LINEAR AND NONLINEAR SPATIAL SUBUNITS IN Y CAT RETINAL GANGLION CELLS

BY S. HOCHSTEIN* AND R. M. SHAPLEY

From the Rockefeller University, New York, N.Y. 10021, U.S.A.

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SUMMARY

1. The mechanism which makes Y cells different from X cells was investigated.

2. Spatial frequency contrast sensitivity functions for the fundamental and second harmonic responses of Y cells to alternating phase gratings were determined.

3. The fundamental spatial frequency response was predicted by the Fourier transform of the sensitivity profile of the Y cell. The high spatial frequency cut-off of a Y cell's fundamental response was in this way related to the centre of the cell's receptive field.

4. The second harmonic response of a Y cell did not cut off at such a low spatial frequency as the fundamental response. This result indicated that the source of the second harmonic was a spatial subunit of the receptive field smaller in spatial extent than the centre.

5. Contrast sensitivity vs. spatial phase for a Y cell was measured under three conditions: a full grating, a grating seen through a centrally located window, a grating partially obscured by a visual shutter. The 2nd/1st harmonic sensitivity ratio went down with the window and up with the shutter. These results implied that the centre of Y cells was linear and also that the nonlinear subunits extended into the receptive field surround.

6. Spatial localization of the nonlinear subunits was determined by means of a spatial dipole stimulus. The nonlinear subunits overlapped the centre and surround of the receptive field and extended beyond both.

7. The nature of the Y cell nonlinearity was found to be rectification, as determined from measurements of the second harmonic response as a function of contrast.

8. Spatial models for the Y cell receptive field are proposed.

* Present address: Neurobiology Unit, Institute of Life Sciences, Hebrew University, Jerusalem, Israel.

INTRODUCTION

Retinal ganglion cells in the cat have been categorized into many groups based on different kinds of tests (Enroth-Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971; Stone & Hoffmann, 1971; Hochstein & Shapley, 1976). In the accompanying paper (Hochstein & Shapley, 1976) we proposed that the classification of cells as X or Y by means of a nonlinearity index is especially useful because it divides the cells into two non-overlapping groups. This paper is an initial study of the underlying mechanisms which make Y cells different from X cells. Three sets of experimental data were critical in defining the unique properties of Y cells: (1) spatial frequency contrast sensitivity functions for linear and nonlinear components of Y cell responses to alternating phase sine gratings, (2) the spatial sensitivity profile for a pattern of dipole stripes (1 cycle of a sine grating), and (3) the response vs. contrast function for the second harmonic response to an alternating phase grating. These and other results which were obtained implied that the typical Y cell receptive field was made up of linear components (a centre and a surround like those of an X cell) and also nonlinear components (small rectifying subunits overlapping both the centre and surround). The nonlinear subunits may be used to account for many of the correlated response characteristics which distinguish Y cells from X cells in the cat retina. The discovery of the nonlinear subunits of Y cells reinforces our belief in the usefulness of the X/Y classification based on the nonlinearity index; it explains why Y cells are qualitatively different from X cells.

METHODS

Methods of surgical preparation, electrophysiological recording, stimulus display, and data analysis have been described in the preceding paper.

In some of the critical experiments, the stimulus was an alternating phase sinusoidal grating produced on the screen of an oscilloscope with electronic circuits designed for the job. The grating position (spatial phase), spatial frequency, and contrast (or modulation depth) were under the experimenter's control, and were systematically varied. The mean luminance of the screen was constant in time at a value of 1 cd/m^3 . A digital computer ran the experiment in the sense that it provided the temporal modulation required to excite the retinal ganglion cell, and it also measured the averaged neural response to several presentations of the stimulus, displayed the average response wave form on a monitor oscilloscope, and stored the response on magnetic tape for later analysis. This later analysis consisted mainly of measuring the Fourier components of the response at the modulation frequency and the next nine higher harmonics of the modulation frequency, to measure possible harmonic distortion produced by nonlinearities in the retinal network. These procedures are described in the preceding paper (Hochstein & Shapley, 1976).

One new stimulus pattern was dipole stripes. The dipole stripes were formed by one cycle of a sine grating, and were the full length of the screen (10°) . The dipole

stripes were alternated in phase by sine wave temporal modulation (dark replacing light and vice versa with a sinusoidal time course) in exactly the same manner as a full sine wave grating. The dipole wave form was produced by a gated oscillator when the gate was only one period in duration.

The one dimensional sensitivity distribution (or *line weighting* function) was measured in ganglion cells with a thin rectangular bar as a stimulus pattern (the rectangular bar may be viewed as one *half cycle* of a square-wave grating). The bar was produced by a pulse synchronized to the sweep; the delay with respect to the start of the sweep was adjustable and voltage-controllable so that the position of the bar on the screen could be set by the computer. As in the other types of experiment, the luminance of the bar was modulated by the computer in a sinusoidal fashion by multiplying the pulse with a computer-generated, slow modulation signal in an analog multiplier.

In this investigation twenty-four Y cells were studied. Complete spatial frequency sensitivity curves for fundamental and second harmonic responses were collected for fourteen of these cells. The data from one particular Y cell were chosen as representative for illustrations in Figs. 1-3.

RESULTS

Spatial frequency responses : fundamental and second harmonic

Initial experiments were of the type reported in the preceding paper (Hochstein & Shapley, 1976). These involved determining the contrast sensitivity vs. spatial phase for alternating phase sine gratings sinusoidally modulated in time. There were two main components of the Y cell response to such a stimulus as determined by Fourier analysis of the post-stimulus time (PST) histogram: a fundamental component at the modulation frequency, and second harmonic component at twice the modulation frequency. The fundamental component of the Y cell response was similar to X cell responses in that it had a sinusoidal dependence on spatial phase and therefore had two null positions. The second harmonic component was approximately independent of spatial phase.

The second harmonic component of the response of Y cells to alternating grating must have been generated by a process (or processes) essentially different from the processes which led to the fundamental component of the response. No summation of the responses of linear transducers could lead to a frequency doubling. Also the spatial phase dependence of the second harmonic was completely different from the fundamental. It is likely that there are multiple sources of nonlinearity in the retina, and therefore there could be more than one source of the second harmonic component which was measured. However, as a first approximation we have assumed the second harmonic to be generated by a single nonlinear mechanism. This approximation might not have been correct but, as it turned out, it was basically correct, i.e. there was no need to postulate a second nonlinear mechanism in order to explain our results. Under the low contrast stimulus conditions of these experiments, the

10

simplifying approximation of a single source for second harmonic responses is a good one, to be justified by the consistency of the results which are presented below.

For the representative Y cell, sensitivity vs. spatial phase for the fundamental and second harmonic responses at different spatial frequencies are shown in Fig. 1. These data resemble those in Fig. 7B of the preceding paper from another Y cell (Hochstein & Shapley, 1976). From data like these spatial frequency sensitivity functions were constructed.



Fig. 1. Contrast sensitivity vs. spatial phase for a Y cell at two spatial frequencies. The sensitivities for the fundamental component (\times) and second harmonic (D), in response to an alternating phase grating at 0.35 c/deg, are plotted vs. spatial phase. Sensitivities for the fundamental (\Box) and second harmonic (Y) to a 0.7 c/deg grating as a function of spatial phase of the grating, are also plotted on the same co-ordinates. A best fitting sine curve to the 0.35 c/deg fundamental data is also drawn in. The second harmonic sensitivities are roughly spatial phase-insensitive. The temporal modulation in these experiments was 4 Hz, sinusoidal. The data are from an off-centre Y cell located 15° from the area centralis.

For each of several spatial frequencies the contrast sensitivity vs. spatial phase was measured for fundamental and second harmonic responses as in Fig. 1. Then the peak fundamental contrast sensitivity and the average second harmonic sensitivity were graphed vs. spatial frequency. A typical graph is shown in Fig. 2. The main result of this experiment was that the fundamental component of the Y cell response had a lower high spatial

frequency cut-off than the second harmonic component. That is, the mechanism which generated responses at the fundamental frequency resolved high spatial frequencies less well than the mechanism which generated second harmonic distortion.



Fig. 2 Spatial frequency dependence of the contrast sensitivity for the fundamental component and second harmonic component of Y cell responses to alternating gratings. Fundamental sensitivity (\times) and second harmonic sensitivity (\bigcirc) are plotted on log-log co-ordinates versus spatial frequency. The fundamental sensitivity was taken to be the amplitude of the sine function which best fitted the contrast vs. spatial phase curve for the fundamental response (as in Fig. 1). This was approximately the same as the contrast sensitivity for the fundamental when the alternating phase grating was located at the position of peak sensitivity. The second harmonic sensitivity was the average of the values at several spatial phases since harmonic amplitude varied little with spatial phase of the alternating grating. The temporal modulation of the alternation was a 4 Hz sine wave throughout.

It was natural to wonder where in the receptive field of the Y cell these two mechanisms were located. During the experiments there was an immediate indication that the fundamental component was associated with the centre response mechanism. When we listened to response modulation on the audio monitor, the fundamental component had the same sign as the centre response. For instance, when an on-centre Y cell was stimulated with a slowly alternating sine grating which elicited a substantial fundamental response, the cell increased its firing rate when a bright bar of the grating was introduced into its centre region and decreased its firing rate when a dark bar replaced the bright. However, such a crucial point required more lines of evidence. The most direct approach was to relate the sensitivity profile of the receptive field to the spatial frequency contrast sensitivity function.

Line weighting function

The sensitivity of the cell to a $10^{\circ} \times 0.5^{\circ}$ bar was determined. The luminance of the bar was sinusoidally modulated in time; that is, the bar was made alternately brighter or darker than the background, with a sinusoidal time course. Its mean luminance was the same as the background. The bar was placed at different equally spaced locations in the receptive field of the Y cell and sensitivity, reciprocal of contrast required to give a criterion response, was determined as a function of position of the bar. As has been done with grating stimuli, sensitivity is given in units of impulses/sec ÷ contrast. This unit was chosen because response criteria were usually chosen to be in a linear range of response vs. contrast; therefore, one could divide the criterion response by the required contrast and obtain a criterion-independent measure of contrast sensitivity. Since we were hunting the source of the fundamental Fourier component of the response, the sensitivity vs. position function was measured with a certain magnitude of the fundamental as the response criterion. However, second harmonic sensitivity was also measured. Graphs of fundamental and second harmonic sensitivity vs. position are shown in Fig. 3. The amplitude of the fundamental sensitivity is shown in the top part of the graph and the phase shift of the response with respect to the stimulus is indicated in the lower graph. Similar quantitative results were obtained on thirteen other Y cells. One curious finding displayed in Fig. 3 is the relative phase shift between the centre and surround. This was an off-centre cell, so the centre phase shift was approximately π radians, i.e. the central response increased when the luminance of the stimulus decreased. However, the surround response was not completely antagonistic to the centre response because its phase shift with respect to the stimulus was $\pi/2$; the phase shift for the surround would have had to have been near zero for the surround to antagonize the centre. The relative phase of centre and surround depends on temporal frequency; it is common for there to be a $\pi/2$ phase difference around 4 Hz in Y cells. This result is not directly relevant to the remaining results in this paper, but it is an important topic which is still under investigation.

The spatial sensitivity profile shown in Fig. 3 is equivalent to a line

weighting function for a linear spatial filter. If one assumes the mechanism or mechanisms of the Y cell field which respond at the fundamental frequency to be linear, one can calculate a theoretically expected spatial frequency sensitivity function from the measured line weighting function (the two functions are Fourier transforms of one another). The theoretically predicted spatial frequency sensitivity for this cell is shown in Fig. 2



Fig. 3. Line weighting function. This is a graph of the inner core of the Y cell one dimensional sensitivity profile as mapped with a thin (0.25 deg) bar which alternated in luminance from light to dark around the mean level of the 1 cd/m² background. The bar changed luminance with a sinusoidal time course at 4 Hz, and the contrast of the stimulus was, as usually defined, $(L_{max} - L_{min})/(L_{max} + L_{min})$. The amplitude of the sensitivity for the fundamental component is marked with \Box . The sensitivity of second harmonic response is marked with +. Below the amplitude plots is a plot of phase shift of the fundamental response with respect to the stimulus. The phase shift of the surround mechanism was approximately 90°. The Fourier transform of this 'linespread function' is graphed in Fig. 2.

together with the experimentally measured spatial frequency sensitivity of the fundamental component of Y cell responses. The agreement is good. The predicted bump in the spatial frequency sensitivity near 1 c/deg seems to be consistent with the data. However, these are low sensitivities and subject to some uncertainty. The major feature of the curve that is of 272

interest is the steep roll-off around 0.5 c/deg. The predicted and measured spatial frequency sensitivity functions are in particularly good agreement in this region. The sensitivity for the fundamental response in this cell was negligible at spatial frequencies higher than the highest frequency shown in the figure. These experiments are consistent with the idea that the centre mechanism of the Y cell generates the *fundamental component* of the cell's modulated responses at high spatial frequencies, that it is basically a linear mechanism, and that it has a lower spatial frequency cut-off than whatever it is which produces the second harmonic component.

Window and shutter

Two other kinds of experiments were performed to locate the source of the second harmonic distortion and also incidently to confirm that the centre generated the fundamental component. The first of these was the 'window-shutter' experiment. In this experiment we performed a standard null test except that the alternating grating was masked so that only the centre of the receptive field could 'see' the grating, the window experiment, or only part of the receptive field outside the centre could see the grating, the shutter experiment. The part of the screen which did not contain grating was kept blank, at the mean luminance of the grating, 1 cd/m².

The results of this experiment on another typical Y cell are shown in Fig. 4. Insets to the Figure illustrate the spatial stimuli used. Fig. 4A shows that at the spatial frequency used in this experiment (0.35 c/deg) this cell had about equal fundamental and second harmonic component sensitivities. When the grating was shown to the centre of the receptive field through a window $(3^{\circ} \times 3^{\circ})$, both components lost sensitivity but the second harmonic dropped significantly more than the fundamental component. When the grating was shown mainly to the receptive field surround behind a shutter (the shutter was 13° wide and 3° high) the fundamental component was almost gone but the second harmonic component suffered only a small drop in sensitivity. This result further supports the notion of centre linearity in Y cells, and suggests that some part of the receptive field surround is the major source of the second harmonic distortion.

Shutter and window at higher spatial frequencies

The results in Fig. 4A were obtained with a stimulus (0.35 c/deg grating) which was almost equally effective in eliciting fundamental and second harmonic responses. When the stimulus was a 0.7 c/deg grating, the second harmonic was dominant because the fundamental component had died away. The direct measurement of the location of the second harmonic component was then possible. Fig. 4B shows a window and shutter experiment with the 0.7 c/deg grating. When the higher frequency grating was

viewed by the cell through the window it was invisible to the cell. When the grating was obscured only by the shutter, the cell's second harmonic component declined in sensitivity only by 30%. It follows from this experiment also that the source of the second harmonic response in Y cells is located predominantly outside the centre of the receptive field.

To make the results of the window and shutter experiments more understandable, pictures of averaged responses in such experiments are given in Fig. 5. In Fig. 5 are shown the averaged responses for the 0.35



Fig. 4. A, window and shutter experiment with 0.35 c/deg. spatial grating. Contrast sensitivity vs. spatial phase. The contrast sensitivity for the full grating (10° high × 13° wide) is marked with \Box for the fundamental and \triangle for the second harmonic. For the grating seen through a 3° × 3° window, fundamental sensitivity is denoted by \bigcirc , second harmonic by +. The fundamental sensitivity for the grating seen behind a shutter (3° × 13°) was nil and is not plotted; the second harmonic for the grating behind the shutter is marked with \bigtriangledown . B, window-shutter experiment with a 0.7 c/deg. grating. Contrast sensitivity for the 0.7 c/deg. grating was negligible and is not shown. The second harmonic sensitivities for the full grating, window and shutter are respectively \bigtriangledown , *, and \triangle . For both A and B, insets show the appearance of the window and shutter stimuli.

c/deg grating at two positions of the grating and under the three experimental conditions. The positions are those of peak sensitivity and 90° in spatial phase away, the null for the fundamental component. The conditions are full grating, grating through the window, and grating behind the shutter. Fig. 5 also shows one averaged response for each of the three conditions, when 0.7 c/deg was used as a spatial frequency. Only one response per condition was required at the higher spatial frequency because all positions of the grating gave the same response.

Fig. 5. Averaged Y responses to full gratings and gratings seen through a window or behind a shutter. These are the histograms for the same experiment as in Fig. 4. The responses at peak and 'null' for the Y cell for a 0.35 c/deg grating are in the top and middle row. The responses to the 0.7 c/deg grating in the three conditions (full grating, through window, behind shutter) are shown in the bottom row. The stimulus was a 0.5 Hz square-wave alternating grating in each case. The contrast for these runs was 0.55.

Dipole stripes

The next experiment was an attempt to define more precisely the locus of second harmonic generation. One cycle of an alternating phase sine grating, which we call dipole stripes, was placed in different equally spaced positions of the receptive field, and the sensitivity of the second harmonic component for this stimulus was determined. This function which relates sensitivity for the dipole stripes to their position will be termed the *dipole weighting function*. We chose a spatial frequency for the dipole which was high enough to be above the high frequency cut-off of the fundamental response yet low enough to be resolved by the second harmonic mechanism. For the same cells, the line weighting function (with the fundamental as the criterion response) and the dipole weighting function were determined. These results are compared in Fig. 6. Clearly, sensitivity for a second harmonic response to the dipole overlaps the centre and extends into the surround well beyond the boundaries of the

Fig. 6. Dipole weighting and line weighting functions. This experiment began with measurement of the linespread function with a 0.5 deg bar alternating light and dark, as in Fig. 3. For the same cell a dipole weighting function was obtained by stimulating with 1 cycle of a 0.7 c/deg alternating phase grating located in various positions in the receptive field. For the line weighting function, the fundamental component's sensitivity is plotted vs. position and marked by \Box . It is plotted as plus when the response had the phase shift of the centre and minus when it had the phase shift appropriate to surround. For the dipole weighting, the second harmonic sensitivity is plotted with the symbol \triangle . Time course of the stimulus was 0.5 Hz square wave. The inset shows the appearance of the dipole stripes.

conventional centre and surround response mechanisms as measured in the line weighting function.

The second harmonic responses so characteristic of Y cells could be generated by various different nonlinear mechanisms. It is useful at this point to review which of these mechanisms our experiments conclusively disprove, and what possibilities are left. Nonlinear summation of pooled centre and surround signals is one hypothesis which is definitely ruled out by the experiments on spatial resolution of the second harmonic response and by the dipole weighting function. Similarly, a nonlinear transduction on either the pooled centre signals or pooled surround signal would be inconsistent with these two sets of experiments. Moreover, the centre mechanism is absolved of a significant responsibility for the nonlinear behaviour of Y cells by the window and shutter experiments. What one is left with is the necessity for postulating an additional receptive field input in Y cells superimposed on the conventional centre-surround organization. This mechanism is spread out over a large area, as indicated by the shutter experiment and the dipole weighting function, and also has high resolution as indicated by its spatial frequency contrast sensitivity function. It is impossible for a single mechanism to have a wide spatial extent and also high spatial resolution. All of our experiments point to the conclusion that the nonlinear response mechanism of Y cells is made up of a dispersed ensemble of small spatial subunits whose outputs go through a nonlinear transduction before they are pooled. There remain questions about the nature of the nonlinear transduction.

Rectification

There are several possible nonlinear transductions which might generate Y cell second harmonic responses. A pure square law device is one obvious possibility. Another possibility is a saturation type of nonlinearity, either a low power law or logarithmic type of nonlinearity. A third possibility is a linear (or nonlinear) rectifier, i.e. a transduction which is asymmetrical in its response to positive or negative deflexions. This last possibility is equivalent to a linear transduction with a threshold. It is the last possiblity which we favour, because of measurements of the dependence of second harmonic response on contrast (or modulation depth). The result of such an experiment on one representative Y cell is shown in Fig. 7. The second harmonic response was proportional to contrast up to a saturation at 0.2 contrast. No sign of a square law or other power law nonlinearity was detected. Rather, the linear contrast-response function suggests rectification as the nonlinear process which dominates the Y cell behaviour up until the saturation range (which was generally avoided in our other experiments).

Support for rectification as the major nonlinearity in Y cells is forthcoming from other experiments on the manipulation of the time course of grating alternation in the standard null test experiment. In this paper we have concentrated so far on Fourier analysis of responses to 4 Hz sinusoidally modulated alternating sine gratings. However, for 0.5 Hz square-wave modulated alternating gratings, we found that Y responses had not only second harmonic distortion, but also outstanding distortion components at many even harmonics, up as high as the tenth harmonic. Fig. 8 shows such results, which were consistent with rectification though not critical proof of this hypothesis.

Finally, more direct evidence of rectifying subunits in the Y cell receptive field periphery and the nature of the rectification was gleaned from

Fig. 7. Response vs. contrast for the second harmonic component. Here are shown the second harmonic responses as a function of contrast for an alternating sine grating of a high enough spatial frequency (0.7 c/deg) so that it stimulated mainly the nonlinear subunits of the Y cell. The saturation of the second harmonic component above 0.15 contrast is typical. The time course of the stimulus was 4 Hz sinusoidal alternation.

Fig. 8. Post-stimulus time (PST) histogram of Y response at high spatial frequency and 0.5 Hz square-wave temporal modulation, with Fourier analysis. Here is shown an averaged response to a stimulus of 0.55 contrast at 0.7c/deg. The Fourier analysis shows prominent peaks at the even harmonics.

experiments involving stimulation of the cell with two bars placed in the receptive field periphery of cells and square-wave modulated in antiphase. Results from such an experiment are shown in Fig. 9. This cell generated a transient off-response from the surround when each bar alone alternated

Fig. 9. Frequency doubled response generated by the sum of two surround responses: the two bar experiment. Two 1 deg bars $(10^{\circ} \text{ high } 1^{\circ} \text{ wide})$ were located in the periphery of the receptive field of a Y cell. The upper two responses are generated by each bar individually with the other blank. The temporal modulation of the stimulus was 0.5 Hz, square wave. Each bar generated mainly one burst of firing when it flipped from light to dark because this was an on-centre Y cell. When the two bars were modulated in antiphase (one went bright just as the other went dark) the response was on-off. The response to the two in antiphase was almost exactly the sum of the separate responses.

from bright to dark (see linespread data above). When the bars were locked in antiphase, the two asymmetrical off-responses simply added, producing a frequency doubled response. The reason is that there was no symmetrical inhibition at the opposite phase of the response from the off burst, i.e. the responses to the bars alone had gone through the physiological equivalent of a half-wave rectifier which could only generate excitation at light off but not inhibition at light on.

Fig. 10. Spatial model for the Y cell receptive field. The spatial extent of elements of a Y type retinal ganglion cell are shown in this Figure. There is a centre and overlapping nonlinear subunits of the surround, each of them smaller in spatial extent than the centre. Also there is a large linear surround mechanism. The linear centre and surround are drawn with solid curves while the nonlinear subunits are drawn with a dashed curve.

DISCUSSION

The Y cell receptive field

The presence of a widespread nonlinear pathway with high spatial resolution is what characterizes Y cells in the cat retina. From the experimental results already presented one can construct spatial models of the sensitivity profiles of different receptive field mechanisms in Y cells. A model which is consistent with the data in this paper is diagrammed in Fig. 10. There are three types of spatial component in the model: the conventional (linear) centre, the conventional antagonistic (linear) surround, and the nonlinear rectifying subunits. In this model the rectifying subunits have the same sign as the centre mechanism, e.g. in on-centre cells the model's subunits would respond with excitation at the onset of illumination. Pure off-responses from bars or spots placed in the receptive field surround would result from summation of on excitation only, from the rectifying subunits, with symmetric on-inhibition and off-excitation from the linear surround mechanism. This model would also account for the apparent shallow gradient in the centre's sensitivity profile in Y cells (Ikeda & Wright, 1972). The apparent shallow gradient would be caused by incorrect association of subunit responses with those of the centre response mechanism because they are of the same sign. If the model were correct, it would be almost impossible to avoid this error because the centre and the subunits overlap.

If the conventional linear surround mechanism were weak or absent in Y cells, one would have to hypothesize that the subunits had the opposite sign from the centre to account for responses like those in Fig. 9 in this paper. However, we have found a great deal of evidence which reveals a strong Y surround which is antagonistic to the centre. For example, there is the line weighting function in Fig. 6 of this paper. Another measure of the surround is the difference between the centre-dominated responses to gratings and spots and the combined centre-surround responses to modulated diffuse light as shown in Figs. 11 and 12 of the previous paper (Hochstein & Shapley, 1976). The responses to diffuse light were more or less surround dominated. So a linear, conventional receptive field surround is not negligible in Y cells.

Because the receptive field centre, surround, and subunits overlap so much, it is difficult to determine whether the nonlinearity in the subunits is closer to full wave or half wave rectification. For instance, pure-off responses, i.e. half wave rectified responses, from the receptive field periphery could be generated by the summation of a symmetrical, linear response of the linear surround mechanism together with either a pure 'on'-response or an 'on-off' response from an overlapping subunit. In some Y cells, the line weighting functions and the dipole weighting function in the far periphery of the receptive field indicate that the local subunit response is 'on-off'. But there also are Y cells which do not give frequency doubled responses to lines or dipoles in the receptive field periphery, and therefore which probably have half wave rectifying subunits. In this context, it is worth remembering how effective the high spatial frequency alternating phase grating was in isolating the second harmonic response even though there was this considerable overlap of centre, surround, and subunits. The grating worked because the conventional centre and surround mechanisms summed signals over too large an area to be able to resolve the fine grating. Unfortunately the grating cannot help determine the sign of the subunit response. Fortunately, knowledge of the exact wave form of the rectified responses is not required in order to gain insight into the effects of rectification on Y cell responses.

Rectifying subunits can account for many of the peculiarities of Y cell responses. Already we have argued that they can account for the presence of second (and other even) harmonic distortion while still giving a linear response vs. contrast curve for the distortion component. The characteristic 'on-off' response of Y cells to diffuse light probably results from the fact that the nonlinear subunits' responses in on-centre Y cells for instance, add excitation to the centre's response at light on but do not subtract from the surround mechanism's very large excitation at light off. Similarly, rectification in surround subunits may explain the prominent 'on-off' responses seen in response to spots or bars placed in the centre surround overlap region of Y cells. The presence of nonlinear subunits which overlap with the conventional surround mechanism in Y cells may account also for the difficulty encountered by Enroth-Cugell & Pinto (1972) and Enroth-Cugell & Lennie (1975) in their attempts to isolate the pure surround response of cat Y cells. The former authors used centre desensitization and annular stimulation, while the latter authors used subtraction of the response to a small disk from the response to a large disk, in order to obtain pure surround responses. These methods worked in X cells but not in Y cells. From the model in Fig. 10 it is apparent why neither technique would work in Y cells. It is not because of too much centre-surround overlap; there is too much subunit-surround overlap.

This experiment with dipole stripes revealed that some subunits also overlap with the centre response mechanism but that other subunits extend a considerable distance beyond the centre. Even so, the subunits were smaller than the width of the dipole, since they could still resolve the dark from light bar and give their usual second harmonic response. Since the subunits were small but covered a wide area, there must have been many of them.

These nonlinear subunits almost certainly generate the elevation of discharge in response to a drifting grating in Y cells. Our quantitative data on this point are not yet complete. Nevertheless, it is already clear that, qualitatively, the elevation in mean discharge without modulation occurs in just the same spatial frequency region as that in which second harmonic distortion becomes dominant over the fundamental component in the response to an alternating phase grating. We think a sufficient explanation for the difference between the phased (at twice the modulation frequency) response to the alternating grating and the unphased excitation to the drifting grating results from the spatial dispersal of the many subunits. With the alternating grating all the subunits at different spatial positions can add because the temporal modulation at each point of the stimulus is exactly in temporal phase with every other point. This is not the case with the drifting grating and so the responses from the spatially disparate subunits merge into a generalized elevation of mean discharge rate.

Within one subunit spatial summation must be linear. This is deduced from the failure of the subunits to resolve gratings beyond their spatial frequency cut off. The subunits receive convergence from many photoreceptors The smallest subunits we have found could resolve 2 c/deg, though there may be even smaller subunits in more centrally located Y cells from which we were unable to record optic fibre activity. In Y cells, the component of the receptive field with the best spatial resolution is not the centre but rather the nonlinear subunit. The subunits are approximately one third as big as the centre of the Y cell, to judge from the spatial frequency responses we have obtained. When we have recorded X cells and Y cells in close proximity the size of the non-linear subunits in the Y cell roughly corresponded with the X cell centre. Perhaps the size of a Y cell subunit and an X cell centre is roughly that of a single bipolar cell receptive field. Just as X and Y cell centres become larger with retinal eccentricity so too do the non-linear subunits of the Y cells.

Retinal rectification

Others have also found evidence of rectification in retinal signal processing. The most pertinent study is by Toyoda (1974) who recorded intracellularly the response of carp retinal neurones to sinusoidally modulated diffuse light. He found that receptors, horizontal cells, bipolars, and some amacrines responded at the fundamental frequency of modulation, while other amacrine cells responded at the second harmonic frequency. As we have done, he measured the magnitude of the second harmonic response as a function of modulation depth and found it was proportional up to a saturation at high modulation depths. He inferred from this that there must be rectification prior to the appearance of the second harmonic.

Spekreijse (1969) found rectification in goldfish retinal ganglion cells. But then Spekreijse & van den Berg (1971) showed that this rectification occurred fairly late, only after spatial summation which appeared to be linear. They did this with an experiment very much like the null test experiment, with the difference that the spatial pattern was an alternating checkerboard pattern rather than an alternating phase grating. The cells they investigated would correspond to X cells in the cat. Toyoda's finding (Toyoda, 1974) of frequency doubling in some amacrine cells in the carp, a species closely related to the goldfish, raises the possibility that there may be other classes of ganglion cells in these fish which show nonlinearity in spatial summation.

These results suggest that up to the bipolar cell level all the transductions in the retina are linear, in the small signal regime at any rate. However, Toyoda's results imply that there is a rectifying nonlinearity in the inner plexiform layer. This agrees with the popular intuition that Y cell characteristics are determined by some subspecies of the amacrine cells. In the previous paper we argued that the existence of X cells, and the linear component of Y cells, implied that the ribbon synapses were pro-

bably the morphological substrate of a linear synaptic transduction. The inverse of this proposition is that conventional synapses in the inner plexiform layer of the retina might underly nonlinear transductions. It is quite speculative but not inconsistent with the known facts to propose more specifically that amacrine cells which receive conventional synapses from other amacrine cells may be the place where the subunits are born. The size of a subunit may not be set by the dendritic field of one of these amacrines, but rather by the dendritic field of the element presynaptic to the rectifying synapse. Another possibility, suggested by the Journal of Physiology's referee, is that rectification might result from the consequences of action potentials in amacrine cells. If amacrine \rightarrow ganglion cell transmission were of major importance, and if the amacrine cell had a low maintained impulse rate, rectification could be the result of the fact that impulse rates cannot go negative. This proposed mechanism would have to operate before spatial pooling in order to account for the high spatial resolution of the subunits. One consequence of this proposed mechanism is that the rectification might have a very sharp transition, from above threshold to below threshold. A synaptic rectifier might provide a somewhat more rounded transition. Both more precise experiments and some extensive calculations will be required to decide between these alternative models of the nonlinearity in Y cells.

Y cell functions

Cat Y cells are equipped to have a duplex function. They respond in a phase sensitive manner to large objects while giving a generalized elevation of activity when patterns of fine detail move across their receptive fields. Searching for the single function of these cells, as the front end of a central 'motion detector' say, may lead to only partial understanding of their full role in vision. They may be generally involved in signalling the presence of objects. Nevertheless, the Y cells do seem to be involved in the detection of movement or temporal change, as part of this object signalling function.

Recent psychophysical experiments on detection of flicker have shown that there is nonlinear summation of subthreshold stimuli (King-Smith & Kulikowski, 1975). The non-linearity looks like the rectification seen in Y cells, since subthreshold stimuli peripheral to the flickering psychophysical test stimulus can add to its sensitivity when the two stimuli are in antiphase but cannot subtract from the sensitivity when their contrast modulation is reversed, that is, in phase. The widestread belief that Y cells are involved in flicker and motion detection is probably strengthend by the correlation of our neurophysiological findings with these psychophysical results of King-Smith & Kulikowski. This work was supported by grants from the U.S. National Eye Institute, EY 1472 and EY 188. S.H. was supported by a post-doctoral fellowship from the U.S. National Institute of Health. Also, we wish to acknowledge the gift of diallylbis-nortoxiferine from Dr William Scott at Hoffman-La Roche, Inc.

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