A Three-dimensional Physiologically Realistic Model of the Retina

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Abstract: The main purpose of this work is to create a physiologically realistic computational model of the retina by providing a flexible, real-valued three-dimensional architecture. This model exhibits the overall spatio-temporal response of the network as a whole, as well as the temporal responses of individual cells in the different layers of the retina. The network performs both functions in a consistent way. The model will be expanded in the near future to include color vision, Mach Band effects. It can also be used to model other physiological systems and functions. The platform on which this neural network is built is Windows 98 using an object oriented approach.

Introduction: Our current work consists of an object-oriented neural network based on the layer structure, which is a suitable architecture for modeling several aspects of the retina. In particular, we are trying to reproduce waveform responses seen in retinal neurons by Dowling [1] and by using variations of network structures seen in [2-3] and Micheli-Tzanakou [9]. We are also using variations of response functions, as described below, used by Micheli-Tzanakou [9]. The main purpose of this work is to improve our computational models of the retina by providing a flexible architecture that can be easily parameterized and that can be easily viewed in both its overall spatial/time response as well as in the time response of individual neurons. This architecture, as described below, allows us to easily experiment with different degrees of connectivity between the different layers of neurons in the retina. Since we can examine both the inputs and outputs of each neuronal layer, we can easily identify the source of any discrepancies between our simulated results and the experimental data that we are trying to model. One of the main features of this model is that the positions of the neurons are real-valued instead of being placed in discrete intervals. This allows for more realistic determination of the weights and delays of synapses. Furthermore, it precludes the need for the hexagonal pixel approximation of visual stimuli, as used by us and others [9,4-6]. The network is displayed in a graphical and interactive windows-based environment.

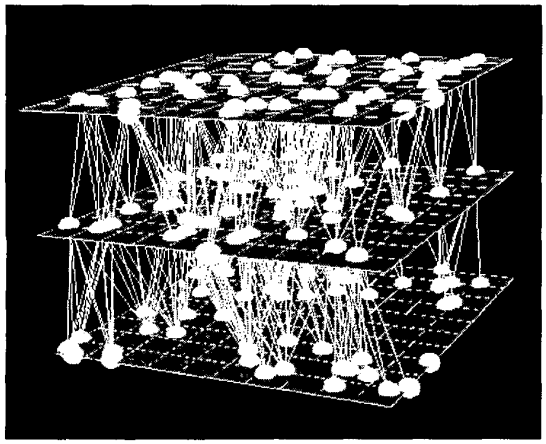
0-7695-0619-4/00 $10.00 © 2000 IEEE

There are several other aspects of the retina that we are modeling, including the accommodation of color vision through the modeling of rods and cones. Also, we are attempting to model the Mach Band effect through the use of lateral inhibition and motion detection. The object oriented structure used makes it possible to easily build in as much detail as we need into the neurons and synapses. These details can range from thresholds, refractory periods, synaptic weights and delays to resting potentials and specific waveforms to even include synaptic chemical concentrations and active transport through the neuronal membrane. This flexibility is being used to try to find a principled way to generate single-neuron effects, such as habituation and the exponential decay rate in the frequency of a spike train. Elaboration on the network architecture and the response functions that we are currently experimenting with can be found below.

Network Structure

In order to generalize our network design and expand its capabilities beyond the module-based designs used in previous work, we have designed our network utilizing a conceptualized three-dimensional model. Our aim was to design a network structure that more closely resembles the architecture found in the actual retina. We felt that a three-dimensional model would achieve these aims far more naturally and accurately than the previous models referenced [4-8].

The module-based retina model is constructed by replicating small modules consisting of a small number of explicitly interconnected characteristic neurons [7]. Although relatively simple to construct and very interesting to study, such a design has certain limitations. Firstly, although the design of an individual module may allow for a great deal of design variety, the use of repeating modules creates a network that is somewhat rigid in its structure. Thus, although the parameters of a single module may be permutated indefinitely, a macroscopic retinal model consisting of the replication of a single unit will inevitably be restricted to be uniform at all points in space. Secondly, the use of individual modules poses a problem when it comes to the interconnection of modules. The process of interconnecting multiple modules to create a larger retinal surface is not straightforward, and will almost always lead to points of interconnection. For example, a single module may consist of two photoreceptors, one horizontal cell, two bipolar cells, one amacrine cell, and three ganglion cells. Thus the ratio of cells is 2:1:2:1:3, respectively. By expanding a network based on such a module, we would either be restricted to creating a network of a fixed ratio of cells, or we would have to fabricate an intricate method of interconnecting modules which would somehow merge the modules in a nonlinear manner. In the first case, we would be unable to create a network with hundreds of input cells, and only a few output integrating cells. In the second case, the interconnection method would have to be explicitly defined depending on the model and the desired arrangement, resulting in a non-general program design.



The three-dimensional neural network model resolves all of these problems, resulting in a very generalized and powerful network structure. It is based on a conceptualized three dimensional model, in which neurons are organized into functional groups called layers. Essentially, a layer represents a collection of neurons that exhibit the same "cellular" properties, as well as qualitatively forming the same types of synaptic interconnections. In our case this would indicate that all the neurons on a particular layer would process their output responses using the same algorithm. Also, all the cells on a given layer would generally form connections of the same type (i.e. excitatory or inhibitory) with neurons on other layers (or within the same layer as in lateral inhibition). Thus, for a preliminary retina model, we have six layers to represent photoreceptors, horizontal cells, bipolar celof ls, two different layers amacrine cells, and two different types of ganglion cells: G1 and G2. Each type of cell is characterized by its function, the types of interconnections it forms, and the method by which it generates its response to its given inputs. Thus, photoreceptors would receive input from a separately defined stimulus; horizontal cells would receive excitatory inputs from photoreceptors; bipolar cells would receive excitatory input from photoreceptors and inhibitory input from horizontal cells; and so on. The distinction between G1 and G2 cells would be predominantly in the connections that they form: G1 cells would receive inputs from both bipolar and amacrine cells, while G2 cells would receive input from only amacrine cells. This design can easily be expanded to include color vision by replacing the single layer of photoreceptors with four layers representing rods and the three different types of cones (red, green, and blue). All of the network design considerations, such as the relative density of each type of neuron, the types of cells which form synaptic junctions, the weighting and delay of the synaptic connections, and the neuron response functions themselves can be specified by adjusting various network parameters.

A key feature of this three-dimensional model is that the neurons can be positioned at any real-valued coordinates within their given layer. This has two paramount advantages. Firstly, this allows a network to be constructed in which the density of neurons can be variable over different spatial locations in a layer. Thus, photoreceptors can be created using a layer-centered gaussian distribution function, resulting in a high concentration of cells in the center, and a diminishing concentration in the periphery, thus modeling the natural existence of a fovea. Another interesting possibility would be the design of a color vision scheme that mimics the human concentrations of cells, with a high concentration of cones and low concentration of rods in the fovea, and a high concentration of rods in the inner periphery. Other interesting effects, such as the existence of a blind spot or even retinal damage, can be modeled by introducing an area with a vacancy of photoreceptors.

The second advantage to this design is the fact that the neuron's assigned coordinates can be utilized in the construction of the synaptic connections. Thus the layer of bipolar cells, for example, can be connected to the layer of photoreceptors by using a distance-based gaussian weighting function with a threshold. This results in the formation of strong synaptic connections to cells that are in close spatial proximity, and weak synaptic connections to cells that are further away. The threshold level indicates the connection strength under which no connections will be made, thus serving the functional purpose of defining a neuron's "connective field." Furthermore, the delay assigned to the synaptic connections can be determined as a function of distance, thus modeling the natural fact that synaptic delay is directly proportional to neuronal distances.

The entire network is iterated in a pseudo-parallel fashion by storing a time variable which is incremented only after all of the neurons have collected their respective inputs from other neurons and calculated their response functions. The network can be visualized using both a time-varying colorized spatial display (an example frame of which is included above), as well as with neuron-specific time response windows, which display a graph of a neuron's output versus time. Thus both spatial and temporal effects can be easily monitored and analyzed. The network structure itself is very general and can be utilized in endless neural modeling applications. Thus, the modeling of the retina is only a starting point in the endless variety of experiments that can be explored.

Methods: This three-dimensional neural network is based on a multi-layer architecture, in which each two-dimensional layer represents a collection of neurons that exhibit the same "cellular" properties. All of the network design considerations, such as the relative density of each type of neuron, the types of cells which form synaptic junctions, the weighting and delay of the synaptic connections, and the neuron response functions themselves can be specified by adjusting various network parameters. As can be seen in figure 1, the neurons have real-valued coordinates, thereby eliminating the need for our previous module-based network architectures. Instead, we use Gaussian or polynomial distributions for the placement of neurons on each layer. Thus, for a preliminary retinal model, we have six layers to represent photoreceptors, horizontal cells, bipolar cells, two types of amacrine cells, and two different types of ganglion cells, differentiated only by the origin of their inputs. Each type of neuron is defined by its connectivity to other layers and by their individual response functions, which are designed to model physiological data.

Results: Figure 2 shows the results of an experiment verifying the validity of the three dimensional retinal architecture. The network utilized here is very simple, consisting of three layers each containing 50 neurons positioned using a uniform random distribution function. Each layer of neurons receives, as input, the outputs of neurons of relatively close proximity from the layer immediately above. To be physiologically realistic, all of the synaptic weights are proportional to the geometric distance of the two neurons connected. Although the synaptic delays are all fixed at five time units, they can also be varied in the same way. Each of the neurons generates its response using a very simple weighted summation. The topmost layer, however, represents the photoreceptor layer and does not receive any input from other neurons. Instead, it receives input from a separately defined two-dimensional time varying image. The stimulus used in this experiment is a narrow line that moves transversely across the width of the visual field. As is expected, the photoreceptors are excited by the bright line in a pattern very similar to the stimulus itself. It can clearly be seen that this excitation propagates down through the remaining two layers only after the designated synaptic delay. Thus, only the first layer is excited at time T1, while at T6, there is still residual activity in the remaining layers even though the stimulus is no longer present. Most importantly, we can see that all the neurons in each layer do not exhibit exactly the same behavior. Instead, the random component in each neuron's location leads to independent behavior due to the number of connections and the neighborhood of that neuron.

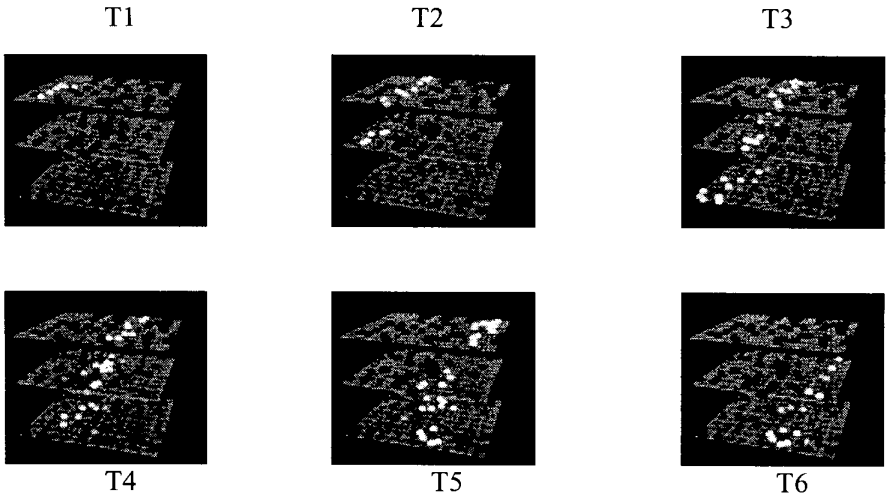


Figure 2: Spatiotemporal characteristics of a moving line through the layers of the retina

New Aspects: Because of the real-valued coordinates of our neurons, we have a very physiologically accurate model with which to test theories and experimental results. We have also facilitated the evaluation of these theories through our graphical representation of the spatio-temporal network responses and the time course of excitation. Figure 3, besides the spatial properties of the network, shows the waveforms that correspond to an edge detection mechanism. The flexibility of this neural network allows us to accurately model many physiological phenomena. For example, we are currently experimenting with lateral inhibition, feed-forward and feed-backward connectivity, adaptation effects and Mach Bands.

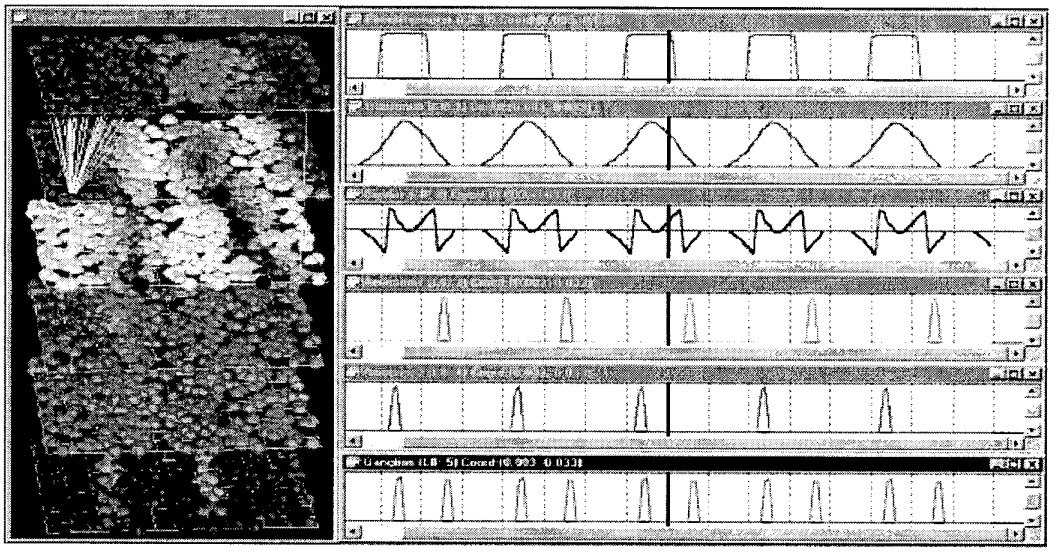


Figure 3: Edge detection and Mach Band effect as indicated in the waveforms.

Conclusions: The flexibility and realistic aspects of this "retina" make a more general neural network that can be used in modeling other areas of the visual system and any other sensory system. Any new network can be defined by changing the response functions of the different types of cells and the connectivity distributions between the layers.

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