoid at a frequency of 4 Hz. The temporal phase of the response is different for each spatial frequency because the center of the receptive field is not at the origin of the stimulus coordinate system; the temporal phase of the response consequently has a component that is proportional to spatial frequency.

lower panel of Fig. 2 shows that at each temporal frequency, there was little variation in the temporal phase of the response with spatial frequency and that the phase of the spatial transfer function simply shifted vertically with temporal frequency.

FIGURE 2. Spatial transfer functions of a luminosity horizontal cell measured at 0.25, 1, 4, 8, and 16 Hz. The amplitude of the fundamental Fourier component of the response is plotted (on log-log coordinates) in the upper panel and the phase (on linear-log coordinates) in the lower panel. Data points are plotted with filled symbols for zero spatial frequency and open symbols for spatial frequencies > 0 . Continuous lines come from a cable model for the horizontal cell network. In this and all subsequent figures, the contrast values of the stimuli varied between 0.3 and 0.9, depending upon the sensitivity of the response at the spatial and temporal frequency of the stimulus. The amplitude per unit contrast does not depend on the contrast of the stimulus, because horizontal cells respond approximately linearly and because we pick out the amplitude of the fundamental component of the response with Fourier analysis.

We measured spatial transfer functions at several different temporal frequencies in the range of 0.25–8 Hz for 11 luminosity horizontal cells. In all cases, as in Fig. 2, the shape of the spatial transfer function depended little on temporal frequency in this range. Spatial transfer functions were measured at temporal frequencies >8 Hz (12 and/or 16 Hz) for 5 of these 11 cells. The invariance of the shape of the spatial transfer function with temporal frequency extended to frequencies >8 Hz for three of these cells and broke down for two cells at >8 Hz.

The amplitude curve of the spatial transfer function, which was measured at 16 Hz (Fig. 2), cut off more abruptly with spatial frequency than did those curves measured at lower temporal frequencies. This is an indication that, for this cell, the receptive field spatial sensitivity profile is somewhat broader for higher temporal frequency signals. The smooth curve drawn through the 16-Hz data points is similar to the curves for the lower temporal frequencies, except that it is shifted to the left by a factor of ~ 1.7 on the spatial frequency axis. Thus, the receptive field was $\sim 70\%$ larger for 16-Hz signals than it was for signals between 0.25 and 8 Hz. We observed a similar broadening of the receptive field at a high temporal frequency for one other cell.

The approximate invariance of the spatial transfer function over a wide range of temporal frequencies is an indication that feedback from horizontal cells to cones does not play a major role in determining the shape or extent of the receptive field spatial sensitivity profile for signals in that range of temporal frequencies. Consider how we would expect the spatial transfer function to behave if feedback did play a significant role. If, for example, feedback were strong and the feedback loop acted as a low-pass temporal frequency filter, then feedback would play its most significant role at low temporal frequencies. As the low temporal frequency signal propagates in the network, the effect of feedback would be to add, at each point, an antagonistic signal to the direct signal generated by light. Consequently, low temporal frequency signals would suffer greater attenuation with distance than high-frequency signals. Thus, at low temporal frequencies the receptive field would be narrower and the corresponding spatial transfer function would be broader than at high temporal frequencies, which is contrary to what we found in most cases.

Temporal Properties of Luminosity Horizontal Cells

Fig. 3 shows the full-field temporal transfer function of a luminosity horizontal cell (in a Bode plot format). The upper panel plots the amplitude (per unit contrast) and the lower panel the phase of the response to sinusoidal modulation of spatially homogeneous retinal illuminance, as a function of temporal frequency. The temporal transfer function of this cell (as well as all others) had band-pass characteristics. There was a decline in temporal frequency sensitivity in the low-frequency range between 4 and 0.125 Hz; the amplitude of the response at 4 Hz, the peak frequency, was approximately twice that at 0.125 Hz. There was a steep decline in temporal frequency sensitivity at >4 Hz; the amplitude of the response at 32 Hz was ~ 500 times

smaller than that at 4 Hz. The phase of the response led that of the stimulus slightly at 0.125 Hz, and the phase lead decreased with increasing temporal frequency. At 1 Hz the phase of the response began to lag, and the phase lag increased sharply with increasing frequency. At 32 Hz the phase of the response lagged by $\sim 3.5 \pi$ rad.

FIGURE 3. Temporal transfer function of a luminosity horizontal cell. Amplitude of the fundamental Fourier component of the response is plotted (on log-log coordinates) in the upper panel, and phase (on linear-log coordinates) is plotted in the lower panel. Data points are plotted with open circles for each frequency and also with open squares for those frequencies at which we made two measurements (1, 2, 12, 20, 24, 28, and 32 Hz). The continuous lines come from a discrete-stage model for horizontal cell dynamics (Eq. 1).

FIGURE 4. (A) Temporal transfer function of a luminosity horizontal cell measured at 0 cycles/mm (filled circles) and at 1.0 cycles/mm with drifting gratings (open circles). Amplitude is plotted in the upper panel and phase in the lower panel. When a temporal transfer function is measured with drifting gratings, there is a constant offset in the temporal phase of the response unless the center of the receptive field is at the origin of the stimulus coordinate system. The temporal phase plot for the grating temporal transfer function was obtained by subtracting from the measured phase the constant phase that gives the best superposition of the grating and full-field phases at low temporal frequencies. (B) (*opposite*) Amplitude of the response for the two conditions replotted after shifting the amplitude curves for the two conditions so that they nearly superimpose at low temporal frequencies. The continuous and dashed lines in A and B are cubic splines and are drawn as a visual aid.

Recall that Fig. 2 showed that the spatial transfer function is approximately independent of temporal frequency over the range of 0.25–8 Hz. This implies that over the 0.25–8-Hz range, the temporal transfer function should simply scale in amplitude with spatial frequency. That is to say, the amplitude of the

temporal transfer function should shift vertically on the log-amplitude axis with a change in spatial frequency, whereas the phase should remain unchanged. We found this to be the case.

Fig. 4A shows temporal transfer functions of one cell (the same cell as in Fig. 3) measured at zero spatial frequency and at a spatial frequency of 1 cycle/mm with drifting gratings. Notice that the 1-cycle/mm curve is shifted in amplitude by a factor of ~ 16 . The phase curves for the two conditions are nearly identical. Fig. 4B shows the amplitude curves for the two stimulus conditions replotted after shifting the grating curve vertically. Notice that

FIGURE 4.

the temporal transfer functions for the two conditions are very similar over the 0.125–8-Hz range after this shift operation. The two curves begin to separate above 8 Hz, with the temporal transfer function for the grating condition declining slightly more steeply than the full-field transfer function.

IMPLICATIONS WITH RESPECT TO FEEDBACK AND MEMBRANE IMPEDANCE Cones have much smaller receptive fields than horizontal cells (Detwiler and Hodgkin, 1979; Lamb, 1976). Therefore, a high spatial frequency grating that produces a barely measurable response in the horizontal cell will produce a robust response in the cone. When the retina is stimulated

with such a grating, the direct response of the cone is hardly antagonized by a modulating component of horizontal cell feedback. Thus, the temporal transfer function measured at a high spatial frequency measures the dynamics of the horizontal cell response in the absence of temporal filtering introduced by feedback. Strictly speaking, this is correct only if the magnitude of feedback depends on the horizontal cell membrane potential in the region of the neuron from which one records with a microelectrode.

For the cell in Fig. 4, 1 cycle/mm was high enough that the temporal transfer function at this spatial frequency was a good indication of the response dynamics of this cell in the absence of the effects of feedback. The response amplitudes for the grating condition were attenuated by a factor of ~ 16 compared with the full-field responses. We have measured spatial transfer functions of red-sensitive cones in the turtle retina and have found that the amplitude of the response to a 1-cycle/mm grating was approximately equal to the amplitude of the response to full-field modulation. The fact that the full-field and grating temporal transfer functions of the horizontal cell were virtually identical in shape indicates that the decline in temporal frequency sensitivity at low temporal frequencies cannot be attributed to feedback; this feature of the horizontal cell temporal transfer function must result from a property intrinsic to the feed-forward pathway between the cone and horizontal cell. The feed-forward synapse between cone and horizontal cell may be responsible for part of this low-frequency filtering (Schnapf and Copenhagen, 1982).

The fact that the amplitude of the full-field temporal transfer function declined less steeply than did the grating transfer function above 8 Hz suggests that feedback and/or the horizontal cell membrane impedance improved the frequency response at high temporal frequencies. The amplitude of the full-field response at 12 Hz in this cell was boosted by a factor of ~ 2 . Similar measurements made on two other cells gave similar results.

To interpret these results, it is helpful to examine the consequences of feedback and membrane impedance in the time domain as well as in the temporal frequency domain. The temporal impulse response at 1 cycle/mm spatial frequency is computed by taking the Fourier transform of the grating temporal transfer function; this impulse response represents what the waveform of the response to a flash of spatially homogeneous light would be like in the absence of feedback and filtering by the horizontal cell membrane impedance. The time to peak of the full-field impulse response (Fig. 5) was 90 ms, and the time to peak of the grating impulse response (not shown) was 102 ms. Thus, feedback and/or horizontal cell membrane impedance sped up the dynamics of the response by $\sim 10\%$.

A DISCRETE-STAGE MODEL FOR HORIZONTAL CELL DYNAMICS We characterized the dynamics of each horizontal cell by fitting the cell's measured temporal transfer function with an analytic function, $T(\omega)$, of the form:

$$T(\omega) = G T_H(\omega) T_L(\omega). \quad (1)$$

G is a constant gain factor, which determines the contrast sensitivity of the response. Changing G simply shifts the amplitude on the Bode plot vertically.

$T_H(\omega)$ is the transfer function of a one-stage high-pass filter and has the form:

$$T_H(\omega) = \frac{\tau_b(1 + i\omega\tau_a)}{\tau_a(1 + i\omega\tau_b)}, \quad (2)$$

where τ_a and τ_b are two time constants that characterize the high-pass filter, and $\tau_a > \tau_b$. At zero temporal frequency, the amplitude of $T_H(\omega)$ is equal to τ_b/τ_a , and as the frequency increases, the amplitude of $T_H(\omega)$ grows monotonically to its asymptotic value of 1. The stage of high-pass filtering is used to fit the low-frequency end of the horizontal cell temporal transfer function.

$T_L(\omega)$ is the transfer function of a multistage low-pass filter, which is used to fit the high-frequency end of the horizontal cell temporal transfer function and has the form:

$$T_L(\omega) = \prod_{k=1}^N 1/(1 + i\omega\tau_k). \quad (3)$$

FIGURE 5. Temporal impulse response corresponding to the temporal transfer function in Fig. 3. The amplitude (in arbitrary units) of the response to a brief increase in retinal illuminance above the mean level is plotted as a function of time. This impulse response was computed by taking the inverse Fourier transform of the temporal transfer function plotted in Fig. 3.

For each cell we chose τ_k according to two simple schemes (Baylor et al., 1974). In scheme A, $\tau_k = \tau$ for all k , and in scheme B, $\tau_k = \tau/k$. In some cases, one or the other scheme fit the data better, but in a few cases the two schemes fit almost equally well.

The impulse response of a low-pass filter with a temporal transfer function of the form given by scheme A, which we will call $I_A(t)$, is given by:

$$I_A(t) = \frac{1}{(N-1)!} \left(\frac{t}{\tau}\right)^{N-1} e^{-t/\tau}. \quad (4)$$

The impulse response of the low-pass filter with a temporal transfer function of the form given by scheme B, which we will call $I_B(t)$, is given by:

$$I_B(t) = \frac{N}{\tau} e^{-t/\tau} (1 - e^{-t/\tau})^{N-1}. \quad (5)$$

In summary, the temporal transfer function is characterized by five parameters: G , the gain; τ_a and τ_b , two time constants for the high-pass filter; N , the number of low-pass filter stages; and τ , a time constant of the low-pass filter.

The continuous curve in Fig. 3 was computed from a particular equation of the form of Eq. 1 in which scheme A was used for choosing the time constant of the low-pass filter. In this case,

$$T(\omega) = G \frac{\tau_b (1 + i\omega\tau_a)}{\tau_a (1 + i\omega\tau_b)} \left(\frac{1}{1 + i\omega\tau} \right)^N,$$

where $G = 16.3$ mV per unit contrast; $\tau_a = 221$ ms; $\tau_b = 80$ ms; $N = 10$; and $\tau = 8.6$ ms.

To compare our results on horizontal cell dynamics with those of others who did their analysis in the time domain, Fig. 5 shows the full-field impulse response, which corresponds to the temporal transfer function of the cell in Fig. 3. [This was computed by taking the Fourier transform of the equation for $T(\omega)$ above.] This impulse response corresponds to the response one would measure to a brief flash of light superimposed on the mean level of retinal illuminance used in this study. The slow rise of the impulse response to its peak is a reflection in the time domain of the steep decline in temporal frequency sensitivity at high frequencies. The depolarizing overshoot is a reflection of the low-frequency decline in temporal frequency sensitivity.

Table I lists the best-fit values of five parameters, G , τ_a , τ_b , N , and the first moment t_L of the impulse response of the low-pass filter stage, for the two curve-fitting schemes A and B, for each of 10 luminosity horizontal cells. Also listed in Table I is the time, t_p , at which the full-field impulse response of each cell [computed by taking the Fourier transform of $T(\omega)$, i.e., Eq. 1] reached its peak value. The time constants for the high-pass-filter stage were large compared with those of the low-pass stage. This indicates that the mechanism that is responsible for high-pass filtering operates on a slow time scale. The high-pass filtering is probably a manifestation of a form of light adaptation (Normann and Perlman, 1979). The ratio τ_a/τ_b , which measures the extent of high-pass filtering and is roughly equal to the ratio of amplitude of the response at the peak frequency to that at the lowest measured frequency, had an average value of ~ 2 . The number of stages of low-pass filtering, N , had an average value of 10. This large number of stages was necessary in order to fit the large phase lag of the response at high frequencies; this is a reflection in the temporal frequency domain of the slow rate at which the temporal impulse response reaches its peak value. The time to peak of the horizontal cell impulse response had an average value of 86 ms.

The exponential space constant (see next section), which characterizes the extent of the receptive field spatial sensitivity profile, had an average value of 460 μm . For the 10 cells in Table I, there is no apparent correlation between response dynamics and receptive field size.

TABLE I
*Temporal Properties of Luminosity Horizontal Cells**

Cell	<i>G</i>	τ_a	τ_b	<i>N</i>	Scheme	t_L	t_P	σ	Relative error
	<i>mV/contrast</i>	<i>ms</i>	<i>ms</i>			<i>ms</i>	<i>ms</i>	μm	
2	9.9	452	218	10	A	96	86	522	0.06
	11.6	312	139	13	B	105	82		0.10
8	18.8	503	217	10	A	102	90	440	0.08
	22.3	371	142	13	B	112	86		0.12
10	11.2	694	407	8	A	106	90	419	0.06
	12.2	530	298	10	B	113	86		0.05
11	20.1	711	367	10	A	106	94	629	0.08
	22.1	535	265	13	B	114	90		0.06
14	8.6	906	555	8	A	104	90	431	0.05
	9.3	648	385	9	B	111	86		0.04
15	9.6	670	383	9	A	88	78	407	0.11
	10.5	516	282	10	B	94	74		0.08
18	12.2	262	116	10	A	88	78	517	0.14
	16.6	184	64	13	B	100	74		0.18
19	11.2	743	399	8	A	123	106	343	0.07
	12.0	591	308	11	B	128	102		0.08
20	11.2	477	248	8	A	116	98	387	0.06
	14.2	305	134	8	B	132	94		0.10
21	16.3	221	80	11	A	86	74	504	0.14
	23.5	172	46	16	B	98	74		0.17

* These data are from a collection of 21 cells for which we measured temporal and/or spatial transfer functions.

A Cable Model for Horizontal Cells

We found that a cable model for luminosity horizontal cells was useful for interpreting the spatiotemporal properties of these cells quantitatively.

THE CONTINUUM APPROXIMATION The lateral spread of signal in a network of electrically coupled horizontal cells has been treated analytically by approximating the network as a single flat cell (Naka and Rushton, 1967; Marmarelis and Naka, 1972; Lamb, 1976; Nelson, 1977; Krausz and Naka,

1980). The network of cones has been analyzed using a similar continuum approximation (Detwiler and Hodgkin, 1979). The receptive fields of red-sensitive cones are small enough compared with those of luminosity horizontal cells that the electrical coupling of cones can be ignored without any serious loss of accuracy in the spatiotemporal model for the luminosity horizontal cell. We measured the responses of horizontal cells to visual stimuli, which varied in one spatial dimension. Under these stimulus conditions, the continuum approximation for the horizontal cell amounts formally to approximating the horizontal cell network as a one-dimensional cable. The model for the cone-horizontal cell network is depicted in Fig. 6.

EXPONENTIAL LINE-SPREAD FUNCTION One can measure a spatial sensitivity profile (or a line-weighting or a line-spread function) of the horizontal cell receptive field by measuring the amplitude and phase of the response to sinusoidal modulation of the illuminance of a narrow bar as function of temporal frequency and position x of the bar with respect to the center of the receptive field. According to the generalized cable model of Krausz and Naka (1980), which considers both spatial and temporal aspects of signal propagation and takes into account feedback from horizontal cells to cones, the temporal transfer function for this response is given by (see Appendix):

$$W(x, \omega) = \frac{T(\omega)}{2\lambda(\omega)} e^{-|x|/\lambda(\omega)}. \quad (6)$$

$T(\omega)$ is the temporal frequency transfer function for the response to modulation of spatially homogeneous retinal illuminance. $\lambda(\omega)$ is an exponential space scale which is, in general, complex valued. According to the Krausz and Naka (1980) model, λ depends on temporal frequency to the extent that the membrane impedance of the horizontal cell and the strength of feedback from horizontal cells to cones depend on temporal frequency. If membrane impedance does not act as a significant dynamic filter and if feedback is either weak or weakly dependent on temporal frequency, λ is just a real constant. Most of our data are consistent with a real and constant λ .

THE SPATIOTEMPORAL TRANSFER FUNCTION As part of our program of characterizing the response properties of horizontal cells by making measurements in the frequency domain, we have measured cross sections of the spatiotemporal transfer function (Figs. 1–4). The spatiotemporal transfer function (Brodie et al., 1978) is related to the line-spread function by the Fourier transform operation. There are a number of reasons why we prefer to do the analysis entirely in the frequency domain. Visual stimuli, which are periodic both in time and space, are natural stimuli to use when one must present the stimulus repetitively in order to signal-average the response. Fourier analysis of the response to sinusoidal stimuli provides an effective method of digitally filtering the response waveform to separate signal from noise. Finally, it is sometimes difficult to measure a response to the alternative impulsive stimuli with stimulus strengths that do not drive the neuron out of its linear range of operation.

The spatiotemporal transfer function $V(\xi, \omega)$, which corresponds to the

line-spread function above, is given by

$$V(\xi, \omega) = \frac{T(\omega)}{1 + \lambda^2(\omega) \xi^2} \quad (7)$$

FIGURE 6. Local circuit element of the cone-horizontal cell network. The boxes represent transductions performed by the various components in the network. *C* represents the phototransduction process in which light is transformed into cone membrane potential. *F* represents the feed-forward synapse; the input to *F* is the cone membrane potential and the output is post-synaptic current, i_s , across the horizontal cell membrane. *Z* is the horizontal cell membrane impedance, which transforms membrane current into membrane potential. *B* represents the feedback synapse; the input to *B* is the horizontal cell membrane potential, V , and its output is the feedback component of the cone membrane potential. The resistance for the lateral spread of current within the network of electrically coupled horizontal cells is labeled r_l . Σ represents a summation point at which the component of cone membrane potential generated directly by light and the component generated indirectly by feedback are combined. It can be shown (see Appendix in conjunction with Krausz and Naka, 1980, Appendix B; Tranchina, 1981) that this model results in a spatio-temporal transfer function of the form given by Eq. 7.

TEST OF THE CABLE MODEL The cable model for the cone-horizontal cell network can be tested by determining whether experimentally measured spatiotemporal transfer functions of horizontal cells can be fit by the theoretical spatiotemporal transfer function of the model, Eq. 7. The horizontal cell spatiotemporal transfer function can be constructed by measuring spatial transfer functions at a series of temporal frequencies.

At a given temporal frequency, ω_k , the spatial transfer function, according to the model, should be fit by an equation of the form:

$$V(\xi, \omega_k) = \frac{T(\omega_k) e^{-i\xi x_0}}{1 + \lambda^2(\omega_k) \xi^2} \quad (8)$$

The term $e^{-i\xi x_0}$ in the numerator is necessary if the receptive field center is not at the origin of the coordinate system. We measured spatial transfer functions at two to five different temporal frequencies for each of 11 cells and at a single temporal frequency for an additional 8 cells. The various temporal frequencies spanned the range from 0.25 to 16 Hz. Eq. 8 provided a good fit for all the spatial transfer functions. These results provide evidence that the model gives an adequate description of the spatial and temporal properties of luminosity horizontal cells in the turtle retina. A more exhaustive test of the model would involve showing that Eq. 8 fits experimentally measured spatial functions of each cell at all temporal frequencies of physiological significance. To test the model rigorously, one would have to show that the variations in λ with temporal frequency make good sense in terms of the temporal frequency-dependent behavior of feedback and horizontal cell membrane impedance.

In our fitting procedure we constrain the model to fit the data exactly at zero spatial frequency in order to keep the number of free parameters to a bare minimum. In other words, we regard $T(\omega_k)$ as given by direct measurement of the amplitude and phase of the response to modulation of spatially homogeneous retinal illuminance at frequency ω_k . This leaves us with three free parameters in Eq. 8. Two parameters are the modulus and argument of the complex number $\lambda^2(\omega)$, which we will call $\rho^2(\omega)$, and $2\theta(\omega)$, respectively [i.e., $\lambda^2(\omega) = \rho^2(\omega)e^{i2\theta(\omega)}$]. The third parameter, x_0 , the position of the receptive field center with respect to the origin, is not a completely free parameter in that it is constrained to have the same value at all temporal frequencies. x_0 varies from cell to cell because the cells' receptive field centers are at different positions with respect to the origin of the stimulus display.

Fig. 2 shows experimental and theoretical spatial transfer functions (plotted with symbols and continuous lines, respectively) of one cell at 0.25, 1, 4, 8, and 16 Hz. (In the temporal phase plots the component of phase lag contributed by spatial offset of the receptive field center [i.e., $-\xi x_0$] is subtracted off to reveal more clearly the features of the response, which are physiological in origin.) By visual inspection, we judged the goodness of fit obtained in this case to be typical of that obtained for all 19 cells.

SPATIAL TRANSFER FUNCTIONS AND THEIR DEPENDENCE ON TEMPORAL FREQUENCY The character of the spatial transfer function at a particular

temporal frequency ω_k is completely determined by $\lambda^2(\omega_k)$ (refer to Eq. 8); $T(\omega_k)$ is simply a factor that measures the relative sensitivity of the cell to modulation of retinal illuminance at the frequency ω_k . This is apparent if one defines a normalized spatial transfer function, which is the ratio of the spatial transfer function evaluated at spatial frequency ξ to the spatial transfer function evaluated at zero spatial frequency [i.e., $V(\xi, \omega_k)/V(0, \omega_k)$]. This normalized spatial transfer function is given by $1/[1 + \lambda^2(\omega_k)\xi^2]$. (We are ignoring the component of temporal phase, which is due to spatial offset of the receptive field center and is of no significance in our subsequent discussion.) Therefore, the normalized spatial transfer function depends on the temporal frequency at which it is measured to the extent that $\lambda^2(\omega)$ depends on temporal frequency.

Table II summarizes results obtained in fitting Eq. 8 to experimentally measured spatial transfer functions of 19 cells. For each cell the best-fit values of the parameters, $\rho^2(\omega)$ and $2\theta(\omega)$ [the modulus and argument of $\lambda^2(\omega)$, respectively] are listed. The data presented in Table II indicate that there is relatively little variation in the magnitude and phase of $\lambda^2(\omega)$ over the 0.25–8-Hz range of temporal frequencies. However, in two out of five cells for which spatial transfer functions were measured at frequencies both above and below 8 Hz, the magnitude of $\lambda^2(\omega)$ did increase somewhat at the higher frequencies (cells 2 and 9 in Table II). Nevertheless, the relative variations in $\lambda^2(\omega)$ with temporal frequency were much smaller than those in $T(\omega)$. In cell 9, for example, the magnitude of $\lambda^2(\omega)$ increased by a factor of 2.4 between 2 and 12 Hz, whereas the magnitude of $T(\omega)$ decreased by a factor of 10.5.

DEPENDENCE OF SPACE CONSTANT ON TEMPORAL FREQUENCY Some of the implications of the temporal frequency-dependent behavior of $\lambda^2(\omega)$ may be more clearly understood in the domain of space rather than spatial frequency. The space constant, $\sigma(\omega)$, for the decrement of response amplitude with the distance for a stimulus consisting of a sinusoidal modulation of the illuminance of a narrow bar at frequency ω is determined by $\lambda^2(\omega)$ (see Appendix). In the special case where λ is a real number, $\sigma = \lambda$. Most of our data indicate that λ is very nearly real. When λ is real, $\theta = 0$, and the data in Table II show that θ was usually very close to 0. Table II lists the values of $\sigma(\omega)$ derived from measurements of spatial transfer functions, and Fig. 7 plots the space constants of those cells for which we measured the spatial transfer functions at several different temporal frequencies.

In the 0.25–8-Hz range of temporal frequencies, a typical variation in the magnitude of the space constant σ for a cell amounted to approximately $\pm 10\%$ of the mean value over this range of frequencies. The only large variation we observed in a space constant with temporal frequency was an increase in the size of the space constants of two cells (2 and 9 in Table II) at high temporal frequencies. The increase in the space constant at high temporal frequencies reflects a broadening of the receptive field. A broader receptive field at high temporal frequencies is consistent with low-pass-filter characteristics of the feedback loop, as we discussed earlier.

TABLE II
Spatial Properties of Luminosity Horizontal Cells

Cell	Frequency	$ T(\omega) $	$\rho^2(\omega)$	$\theta(\omega)$	$\sigma(\omega)$
	Hz	mV/contrast	mm ²	π rad	μ m
1	0.25	7.2	0.217	-0.093	470
	1	8.2	0.158	-0.102	402
	4	5.8	0.145	-0.018	381
2	0.25	5.9	0.274	-0.072	527
	1	8.3	0.273	-0.001	522
	4	7.0	0.216	0.087	469
	8	3.3	0.289	0.229	573
	16	0.41	0.783	0.109	898
3	1	7.0	0.273	-0.064	525
	4	6.1	0.219	0.015	468
4	1	9.6	0.628	0.344	924
	8	3.4	0.638	0.281	883
	12	1.3	0.500	0.239	760
5	0.25	8.3	0.623	0.259	859
	8	4.7	0.590	0.249	831
6	0.25	8.5	0.510	0.230	762
	12	1.8	0.477	0.174	717
	16	0.50	0.357	0.168	619
7	0.25	10.7	0.413	0.217	682
	8	6.4	0.397	0.288	700
8	0.25	9.8	0.354	-0.054	597
	2	13.0	0.280	-0.013	529
	16	0.43	0.353	-0.191	622
9	0.25	12.3	0.234	-0.146	496
	2	13.7	0.190	-0.088	440
	12	1.3	0.449	-0.293	748
10	0.25	7.0	0.236	-0.061	488
	1	9.1	0.176	-0.018	419
	8	1.9	0.253	0.216	534
11	0.25	14.4	0.414	-0.074	648
	1	18.5	0.389	-0.083	629
	8	5.1	0.499	0.001	706
12	1	8.2	0.166	-0.148	418
13	1	9.0	0.146	-0.086	380
14	1	8.3	0.184	-0.056	431
15	1	8.3	0.162	-0.056	404
16	1	14.1	0.132	-0.045	364
17	1	7.1	0.131	-0.006	362
18	1	7.4	0.265	0.062	517
19	1	6.0	0.118	-0.005	343

DISCUSSION

Weak Spatiotemporal Coupling through Feedback and Membrane Impedance

On the basis of spectral sensitivity measurements, it has been concluded that luminosity horizontal cells in the turtle retina receive synaptic input primarily from red-sensitive cones (Simon, 1973; Fuortes and Simon, 1974; Yazulla, 1976; Fuortes et al., 1973). Morphological studies of the synaptic connections between luminosity horizontal cells and photoreceptors confirm this conclusion (Leeper, 1978). The synapse between red-sensitive cones and luminosity horizontal cells is sign-preserving, so that luminosity horizontal cells hyperpolarize in response to all wavelengths of light. There is electrophysiological evidence that horizontal cells make inhibitory feedback synapses onto cones

FIGURE 7. Exponential space constants of luminosity horizontal cells (from Table II) plotted as a function of temporal frequency. The data points for each cell are connected with straight lines as a visual aid.

in the turtle retina (Baylor et al., 1971; O'Bryan, 1973). Hyperpolarization of the horizontal cell gives rise to a depolarizing input to the cone. The feedback is thought to be mediated by an increase in the cone's calcium conductance (Piccolino and Gerschenfeld, 1980), and there is evidence that this feedback is from L1-type horizontal cells only (Piccolino et al., 1981). One of our concerns in this paper was to determine to what extent feedback affects the response dynamics and spatial sensitivity profiles of luminosity horizontal cells in the turtle retina.

We observed that the shape of the amplitude curve of temporal transfer function, in a Bode plot format, did not show any appreciable dependence on spatial frequency for temporal frequencies below 8 Hz. The fact that the extent of the decline in temporal frequency sensitivity at low temporal frequencies was the same under conditions of both high and low spatial

frequency indicates that the low-frequency filtering does not arise as a consequence of slow inhibitory feedback from horizontal cell to cone. This filtering must reflect a property of the feed-forward pathway from a cone to a horizontal cell. This low-frequency decline in temporal frequency sensitivity is reflected in the time domain by a depolarizing overshoot in the impulse response of the horizontal cell. Our conclusion concerning feedback is consistent with the observation that under light-adapted conditions, cones respond biphasically to brief illumination of small spots (Baylor and Hodgkin, 1974). It is also consistent with experiments that demonstrated the band-pass temporal filter properties of the feed-forward synapse between cones and horizontal cells (Schnapf and Copenhagen, 1982).

There are a number of studies that seem to show that horizontal cell feedback has a more dramatic effect than we observed on the dynamics of cone and horizontal cell responses (Marmarelis and Naka, 1973; Pasino and Marchiafava, 1976; Lam et al., 1978; Krausz and Naka, 1980). There are several possible reasons for this apparent discrepancy. There may be species differences; there is an unlikely possibility that feedback plays a relatively more important role in the catfish retina and in the retina of tiger salamander. Another possibility, suggested by the work of Piccolino and Gerschenfeld (1980), which demonstrated the lability of feedback from horizontal cells to cones in the turtle retina, is that feedback was not operative in our eyecup preparations. We do not believe this to be the case, because in several preliminary experiments, we found that the effects of feedback on the spatiotemporal properties of luminosity horizontal cells became more apparent when the background light level was raised by one log unit. This result argues against the idea that our preparations were in some way pathological. At brighter background levels, temporal transfer functions had a clear dependence on spatial frequency. This finding makes good sense for the following reason. We would expect feedback to have no apparent effect on the spatiotemporal properties of horizontal cells as long as the dynamics of the feedback loop are fast compared with the dynamics of the feed-forward pathway. As the background light level is raised, the feed-forward pathway becomes faster, as a consequence of light adaptation in the cones (Baylor and Hodgkin, 1974; Normann and Perlman, 1979). At sufficiently high background levels, the feedback loop acts as a significant temporal filter, relative to the feed-forward pathway, and the spatiotemporal effects of feedback become apparent. In other words, these preliminary results are consistent with the interpretation which says that the reason we observed little effect of feedback on the spatiotemporal properties of horizontal cells in the present study was not that the feedback was weak, but rather that it was weakly dependent on temporal frequency. We have not excluded the possibility that the effects of feedback become more apparent at higher background levels in part because of increased feedback strength (Marmarelis and Naka, 1973). In fact, a recent report by Weiler and Wagner (1982) gives electrophysiological and morphological evidence that input from horizontal cells to cones increases with increasing levels of background illumination. We wish to

emphasize that the background level of retinal illuminance used in the present study was not particularly low; the steady hyperpolarization produced in one cell amounted to $\sim 25\%$ of the response to a saturating flash of light.

There is another point to consider with respect to the apparent discrepancy between our results and those of others. That is, in our experiments, the mean illuminance at every point on the retina was always the same, and therefore the mean level of polarization of horizontal cells and cones was constant regardless of the spatial parameters of the stimulus. In particular, our full-field stimulus, which measures responses in the presence of feedback, and our high spatial frequency stimulus, which measures responses in the absence of a dynamic component of feedback, produced the same mean retinal illuminance at each point and the same mean level of polarization in the horizontal cell. Others have used stimuli consisting of modulation of the illuminance of small spots, large spots, or annuli, and in these cases various different regions of the retina outside the area of modulation were in complete darkness. In these latter experiments, different mean levels of polarization for the various stimulus conditions must produce different mean levels of feedback. In our experiments, it is only the dynamic component of feedback (i.e., the component that depends on the variation of membrane potential about its mean level) that varies with stimulus parameters.

The Cable Model

We found a generalized cable model, like that of Krausz and Naka (1980), useful in characterizing quantitatively our experimentally measured transfer functions. However, it is important to note that we were not able to test rigorously some aspects of this cable model. In particular, this model implies that the exponential space constant can depend on temporal frequency in a complex way that is determined by the properties of horizontal cell feedback and membrane impedance; the dynamics of the horizontal cell response can depend on spatial aspects of the stimulus through the same mechanism. We observed little spatiotemporal coupling in horizontal cell responses under conditions of low photopic background illumination. Typical variations in the space constant with temporal frequency were too small to determine whether these variations make good sense in terms of frequency-dependent behavior of feedback and membrane impedance. The spatiotemporal transfer function given by the Krausz and Naka (1980) model cannot be expressed simply as a product of a spatial transfer function and a temporal transfer function when signals are significantly filtered through feedback and membrane impedance. Experimentally, we found that the spatiotemporal transfer function of luminosity horizontal cells in the turtle retina is approximately given by a product of a spatial transfer function and a temporal transfer function. Preliminary results indicate that this spatiotemporal separability breaks down under conditions of higher mean retinal illuminance, but we do not yet know whether the generalized cable model can account for spatiotemporal properties of horizontal cells in the turtle retina under these conditions.

APPENDIX

The Spatiotemporal Transfer Function of the Cable Model

Krausz and Naka (1980) formulated a linear spatiotemporal model for horizontal cell responses. In their Appendix B, they computed the horizontal cell response to one-dimensional rectilinear stimuli moving at constant velocity; that is, visual stimuli of the form $s(t - x/c)$, where c is the velocity. A drifting sinusoidal grating is of this form, as $\cos(\omega t - \xi x) = \cos[\omega(t - \xi x/\omega)]$; the velocity is equal to ω/ξ . The spatiotemporal transfer function measures the amplitude and phase of the response to a drifting sinusoidal grating as a function of ξ and ω .

If we specialize Krausz and Naka's results, we find the spatiotemporal transfer function, $V(\xi, \omega)$, is of the form:

$$V(\xi, \omega) = \frac{T(\omega)}{1 + \lambda^2(\omega) \xi^2}, \quad (\text{A1})$$

where $T(\omega)$ is the temporal transfer function for the response to modulation of spatially homogeneous retinal illuminance. $\lambda(\omega)$ has the dimension length and reflects the temporal frequency dependence of feedback from horizontal cell to cone, the signal transmission from cone to horizontal cell, and the impedance of the horizontal cell membrane.

Exponential Spatial Sensitivity Profile of the Cable Model

The line-spread (line-weighting) function measures the amplitude and phase of the response to sinusoidal modulation of the illuminance of a narrow bar at frequency ω as a function of x , the distance between the bar and the center of the receptive field. The line-spread function, $W(x, \omega)$ is given by the inverse Fourier transform in space of the spatiotemporal transfer function:

$$W(x, \omega) = \frac{T(\omega)}{2\lambda(\omega)} e^{-|x|/\lambda(\omega)}. \quad (\text{A2})$$

According to this equation, the amplitude of the response falls off exponentially with x . To see this, we express the complex number $\lambda(\omega)$ in the following manner: $\lambda(\omega) = \rho(\omega)e^{i\theta(\omega)}$. Then Eq. A2 can be rewritten as

$$W(x, \omega) = \frac{T(\omega)}{2\lambda(\omega)} \{e^{-|x|[\cos\theta(\omega)]/\rho(\omega)}\} \{e^{-i|x|[\sin\theta(\omega)]/\rho(\omega)}\}. \quad (\text{A3})$$

The first term in brackets determines how the amplitude of the response depends on the position of the bar, and the second term in brackets determines how the phase of the response depends on position. According to Eq. A3, for each temporal frequency, the amplitude of the response falls off exponentially with distance, and the space constant, $\sigma(\omega)$, is given by:

$$\sigma(\omega) = \rho(\omega)/\cos[\theta(\omega)]. \quad (\text{A4})$$

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