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Abstract:

The vertebrate retina consists of a series of sheets of neurons, each containing a patterned representation, or "neural image" corresponding to the incoming visual scene. Most of the operations can be described as convolutions implementing small kernels involving local neighborhoods. These patterns become more complex as the visual signal passes through the retina as each new convolution builds upon previous ones. Because we have access only to single cells, these patterns of activity have never been recorded. As a first step in visualizing these patterns we have attempted to simulate them using modern image processors operating in real time, that, like the retina invoke local convolutions, in an effort to understand the mechanisms, and the physiological roles of each of these biological image processing operations. In addition, we have now developed methods for measuring these patterns in living retinas. The comparison between the modeled and measured patterns will show us what components of retinal function have not yet been incorporated into our understanding, as expressed by the models. These studies will help us to understand biological image processing by forcing us to assemble the retina using well-defined physiological functional building blocks, derived from retinal function. A long-term objective of this research is the implementation of biological image processing algorithms for man-made systems such as tracking, target identification, guidance and navigation.

Final Technical Report

AFOSR -91 - 0196

P.I.: Frank Werblin

Computer models of retinal function

- **Objectives:**

The vertebrate retina processes information by passing the visual signal through a series of 2-dimensional sheets of neurons (1) as illustrated in the caricature shown in Figure 1. At each retinal level these neuronal arrays express a pattern of activity the "neural image," that reflects the image processing operations that have been performed. Most of the operations can be described as convolutions implementing small kernels involving local neighborhoods. These patterns become more complex as the visual signal passes through the retina as each new convolution builds upon previous ones. We have attempted to reproduce these patterns of activity using modern image processors operating in real time, that also invoke local convolutions, in an effort to understand the mechanisms, and the physiological roles of each of these biological image processing operations. These studies will help us to understand biological image processing by forcing us to assemble the retina using well-defined physiological functional building blocks, derived from retinal function. A long-term objective of this research is the implementation of biological image processing algorithms for man-made systems such as tracking, target identification, guidance and navigation.

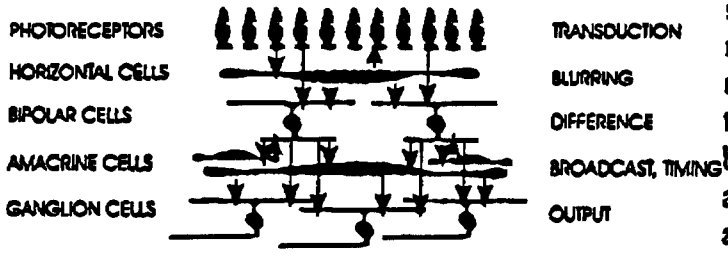

Figure 1. Schematic of vertebrate retina showing the 5 main layers of cells identified by their names (left) and their functions (right). Convolutions at each layer perform image transformations that alter the pattern of activity that exists at each retinal level.

- **Methods:**

The neural images generated by the biological retina are dynamic 2-dimensional patterns formed via convolutions based upon small (neighborhood) kernels. These kernels dictate in what ways the activity at each pixel is a function of the activity of adjacent pixels in its local neighborhood. These operations are best and most easily simulated through the use of currently-available image processing computational systems. We have utilized two different systems for studying retinal processing. Our first computational system was the PIPE (Pipelined Image Processing Engine). This was a digital machine operating in real time that performed local convolutions. More recently

we have utilized the CNN paradigm (4,8), a somewhat more versatile system oprating on similar principles, but with the capability of being implemented in analog VLSI. We adapted the space and time constants derived from physiological single cell measurements taken from the retina of the salamander to form the appropriate convolution kernels, synaptic functions, and interactions mediating retinal function. Both of these systems have generated patterns of activity that simulate the image processing functionsof the biological retina at each level of operation.

Concurrently with the development of the computational retinal models, we have been implementing methods for actually measuring the patterns of activity generated by the biological retinas. The objective here is to compare the patterns generated by the biological retinas with those formed on the image processors. Essentially, we are comparing the measurements with our hypotheses of retinal function. To the extent that the model and hypothesis match, we can be reasonably satisfied that our hypothesis, to the level that it reflects retinal function, is accurate. More interestingly, when there is a mismatch between measurement and hypothesis, we will be led to a new area of retinal functional that had previously been obscure.

So far in this work, our descriptions of outer retinal function seem adquat e because we have matched the measurements taken from the physiological retina with the patterns generated in the model. We are presently working on the measurement of inner retinal function as reflected in the behavior of the output cells, the ganglion cells. It is in this region of retinal function, mediating movement detetion and directional selectivity, where little is known about retinal circuitry or function, that we expect to find disparities between hypothesis and measurement.

- **Results during the grant period**

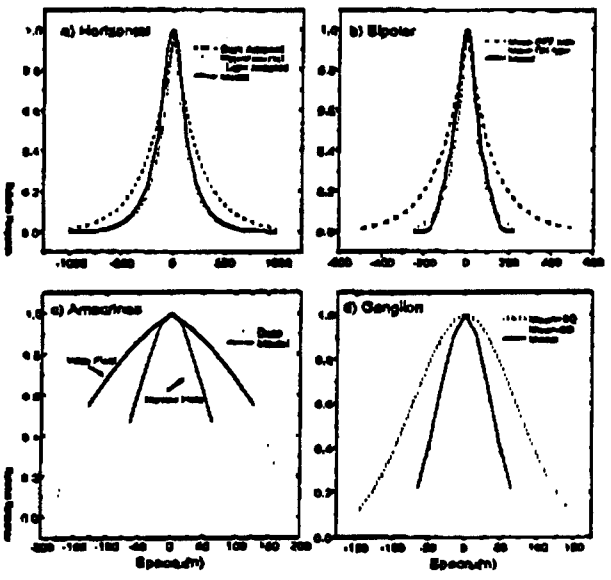

Figure 14

Figure 2. Space constants for retinal networks derived from the physiological data. These space constants are implemented as diffusion templates at each level

Our research has focused upon implementing as much of the image processing capability of the retina as possible in the model system. The results of this work is embodied in Paper #1 included in Appendix I (7), as well as in a videotape that has been widely distributed to the academic community throughout the world. A copy of this tape has already been sent to John Tangney at AFOSR, and a copy is available upon request.

The parameters we used to implement the overall model were taken from the physiological studies of the salamander, perhaps the best-studied vertebrate retina we have today. To illustrate, Figure 2 shows a summary of the space constants incorporated into the model.

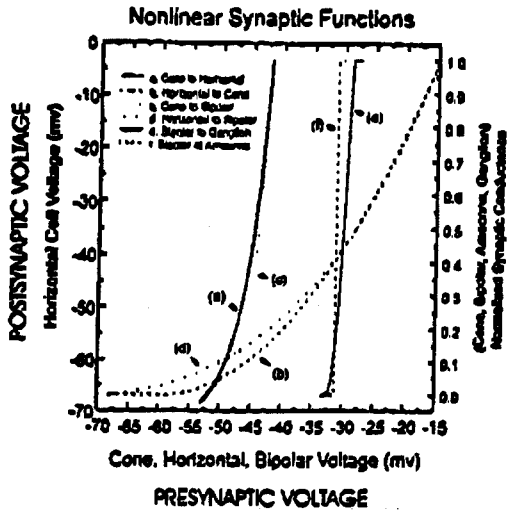

Figure 15

Figure 3. Synaptic functions defining the relationship of activity in each retinal cell as a function of the activity of the cells that drive it. As a general rule, cells in the outer retina were driven by continuous functions over a broad range of potentials, whereas cells in the inner retina were driven by much steeper functions that are almost "threshold" functions.

Timing of retinal signals was also adapted from the physiological measurements, and the data used to implement this timing is discussed in Paper 1. Finally, the synaptic functions, derived from the measured input-output relations between retinal cells, was implemented from lookup tables in the model. A series of these synaptic functions is illustrated in Figure 3.

These three functional relationships defining time, space and relative magnitude of signals, were combined according to the rules of retinal connectivity as well as we know them today (5), to generate the model of retinal function described in Paper I and illustrated in time and space on the videotape. Some of the highlights of these studies are illustrated below.

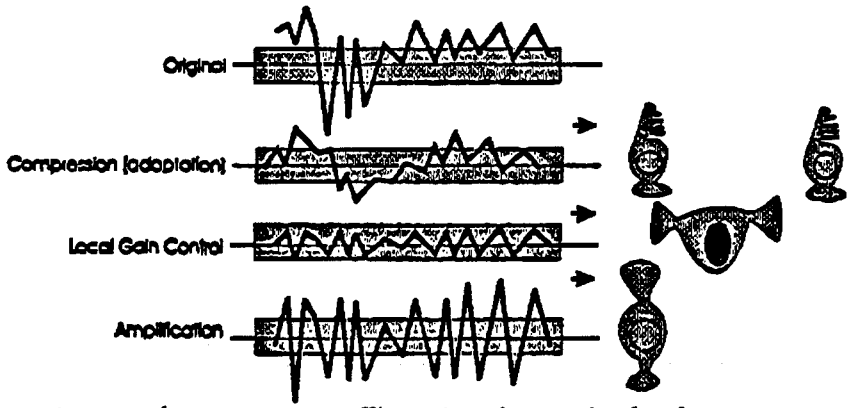

Figure 4. Transformations at the outer retina. The original intensity levels are compressed by adaptation mechanisms in each photoreceptor to generate a series of compressed response levels. These levels are normalized with respect to local average intensities by the action of the horizontal cell network. These locally normalized signals are then amplified at the synapse between photoreceptors and bipolar cells to emphasize the slope of the signal at

- **Outer Retinal Function**

The first major interaction in the retina takes place at the photoreceptor terminals where the broad ranging horizontal cells feed back to the photoreceptors to form a contrast-enhanced version

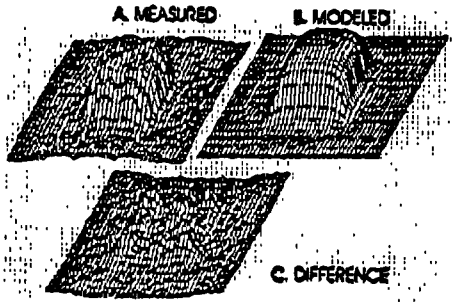

Figure 5. Patterns of activity at the bipolar cells. A. Activity measured in a bipolar cell "array" showing the presence of some inhibition around the edges of the square. B. Patterns generated in the model using lateral inhibition from horizontal cells. C. Difference between the measured and modeled patterns at the bipolar cell array. These differences, mainly spike-like projections at the corners of the responses to a square, represent activity that was not accounted for in the model.

of the original image at the photoreceptor terminals (2,6) as shown in Figure 4. The signals generated across the array of bipolar cells in response to a square patch of illumination are illustrated in Figure 5. This shows the bipolar cell response to the square embedded in a saucer of horizontal cell inhibition. A snapshot of the form of bipolar cell patterns derived from both the hypothetical and actual physiologically-measured results are shown, along with a pattern showing the differences between these two forms of activity at one instant of time. It is through an analysis of these differences that we will be able to learn about retinal function, because the differences are due to components of function that we have not included in the model. For example, in the comparison of Figure 5, there is a set of peaks in the activity of the model that don't exist in the measurements. This indicates that either the space constants for the horizontal cell or bipolar dendrites was in error in our model and should be adjusted based upon a more accurate set of physiological measurments. These results also show that interactions at the outer retina perform more of a gain-setting than an edge enhancing function. It would require a much narrower space constant for the horizontal cells to mediate an edge-enhancing function (3).

- **Activity at the Inner Plexiform Layer**

The inner retina mediates functions associated with timing such as movement detection, change detection, and dynamic contrast gain control. These functions are subserved by two main populations of amacrine cells as shown in Figure 6. One population, generating a sustained response, appears to transmit inhibition over a region about the same dimension over which it receives its input, as shown in Figure 6A. The other population receives input locally, then broadcasts its output over a broad area, but only transiently, as shown in figure 6B. These cells have processes that can extend 1/3 of the way across the retina, and their inhibitory activity dominates the activity of all cells that send signals from the retina to higher centers. The retinal output cells, the ganglion cells, are therefore controlled by these inhibitory signals, and their effects are superimposed upon the activity of the bipolar cells shown in Figure 5, as illustrated in the behaviors of the ganglion cell

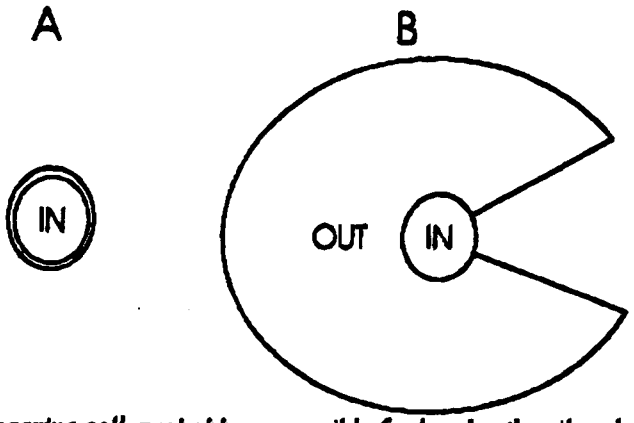

Figure 6. A. Narrow field amacrine cell, probably responsible for local rather than lateral inhibition. Its main role may be to truncate activity in local regions creating transient activity in cells that signal only the arrival or departure of visual targets. B. Wide field amacrine cells. Their function is to receive inputs locally (in) and then to broadcast activity over wide regions of the retina (out). These cells may be involved in directional selective movement detection

mosaic shown in Figure 7. This figure shows the development in time of the ganglion cell response. It begins with a square area of activity corresponding to the excitatory input from the bipolar cells in A. This is followed by a trough of inhibition that begins to develop in B, and proceeds to spread across the retina in C and D. As this trough represents the activity of the amacrine cell system described in B of the previous figure. At the same time, a ridge of activity develops around the original square area of activity. This ridge is mediated by the local inhibition of the narrow field amacrine cells shown in part A of Figure 6. These two inhibitory components, represented by the ridge and trough, are the simplest manifestations of the amacrine cell inhibition.

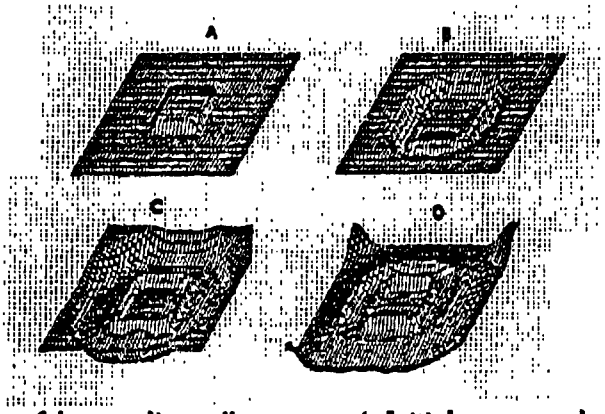

Figure 7. Development in time of the ganglion cell response. A. Initial response showing the excitatory input from a local population of bipolar cells driven by the square stimulus. B,C,D. Development, in time of a broad inhibitory trough mediated by the wide field amacrine cells, as well as a narrower ridge of inhibition near the square itself mediated by the narrow field amacrine cell system.

- **What we've learned from these studies.**

The modeling exercise presented above and described more fully in Appendix I represents a first step in understanding retinal function from a computational point of view. We now have an assembly of functional modules embodied in the model descriptions of the different classes of retinal cell networks. Most of the physiological responses can be approximated by these components, but the actual arrangement, including lateral dimensions, time course, synaptic gains and weightings

can only be determined by comparing the model behavior with that of the living retina. To measure the patterns of activity in the actual retina we have constructed a multielectrode recording apparatus that is capable of measuring the coincident activity of 100 ganglion cells. This will provide us with information about correlative activity and asymmetries in function. In addition, we have developed methods for recording with patch clamp from individual ganglion cells, recordings that can last for hours. By moving the stimulus, i.e. a square box, to every possible position with respect to the ganglion cell, we can use that cell as a representative of all ganglion cells in a grid that would have responded to the stimulus. These recordings, displaying both excitation and inhibition, can then be played back in sequence to provide a pattern of activity which we can compare with the model. These studies will give us a clearer indication of the dimensions and time course of the retinal networks underlying different forms of lateral inhibition, networks that have never been studied before. Thus, the model provides us with a prototype of retinal function as we know it today, which may be useful for generating biologically-based image processing system. But the modeling also leads us to new advances in our understanding of the biology by providing valuable analytical tools that have never before been available to biologists.

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