Dynamics of Turtle Cones

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ABSTRACT   The response dynamics of turtle photoreceptors (cones) were studied by the cross-correlation method using a white-noise–modulated light stimulus. Incremental responses were characterized by the kernels. White-noise–evoked responses with a peak-to-peak excursion of >5 mV were linear, with mean square errors of ~8%, a degree of linearity comparable to the horizontal cell responses. Both a spot (0.17 mm diam) and a large field of light produced almost identical kernels. The amplitudes of receptor kernels obtained at various mean irradiances fitted approximately the Weber-Fechner relationship and the mean levels controlled both the amplitude and the response dynamics; kernels were slow and monophasic at low mean irradiance and were fast and biphasic at high mean irradiance. This is a parametric change and is a piecewise linearization. Horizontal cell kernels evoked by the small spot of light were monophasic and slower than the receptor kernels produced by the same stimulus. Larger spots of light or a steady annular illumination transformed the slow horizontal cell kernel into a fast kernel similar to those of the receptors. The slowing down of the kernel waveform was modeled by a simple low-pass circuit and the presumed feedback from horizontal cells onto cones did not appear to play a major role.

INTRODUCTION

For more than a decade, turtle receptors and horizontal cells have been studied in great detail (Baylor and Fuortes, 1970; Fuortes et al., 1973; Piccolino et al., 1981). Surprisingly, most of these studies have been carried out by using flashes or steps of light given in the dark (Baylor and Fuortes, 1970), and the amplitude and waveform of the responses evoked by these stimuli have been analyzed (Baylor and Hodgkin, 1973) and described for the static aspects of the response, as typically characterized by the Naka-Rushton (1966) equation or its modification (Normann and Perlman, 1979). Notable exceptions are the reports by Tranchina et al. (1981, 1983), who used a sinusoidal stimulus on the horizontal cells, and by Norman and his associates (Normann and Perlman, 1979; Normann and Anderton, 1983; Daly and Normann, 1985), who used step increments superposed on a steady mean irradiance.

Previously, using a white-noise stimulus and the cross-correlation technique (white-noise analysis), we showed that (*a*) the horizontal cell response to modulation around a mean irradiance was linearly related to input white-noise modulation, (*b*) a spot and a large field of light produced different horizontal cell response dynamics, and (*c*) a steady annular illumination made the horizontal cell dynamics evoked by a spot of light similar to those evoked by the large field (Chappell et al., 1985).

The visual environment animals encounter is an undulation of mean irradiance and the visual system would be expected to evolve to respond optimally to such a stimulus. The responses to a short flash of light given in the dark are transient phenomena during which response parameters, including sensitivity, are rapidly changing and are not steady state responses. Evidence has accumulated to show that cells in the distal retina, when adapted to a steady mean irradiance, produce responses linearly related to the modulation of light stimulus (Naka et al., 1975; Naka, 1985; Mizunami et al., 1986). In this article, we examine the steady state dynamics of turtle receptor response evoked by a modulation of mean irradiance.

We will show that: (*a*) The cone photoreceptor response to modulation around a mean irradiance is linear. This is a piecewise linearization. (*b*) Incremental sensitivity follows roughly a Weber-Fechner relationship. (*c*) The response dynamics change with an increase in the mean irradiance. (*d*) A small field and a large field of light produce almost identical kernels from receptors, whereas horizontal cell kernels produced by a small spot are much slower than the receptor kernels produced by the same stimulus. (*e*) A steady annulus of light transforms the slow horizontal cell kernels into a fast kernel. This transformation is equivalent to a removal of a simple low-pass circuit by a steady annulus of light. (*f*) The feedback from horizontal cells onto cones proposed for catfish horizontal cells by Marmarelis and Naka (1973) does not appear to play a major role in the transformation of the kernel waveform by the steady annular illumination.

MATERIALS AND METHODS

Biological

The preparation used was the eyecup preparation of red-eared turtle, *Pseudemys scripta elegans*. Turtles were imported from the United States and kept in a greenhouse aquarium at the National Institute for Basic Biology, Okazaki, Japan. Recordings were made through conventional 2-M citrate-filled glass pipettes, and responses together with light signals were initially stored on analog tape on a Sony tape recorder (NFR 3000 data recorder, Sony Corp., Tokyo, Japan). The responses and signals were analyzed off-line on a DEC VAX 11/780 computer (Digital Equipment Corp., Marlboro, MA) using a software system, STAR, developed for time series analysis of neurophysiological data by Y.-I. Ando and M. Sakuranaga.

Stimulus

Two types of white light stimuli were used. One was a small or a large spot of light from a glow modulator tube (R-1130B, Sylvania/GTE, Exter, NH), which was flashed from the dark or modulated by a Gaussian white-noise signal obtained from a noise generator (WG-772, NF Circuit Design Block, Tokyo, Japan). The maximum irradiance of the white-

noise stimulus was 40 μW/cm^2. The small spot (which will be referred to simply as a spot) had a diameter of 0.17 mm and the large spot (which will be referred to as a field) was 4.5 mm in diameter. The other stimulus was a one-dimensional random grating traveling at a constant speed of 1.0 mm/s (Davis and Naka, 1980). A correlation was performed between the grating signal measured by a photodiode with a small aperture and the cellular response. The responses evoked by a drifting random grating had temporal as well as spatial components, a situation similar to the responses evoked by a solitary moving bar of light (Davis and Naka, 1980). If there was no contamination from the temporal component and if the cell's field was symmetric, the receptive field profiles measured here should be symmetric around the peak (the receptive field center). The slight asymmetry of the measured profile (Fig. 2C) suggested a small degree of temporal contamination. However, this did not complicate our identification of cell types because the difference in receptive field sizes was much larger than the asymmetry produced by the temporal contamination. The autocorrelation function had a half-width of 30 μm, which set the lower limit of the size of the field measured. Irradiance of both beams was attenuated by a series of neutral density filters. Light signals were monitored by a photodiode (model 750, United Detector Technology, Culver City, CA) before they were attenuated by the neutral density filters. For surround enhancement experiments, a steady annulus of light obtained from a tungsten lamp with inner and outer diameters of 0.4 and 5 mm, respectively, was used.

Analysis

A white-noise stimulus is a modulation of a mean irradiance, I_0, by a Gaussian white-noise signal, $I(t)$. The resulting response is composed of a steady mean hyperpolarization, V_0, and a modulation response, $V(t)$, as shown in Fig. 2. The relationship between I_0 and V_0 gives the static (DC) sensitivity. This relationship, often compared with the Naka-Rushton (1966) or Michaelis-Menten equation or its modification (Baylor and Hodgkin, 1973), has been used extensively to describe the static input-output relationship in previous turtle studies (Baylor and Fuortes, 1970; Baylor and Hodgkin, 1973; Normann and Perlman, 1979). The incremental sensitivity, $S_i(t)$, is the relationship between a response, $\Delta V(t)$, and the modulation, $\Delta I(t)$, around a mean background, I_0. For a white-noise input with a mean, I_0, the incremental sensitivity can be obtained by cross-correlating the input against the output to compute the first-order kernel, $h(\tau; I_0)$. Therefore, the incremental sensitivity at a mean irradiance, I_0, can be defined as:

$$S_i(t) = \Delta V(t)/\Delta I = h(\tau; I_0). \tag{1}$$

If a cell's response around a mean luminance is linear, the kernel is an impulse response as produced by an impulse input. The physical dimension of $S_i(t)$ is (millivolts times seconds)/(microwatts per square centimeter). Although to be mathematically rigorous, an impulse response is infinitely short in duration, in practice it is an autocorrelation function of input white noise with units of microwatts times seconds. This is equivalent to the situation for the white-noise input. Mathematically, it contains all frequencies with equal power and its autocorrelation function is infinitely short in duration. The white noise used here is band-limited and is often referred to as pink noise. The autocorrelation function of the noise, ΔI, has a finite duration and is obtained by a low-pass operation performed on an idealized white-noise signal. ΔI is also an impulse response of the low-pass filter. Neutral density filters attenuate the amplitude of ΔI as well as the mean by the same factor to keep the contrast, $\Delta I/I_0$, constant. The contrast sensitivity, $S_c(t)$, is the change, $\Delta V(t)$, generated by $\Delta I/I_0$ and is given by:

$$S_c(t) = \Delta V(t)/(\Delta I/I_0) = I_0 \cdot h(\tau; I_0). \tag{2}$$

The physical dimension of $S_c(t)$ is millivolts times seconds. In this experiment, a correlation was performed between the light input before attenuation and the resulting response. Interposed neutral density filters attenuated ΔI and I_0 by the same factor to keep the contrast, I/I_0, constant as discussed above. Eqs. 1 and 2 show that the incremental and contrast sensitivity differ only in the ordinate units because I_0 is a constant and one can be converted into the other if the attenuation factor of the interposed neutral density filters is known. The details of this analysis can be found in Sakuranaga and Ando (1985). With interposed neutral density filters with a density of 10^n (n-log neutral density filters), the kernel, $h(\tau; I_n)$, is computed as:

$$h(\tau; I_n) = \frac{10^n}{P} \overline{I(t - \tau)[V(t) - V_0(I_n)]}. \tag{3}$$

Here the bar is to denote the time average over t and P is the power spectral density. In the actual measurements, a correlation was made, however, between the unattenuated input light signal and the response: noise in the input signal is a serious source of error in kernel estimation (Marmarelis and Marmarelis, 1978, p. 131). If a cell's incremental sensitivity follows the Weber-Fechner law, kernels computed by Eq. 3 should have identical amplitudes for the range of mean irradiance used. A deviation from the function produces kernels (plotted on the contrast sensitivity scale) of different amplitudes (Sakuranaga and Ando, 1985).

Eq. 3 computes kernels by cross-correlating the response against an unattenuated white-noise input because its right-hand term is multiplied by 10^n, an attenuation factor of the neutral density filter interposed. For example, if the 1-log filter is interposed, the amplitude of the kernel computed is compressed by $1/10$ and the real amplitude is obtained by multiplying the amplitude axis by a factor of 10. This will produce the real relationship between $I(t)$ and $V(t)$ or the incremental sensitivity. The contrast and incremental sensitivities, therefore, are different only in the kernel's amplitude (ordinate units) and not in their waveforms or kinetics.

The algorithms for computation and definition of terms used in this article can be found in Chappell et al. (1985).

RESULTS

We used two criteria to identify the receptors: (a) receptive field profiles determined using a moving random grating, and (b) the size of the responses evoked by a small spot and a large field of light. Fig. 1 shows the receptive field profiles produced by cross-correlating the traveling grating signal against the resulting response. In this figure, receptive field profiles from seven receptors are shown together with four each for the small- and large-field horizontal cells. The half-width of the receptor receptive field was ~50 μm, whereas those of the small- and large-field cells were 150 and 320 μm, respectively. The half-width of the receptor receptive field was slightly larger than the value obtained by a 7-μm test spot (Baylor and Hodgkin, 1973). The large-field cell is the cell body and the small-field cell is the axon terminal of luminosity-type horizontal cells (Simon, 1973; Saito et al., 1974; Ohtsuka, 1983). The difference in their receptive field sizes provides us with a way to functionally identify three units—receptors and the small- and large-field horizontal cell units. In a small number of cases (fewer than 30%), receptive field profiles, which could not be superposed on any of the three groups shown in Fig. 1, were obtained. The results from

these anomalous cells are not included in this article. Although we did not explore the types of receptors, preliminary tests with chromatic filters (an R-62 filter with a cut-off at 620 nm and a D-490 bandpass filter with a 470-nm peak, Hoya Corp., Tokyo) showed that we were recording from red cones.

A turtle cone photoreceptor response to a white-noise–modulated field of light is shown in Fig. 2. First the cell was identified as a receptor based on its flash response to a spot (dashed line) and a field (continuous line) of light (Fig. 2*A*). The amplitudes of the responses produced by these two stimuli were similar, 16 mV for the spot and 18 mV for the field stimulus, although the response produced by the later stimulus had a faster rise time. These are in contrast to the small-field horizontal cell in which the spot of light produced a response of much smaller amplitude than the one produced by a field of light (Fig. 4). Under the present experimental conditions, the amplitude of the spot-evoked response from the small-field horizontal cell was less than half that produced by the field
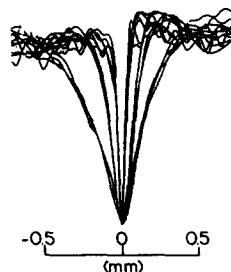

FIGURE 1. Receptive field profiles of receptors (seven examples superposed), small-field horizontal cells (four examples superposed), and large-field horizontal cells (four examples superposed). Profiles were produced by cross-correlating the traveling random grating signal measured by a photodetector having a narrow window against the resulting cellular response. The half-width of the receptors' receptive field profiles was 50 μm and those for the small- and large-field horizontal cells were 150 and 320 μm, respectively. The mean irradiance of the grating was 0.01 μW/cm^2.

stimulus. The differential in the response amplitude was much greater in the large-field cell. Together with the receptive field size, the difference in the response amplitude provides us with a reliable means to identify three elements in the turtle outer retinal layer.

Fig. 2*C* shows the receptor's receptive field profile plotted using data obtained from a traveling random grating. The half-width of the receptive field obtained was 50 μm. The data from this figure, with the information from Fig. 2*A* above it, show how photoreceptors were identified. Fig. 2*B* shows the initial part of the cell's response to the white-noise stimulus. The response was composed of two parts, the initial transient, V_p, and the dynamic steady state that followed it. The initial transient peak is similar to the one produced by a step of light and is produced by a sudden appearance of the stimulus, I_0. The membrane potential settles down to a steady mean level, V_0, in a few seconds, which is maintained as long as the stimulus is on. This is the process of field adaptation (Rushton, 1965),

during which sensitivity is changing rapidly. The decrease in the static sensitivity is seen by the repolarization of average membrane potential from V_p to V_0 and the increase in the dynamic sensitivity is seen by the increase in the modulation response. These general characteristics are similar to those found in step-evoked responses (Fig. 1 in Normann and Perlman, 1979). As described in Materials and Methods, the relationship between I_0 and V_p or V_0, the cell's static (DC) sensitivity, relates to the Naka-Rushton (1966) equation or its modification. The
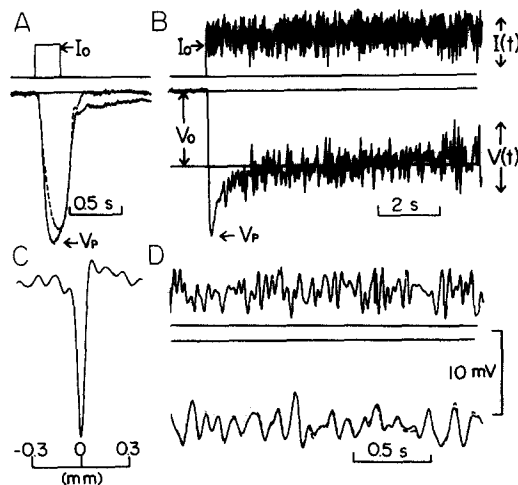

FIGURE 2. Receptor response evoked by a white-noise–modulated field of light. Panel A shows step-evoked responses from the receptor; the dashed line is for the spot and the solid line is for the field response. The receptive field profile of the cell is shown in C. The profile is similar to those from receptors in Fig. 1. The slight asymmetry of the profile was due to contamination from temporal (differentiating) dynamics. B shows the early part of the response to a white-noise stimulus. The initial response is a hyperpolarizing peak, V_p, evoked by a sudden appearance of irradiance, I_0. The transient is similar to the one produced by the field of light in A. A few seconds after the initial transient, the membrane potential settles down to a steady level, V_0. The retina is now in a steady dynamic state. D shows the stimulus and response on an expanded time scale. On the response trace, a model response predicted by the first-order kernel is superposed using a dashed line. The two traces match very well, even for the part of the response with an amplitude of 5 mV, peak to peak. The white-noise–evoked response is linearly related to the stimulus. The mean irradiance of the white-noise stimulus was 40 μW/cm^2.

relationship between $I(t)$ and the response, $V(t)$, is the dynamic incremental sensitivity and is described by the kernels obtained by cross-correlating the input, $I(t)$ against $V(t)$. The correlation does not take into account the steady values, I_0 and V_0. In Fig. 2D, the white-noise stimulus and the resulting response are shown on an expanded time scale. The prediction (to the same white-noise stimulus) by the first-order kernel is superposed on the response trace (dashed line). Although there are a few minor deviations between the two traces, the cellular response and the linear prediction, the fit is quite good. Indeed, the mean square error

(MSE) for the whole record of 65 s is 6.5%. The receptor's modulation response is linearly related to the stimulus modulation.

Table I shows the MSEs of the first-order (linear) models produced by convolving the original white-noise stimulus with the first-order kernels from the receptor and horizontal cells. Smaller MSEs indicate a smaller error in the first-order model, whereas larger MSEs indicate the presence of nonlinear components or noisy recording. For 15 receptors, both spot and field illumination produced responses with MSEs of ~8% that were similar to the MSEs from both the small- and large-field horizontal cells, the exception being the large MSE for the spot-evoked responses from the large-field cells. The presence of a steady annular light reduced the large-field horizontal cell MSE to <10%; the surround stimulus linearized the response. In the small-field cells, a steady annulus of light made the spot kernels faster and larger, but improvements in MSEs were small since the spot MSEs were already <10%. Small MSEs observed from the receptors show that the receptor responses are as linear and as stationary as those from the horizontal cells.

TABLE I

Mean Square Errors of Responses Predicted from a Linear Model

Cell type	Receptor	Horizontal cell	
		Large	Small
Number	15	5	7
Spot MSE	8.33	19.1	9.98
SD	2.15	2.50	2.83
Field MSE	8.01	7.30	8.24
SD	2.76	3.01	2.08
Spot with annulus ($r = 2$)		8.9	—

MSEs for the linear prediction obtained by convolving the original white-noise light stimulus with the first-order kernel obtained by cross-correlating that stimulus with the cellular response. Responses were evoked by a white-noise stimulus of 40 μW/cm^2.

Fig. 3A shows the power spectra of input white noise ("light"), of the actual response, and of the model computed from the first-order kernel. The response and model power spectra, which are bandpass with a peak at 9 Hz and a roll-off at ~11 Hz, matched very well, the MSE of the linear model being 8.6%. In Fig. 3B, three traces are superposed: two are probability density functions (PDFs) for the response and linear model shown in Fig. 2, B and D, and the third is the Gaussian distribution (smooth line) fitted to the response PDF. If a system is linear, the PDF of the system's response to a white-noise stimulus must also be Gaussian. The three curves were similar, which showed that the response from turtle receptors produced by the white-noise stimulus is Gaussian. The PDFs were symmetrical at least for a range of 8 mV, peak to peak. As the mean hyperpolarizing level, V_0, is 7 mV for the cell (Fig. 2B), the linear range of the modulation response is not small.

Fig. 4 shows the step-evoked responses from a receptor (A) and a small-field horizontal cell (B) evoked by a small spot (traces marked "S") and a field of light (traces marked "F"). The responses from these cells were obtained successively

during a single electrode penetration. Although the initial peak was sharper in the field-evoked response, the photoreceptor produced responses of almost identical amplitude as well as of waveform (cf. Fig. 2A). In the horizontal cell, on the other hand, the same stimuli produced responses of very different amplitudes as well as of different waveforms. Similarly, the spot and field of light produced almost identical kernels obtained from photoreceptors (Fig. 4C, solid lines marked "S" and "F"), whereas these stimuli produced very different kernels from horizontal cells (Fig. 4C, dashed lines marked "S" and "F"). As previously reported by Chappell et al. (1985), the field kernel from horizontal cells is faster, larger, and biphasic, and the spot kernel is smaller, slower, and monophasic. The larger amplitude of the field kernels can be accounted for by a simple response summation in the horizontal cell lamina (S-space of Naka and Rushton, 1967),
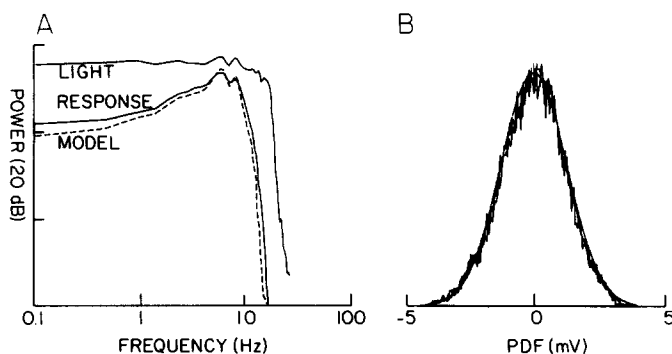

FIGURE 3. Panel A shows the power spectra of the light stimulus (upper trace), of the cellular response (solid line, middle), and of the model predicted by the first-order kernel (dashed line). The response and model power spectra are in good agreement. The response power spectrum is bandpass with a peak at ~10 Hz. The MSE for this response is 8.9%. B shows the PDFs for the cellular response and for the linear model. The smooth line is a Gaussian curve fitted to the response PDF. The three traces are in good agreement. Around the two extreme ends, the response PDF is slightly asymmetrical. PDFs are from the records shown in Fig. 2B. Responses were evoked by a white-noise stimulus of 40 μW/cm^2.

but the difference in the kernel waveforms cannot. In all cells that we identified as receptors, both the spot and the field of light produced kernels that were similar in their amplitudes as well as waveforms, the difference in kernel amplitudes always being <20%.

Fig. 5 shows the kernels from two receptors (A) and a horizontal cell (B) obtained at four mean irradiance levels. The kernels plotted on a contrast sensitivity scale were different in their amplitudes and waveforms for different mean levels. If incremental sensitivity obeys the Weber-Fechner relationship exactly (see Discussion), all the kernels plotted on the contrast sensitivity scale must have identical waveforms and amplitudes; i.e., for a 10-fold increase in the mean irradiance, the amplitude of the kernel must be attenuated by 1/10 to keep the contrast sensitivity constant. As the mean increased, the amplitude of

the kernels in Fig. 5 also increased, which shows that the contrast sensitivity increases as the mean increases. For the two receptor kernels at 0 and −1 log (Fig. 5A), the Weber-Fechner relationship held approximately for the kernel amplitudes but not for their waveforms. Similar observations hold for the horizontal cell kernels (Fig. 5B). This means that the incremental sensitivities of photoreceptors and horizontal cells were almost identical and the Weber-Fechner relationship holds only for the amplitudes of responses obtained at a bright mean irradiance. As in the case of horizontal cells, receptor kernels are monophasic
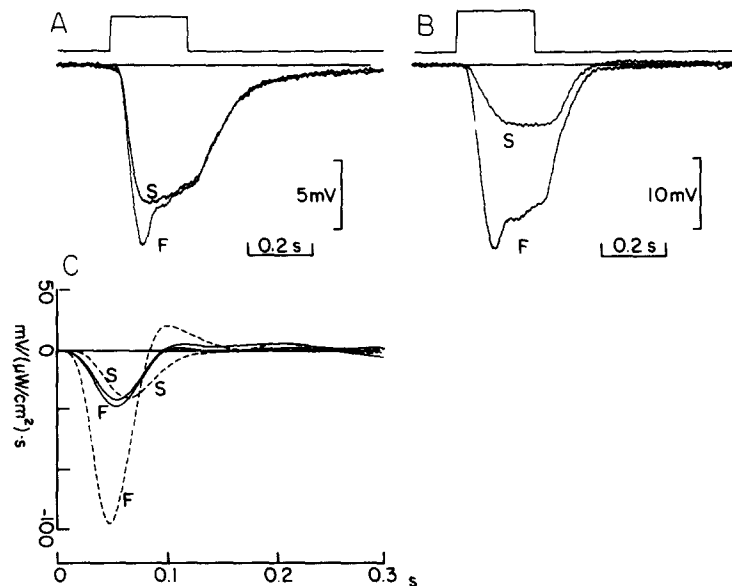

FIGURE 4. Responses from a receptor (A) and a small-field horizontal cell (B). In A and B, responses were evoked by steps of light given in the dark. Traces marked "S" were evoked by a spot and those marked "F" were evoked by a field of light. The cells' first-order kernels are shown in C; receptor kernels are shown in the solid line and horizontal cell kernels are shown in dashed lines. Kernels marked "S" were evoked by a spot and those marked "F" were evoked by a field stimulation. Recordings were made during a single electrode penetration. Irradiance of the step stimulus was 4 and 4.2 μW/cm^2 for A and B, respectively, and the white-noise stimuli had a mean of 4 μW/cm^2.

(integrating) at low mean irradiance and biphasic (differentiating) at a bright mean irradiance.

The amplitude of the kernels can be used as an index of incremental sensitivity. The amplitudes of kernels obtained at various mean irradiances are plotted in Fig. 6. The incremental sensitivity is obtained by multiplying the kernel amplitude, measured as the contrast sensitivity, by the attenuation factor, 10^n. The incremental sensitivity of both the receptor and horizontal cells is approximated by the Weber-Fechner law, but the fit is not exact, as we have already noted for the kernels shown in Fig. 5. The deviation can be explained by the modified
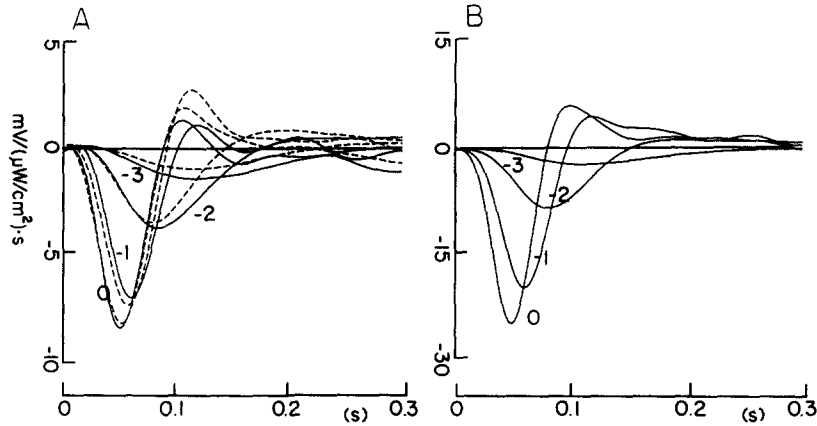
FIGURE 5. First-order kernels from two receptors (A), one in solid and the other · in dashed lines, and one horizontal cell (B), plotted on a contrast sensitivity scale. Kernels are the product of cross-correlation between the light signal before attenuation and the resulting cellular response. Traces marked 0 through −3 are for the 0-log mean irradiance of 40–4 × 10^{-2} μW/cm^2, attenuation being in 1-log steps. The ordinate units are for the 0-log (no neutral density filter) records only. For traces obtained with a 1-log filter, the ordinate values are to be multiplied by 10 and those with 2-log filters by 100, etc. For the receptor kernels in dashed lines, the ordinate values are to be reduced by 20%.

Weber-Fechner relationship, which includes the equivalent background luminance (Rushton, 1965).

In Fig. 7, A and B, kernels from a receptor plus both a small- and a large-field horizontal cell are shown. Recordings from these cells were made successively
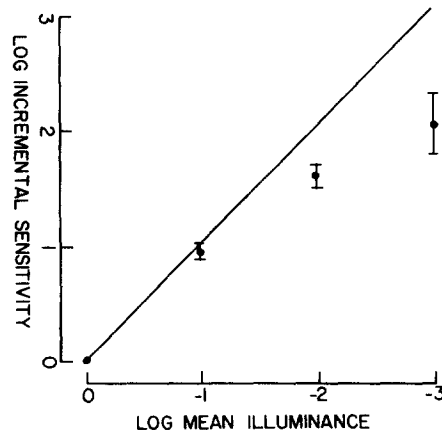

FIGURE 6. Kernel amplitude plotted on an incremental sensitivity scale. The ordinate is the amplitude of kernels and the abscissa is the log mean irradiance. Data from four receptors and one horizontal cell are shown. The maximum mean irradiance, 0 log, was 40 μW/cm^2. Sensitivity was normalized by taking the value at 0 log as 1.

from the same location so that the recordings were made at the same state of adaptation. In the figure, receptor kernels evoked by a small spot (*A*) and a large field (*B*) of light are shown by the dashed lines and are identical. To facilitate comparison of waveforms, the amplitudes of the horizontal cell kernels were normalized to those of the receptor. The kernels produced in the two horizontal cells by a spot stimulus were identical (Fig. 7*A*), but, unlike the receptor kernels,
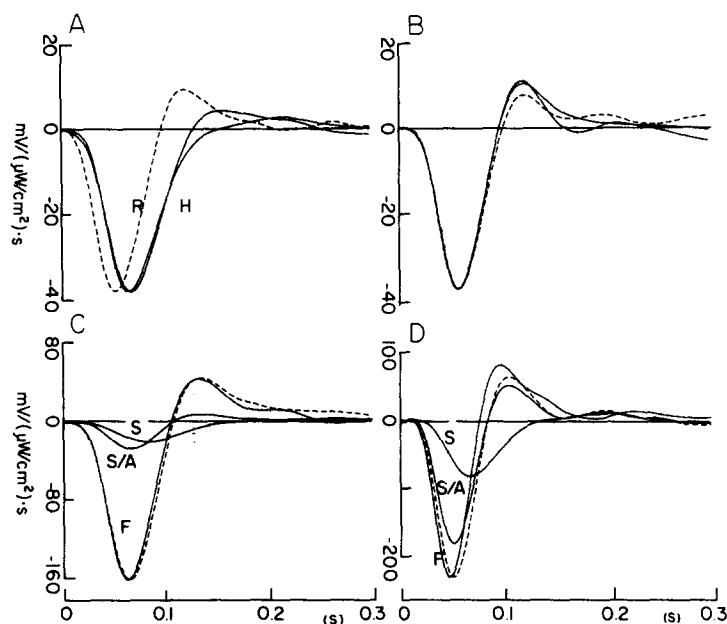

FIGURE 7. Comparison of kernels produced by spot and field stimuli. Panels *A* and *B* show kernels from a receptor (dashed lines) and small- and large-field horizontal cells (solid lines). The kernels in *A* were produced by a spot and those in *B* by a field of light. The amplitudes of the horizontal cell kernels were normalized to those of the receptor kernels. The ordinates apply only to receptor kernels. The three recordings were made in the same location and recordings were within 10 min of each other. *C* and *D* were recorded, respectively, from large- and small-field horizontal cells from different retinas. Traces marked "S" were produced by a spot and those marked "F" by a field of light. Traces marked "S/A" were produced by the spot of light in the presence of a steady annulus of light. White-noise stimuli had a mean irradiance of 4 μW/cm^2 and the steady annulus was 0.4 μW/cm^2. The S/A kernels normalized to the field kernels are shown in dashed lines.

they were monophasic, with a peak response time of 50 ms. All three kernels produced by a field of light, on the other hand, were identical (Fig. 7*B*). Since the receptor kernels were identical whether they were produced by a spot or a field of light, the slower and smaller (spot-evoked horizontal cell) kernels were not due to slower and smaller receptor inputs. Larger horizontal cell kernels in response to modulation of a larger field stimulus can be accounted for by the spatial summation of signals for the kernels evoked by a large field of light.

However, there must be another mechanism to degrade the faster receptor input when it is transmitted to the horizontal cells. Chappell et al. (1985), working in turtle retina, and Kawasaki et al. (1984), working in catfish retina, have shown that the slow kernels could be made as fast as those produced by a field of light by the presence of a steady annulus of light. Results from similar experiments are shown in Fig. 7, in which the kernels in C and D were obtained from a large- and a small-field horizontal cell, respectively. The kernels marked "S/A" were produced by a small spot of light in the presence of a steady surround. In both the large- and small-field cells, the steady surround made the spot kernel faster and larger. These kernels, normalized in amplitude to the field kernels (dashed lines), were similar to those of the large field of light. Since the receptor kernels were identical for both spot and field stimulation, these results suggest that the mechanism that degrades the spot-evoked response is removed by the steady annulus of light.

DISCUSSION

Cones and horizontal cells in the turtle retina have been studied extensively and the following consensus has emerged: (a) The static (DC) sensitivity, the relationship between V_p or V_0 and I_0, is described by the Naka-Rushton equation or by its modification (Baylor and Fuortes, 1970; Baylor and Hodgkin, 1973). This includes both incremental and decremental responses from a given mean (Normann and Perlman, 1979; Daly and Normann, 1985). (b) A change in static sensitivity appears as a lateral shift of the curve along the log I axis, a change in the value of σ in the Naka-Rushton equation. (c) A dim stimulus, step or incremental, produces much slower responses than those produced by a brighter stimulus (Baylor and Hodgkin, 1973; Normann and Anderton, 1983). (d) The Weber-Fechner relationship approximates the incremental sensitivity (Normann and Anderton, 1983). In the past studies, measurements were made on the "linear range" response, whereas in this analysis, a first-order correlation extracted the linear components and the degree of linearity, or the proportion of the linear component in a response was evaluated using the MSE, the degree of deviation of the linear component (or "model") from the actual response. The "linear range responses" reported in earlier studies were produced by flashes given in the dark, except for those in the reports by Normann and his co-workers (Normann and Anderton, 1983; Daly and Normann, 1985), and the peak response times of these linear range responses were ≥100 ms, which corresponds to the kernels obtained at −3 log mean irradiance in this article. The kernels with peak response times of 50 ms predicted actual responses with MSEs of <10% and the peak-to-peak excursion of the white-noise–evoked response was >5 mV, whereas the linear range responses obtained by the flash method were <1 mV in amplitude (Baylor and Hodgkin, 1973; Fuortes and Simon, 1974; Normann and Anderton, 1983). The linear responses we show here are therefore for a large range of amplitude excursion as well as for a much larger range of mean and modulation irradiance. The same degree of linearity is found in the modulation responses evoked by either a small spot or a field of light. Two factors could be involved in the difference in response linearity found in the

early flash experiments and our white-noise experiments: (*a*) a short step of light flashed in the dark evokes a response that is transient and inherently nonlinear, whereas the white-noise stimulus is a modulation around a mean; (*b*) the step stimulus involves an integration of the impulse response while white noise is differentiating, so that responses produced by a white-noise stimulus are never held stationary at a certain level. This minimizes the static compression nonlinearity caused by large response excursions.

These two factors have probably contributed to the finding that turtle horizontal cell responses produced by a modulated light were linear (Tranchina et al., 1981; Chappell et al., 1985). The findings in horizontal cells substantiate the present observation that turtle receptors produce linear responses to a modulated stimulus because the waveforms of receptor and (field-evoked) horizontal cell responses are very similar (Fig. 7). Taking into account the low signal-to-noise ratio in receptor recordings, MSEs of 8% compare favorably with the best MSE of ~5% for horizontal cells (Chappell et al., 1985). The static relationship between I_0 and V_0 is nonlinear, as it is approximated by the Naka-Rushton equation, whereas the dynamic relationship between $I(t)$ and $V(t)$ is linear. The activation of a large number of horizontal cells (by a stimulus with large area coverage) has been suggested to initiate a feedback from the horizontal cells to receptors (Marmarelis and Naka, 1973; Lam et al., 1978). This study showed that the feedback did not appear to interfere with the response dynamics because a spot and a field of light produced identical receptor kernels. Tranchina et al. (1983) also found that the effects of feedback, if there are any, are small in the turtle horizontal cells.

Since the work of Fechner (1860), it has been known that $\Delta I/I_0$ has to be roughly constant for the flash, ΔI, to remain at threshold when the background, I_0, changes. In that formulation, sometimes referred to as the Weber-Fechner relationship or Weber's law, the measure was the threshold, whereas in our case the measure is the kernel's amplitude scaled as the contrast sensitivity (Eq. 2). Kernels (plotted on the incremental sensitivity scale) are the comprehensive measure of incremental sensitivity, their amplitude being an approximation of the magnitude of incremental sensitivity and their waveform reflecting the dynamics (Sakuranaga and Ando, 1985). The incremental response becomes faster as the mean is increased but the magnitude of the kernels becomes smaller. The decrease in the incremental sensitivity is a general phenomenon in the visual system, a classic example being the Weber-Fechner relationship.

The incremental sensitivity of both turtle receptor and horizontal cells, indexed by the kernel amplitude, follows roughly the Weber-Fechner relationship. The fit, however, is not exact in two respects because at different mean levels (*a*) the amplitudes of kernels plotted on the contrast sensitivity scale are different and (*b*) the waveforms are different. The fit is therefore approximate. This is not due to the failure of our methodology, because in the cockroach ocellar second-order neurons, the waveform of kernels remained unchanged and their amplitudes were fitted exactly by the Weber-Fechner relationship over a mean irradiance range of 4 log units (Mizunami et al., 1986).

The changes in kernel waveform and amplitude for different mean levels are

similar in receptors and horizontal cells, which shows that these changes originate in the receptors and little transformation of signals takes place when the signal is transmitted from receptors to horizontal cells. Chappell et al. (1985) modified the model proposed for the human visual system by Kelly (1971) so that turtle horizontal cell kernels (the impulse response) could be fitted by the equation. They found that Kelly's model could predict the turtle kernels obtained over a mean irradiance range of 4 log units. Therefore, the modified Kelly model must also be an adequate description of the receptor incremental response.

Chappell et al. (1985) reported that by adding surround illumination (either modulated or not), the slow kernels from spot-evoked turtle horizontal cell responses could be made as fast as the turtle receptor kernels reported here. A similar speeding up of spot-evoked incremental responses has been reported in catfish cone horizontal cells (Kawasaki et al., 1984). The dynamics of receptor
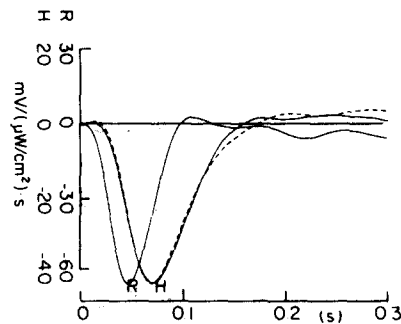

FIGURE 8.   Receptor (R) and a small-field horizontal cell (H) kernels evoked by a small spot of light (both in solid lines). The dashed line shows the results of a low-pass operation on the receptor kernel. The two traces, the spot-evoked horizontal cell kernel and the transformed kernel, are in good agreement. The low-pass filter was a cascade of two low-pass filters with time constants of 1.4 and 25 ms. Kernels are normalized to facilitate the comparison of their waveforms. The ordinate scale marked "R" applies to the receptor and the one marked "H" applies to the horizontal cell kernel.

incremental response were not dependent upon the retinal area stimulated (if it was larger than 0.17 mm in diameter), whereas the dynamics of the horizontal cells were. Therefore, there must be a filter that makes the spot horizontal cell kernels slower than those in the receptors. We found that the filter can be substituted by a simple low-pass circuit. Fig. 8 shows an example in which a receptor kernel (R) was passed through a low-pass filter (dashed line) to match a spot-evoked kernel from a small field horizontal cell (H). The two traces are similar, which suggests that a simple low-pass circuit is capable of such a transformation. We tried several pairs and we could always make reasonable matches.

There are several possible explanations for the influence of steady illumination on the spot response. A larger junction resistance and hence capacitance of the horizontal cell gap junctions brought about by the local discontinuity of membrane potential is one possible mechanism. Whether a similar enhancement of

spot incremental responses observed in other retinas can also be explained by such a simple mechanism is unknown. It has been suggested (Lam et al., 1979) that the postulated faster field kernel from catfish receptors could have been due to feedback from the horizontal cell. This is not the case in turtle, because the slow horizontal cell spot kernel is produced by a mechanism that slows down the fast receptor kernel. Similarly, the assumed feedback from horizontal cells onto cones does not appear to play a major role in the transformation of the turtle horizontal cell kernel by a steady surround, as suggested when we first reported the surround enhancement effect in turtle horizontal cells (Chappell et al., 1985). The visual scene turtles encounter in the natural environment consists of a mean illuminance with local modulations, and a spot of light against a dark background is an unnatural stimulus. It is logical, therefore, that the animal's visual system is optimized for the detection of changes around a mean intensity of retinal ambient illumination.

White-noise or similar analysis performed so far on distal neurons in the turtle receptor and cone horizontal cells (Tranchina et al., 1981, 1983; Chappell et al., 1985), on catfish cone horizontal and bipolar cells (Naka et al., 1975; Naka, 1985), and on the ocellar second-order neurons (Mizunami et al., 1986) has produced similar results. (*a*) The cells' response to white-noise–modulated light is linearly related to the modulation. Since the white-noise stimulus is "natural" by comparison with the much-used step inputs, the linear response describes the cells' normal operation. (*b*) With the exception of the ocellar neurons, the response dynamics change with changes in mean irradiance. (*c*) The incremental sensitivity decreases as the mean irradiance increases. The relationship ranges from being exactly a Weber-Fechner relationship in ocellar neurons (Mizunami et al., 1986) to being the local slope of the Naka-Rushton equation in catfish cone horizontal cells. The impulse response of the human visual system (Kelly, 1971) shares many of these features and Kelly's model roughly describes the response characteristics. We conclude that the linear modulation response around a mean irradiance is the most basic property of the initial signal processing in the visual system. The linear modulation response is then transmitted to the inner retina via bipolar cells or horizontal cell axons and the characteristic nonlinearities are produced in the amacrine cells (Sakai and Naka, 1985; Sakuranaga and Naka, 1985).

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