First Stage of a Human Visual System Simulator: The Retina

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Abstract. We propose a configurable simulation platform that reproduces the analog neural behavior of different models of the Human Visual System at the early stages. Our software can simulate efficiently many of the biological mechanisms found in retina cells, such as chromatic opponency in the red-green and blue-yellow pathways, signal gathering through chemical synapses and gap junctions or variations in the neuron density and the receptive field size with eccentricity. Based on an image-processing approach, simulated neurons can perform spatiotemporal and color processing of the input visual stimuli generating the visual maps of every intermediate stage, which correspond to membrane potentials and synaptic currents. An interface with neural network simulators has been implemented, which allows to reproduce the spiking output of some specific cells, such as ganglion cells, and integrate the platform with models of higher brain areas. Simulations of different retina models related to the color opponent mechanisms, obtained from electro-physiological experiments, show the capability of the platform to reproduce their neural response.

Keywords: Retina simulator · Human visual system · Color opponency · Neural network · Spikes

1 Introduction

The first stages of the Human Visual System (HVS), from the retina up to the primary visual cortex, have been extensively studied and there exist numerous models that characterize their anatomy and most of their biophysical functions. Considering the retina, for example, it is possible to find models able to reproduce a specific physiological experiment in great detail [3,6,33,36] and models that aim to mimic the retina processing as a whole [4,11,17,20,21,27,28,39]. Computations performed by these models reproduce those retina behaviors that they have been intentionally designed for, but lack the configurability to modify their simulation circuitry and adapt to new experiments.

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Among all retina simulators that include all retina stages, Virtual Retina [39] is probably the most complete and detailed one, which is able to reproduce the biological complexity while maintaining the efficient filtering scheme of functional models. One of the contributions of Virtual Retina is the shunting feedback mechanism via amacrine cells towards bipolar cells, also called fast adaptation layer, which allows to reproduce the contrast gain control performed by the retina. At small contrasts, the system has a quasi-linear transformation function but at higher contrasts the retina starts responding sub-linearly and the gain in the bipolar transformation curve is lowered, saturating the output.

We find fewer references of retina simulators that include color processing. Color components are often disregarded in most of retina models, e.g. Virtual Retina, and when they are considered the model simply matches RGB image components with the three types of cones. However, there are remarkable exceptions such as the multi-stage color model by De Valois[11] that includes a quite detailed study of color mechanisms present in the retina, including for instance luminance and color separation of the input visual stimuli by adding the opponent responses of midget bipolar cells. This model also considers random peripheral connectivity for midget bipolar cells, proposing that both type of cones, L and M, connect to the surround of the receptive field and this fact could be enough to generate a cone-opponent signal. Other authors have also implemented the chromatic opponency, red-green and blue-yellow, based on random peripheral connectivity and similar density schema of cones in the fovea [26,29,40] but considering more than one type of cone in the center of the receptive field.

Neural network simulators, on the other hand, describe the low-level biophysics of large and heterogeneous networks of neurons. The user can create neurons individually, or in layers, and then establish connections among them. These simulators have been widely used to simulate, for example, models of the visual cortex. Some of the best known neural network simulators are Neuron[22], STEPS[37], NEST[18], PyNN[9] and Topographica[5]. However, these simulators are computationally time consuming and in most of cases the user needs a background knowledge in Neuroscience.

The platform we propose is halfway between these two approaches and combines the efficient filtering scheme of retina simulators based on image-processing techniques and some biological concepts and implementations considered in neural network simulators. In agreement with other authors [19], we consider that there are sufficient examples of single cell types that serve quite different roles in retina processing to motivate the generalization of basic retinal circuits. Moreover, many retina models are composed of similar processing modules that only change their connection scheme. The platform we describe in this paper is a general-purpose simulation environment that adapts to different retina models and provides a set of elementary simulation modules. The software can be easily used as an efficient benchmark to simulate and understand the visual processing at low-level.

The rest of the paper is organized as follows. In section 2 we describe the biophysical functions of retina cells that have been implemented in the platform.

A general overview of the software is included in section 3. Section 4 explains some of the simulations conducted to evaluate the platform and in section 5 we discuss the conclusions and future work.

2 Anatomy and Physiology of the Retina

In the retina, neurons are arranged in layers that contain cells of the same type. In the brain, most neurons fire action potentials, or spikes, which are electrical impulses well suited to relay the neural signal over long distances. By contrast, most retinal cells form organized maps, with only local interactions between neighboring cells that modify their membrane potential. Neighboring cells are then linked together through two types of synapses: gap junctions (also called electrical synapses) and chemical synapses.

In the simulator, non-linear temporal models can be defined based on single-compartment equations. The basic equation that explains the temporal evolution of a single-compartment model is [10]:

$$C_m \frac{dV(t)}{dt} = \sum_i I_i(t) + \sum_j g_j(E_j(t) - V(t))$$

where the index i indicates the input ionic channel, C_m is the membrane capacitance, V the membrane potential, g_j is the conductance of the channel, E_j the reversal potential of the channel and the term $\sum_i I_i$ denotes external input currents to the neuron. Both the input currents to the neuron and its ionic conductances can be modified by other neurons to model different temporal neural responses.

For some type of cells, the membrane potential integration from controlled physiological experiments can be approximated by linear models. A linear approximation of this neural response of a cell, $L(t)$, can be defined based on the linear kernel $K(x, y, \tau)$ [10,38]:

$$L(t) = \int_0^\infty \mathrm{d}\tau \int_{(x,y)\epsilon RF} K(x, y, \tau) s(x_0 - x, y_0 - y, t - \tau) \mathrm{d}x\mathrm{d}y$$

where $s(x, y, t)$ is the visual stimulus and RF the receptive field of the cell. The neural response of the cell depends linearly on all past values of the input stimulus located in the cells receptive field RF. This integral corresponds to the well-defined convolution operation:

$$L(t) = (s * K)(x_0, y_0, \tau)$$

For some neurons $K(x, y, \tau)$ can be broken down as a product of two functions, one that accounts for the spatial receptive field and the other one for the temporal receptive field:

$$K(x, y, \tau) = K_s(x, y) K_t(\tau)$$

The linear temporal receptive field can be simulated by exponential and gamma filters that model effects such as the membrane signal integration and synaptic transmission. For the spatial receptive field we have considered a set of spatial filters that are based on Gaussian functions, similarly to the kernels used in the receptive field model proposed by Rodieck [30] and Enroth-Cugell and Robson [15]. These filters model spatial integration from chemical synapses in the receptive field and also gap junctions. The three kernels included in the simulation platform are: Gaussian, approximation of a Gaussian and sum of two Gaussians. These three kernels have been implemented based on the recursive approach by Deriche [12–14,32,34].

The software also models the retina morphological and physiological variations associated with eccentricity. It is possible to simulate the spread of neuron dendrites with eccentricity and its consequent increase of the receptive field size. We can also configure the spatial distribution of cells according to predefined density functions and probabilistic connections among neurons. Experiments that simulate inter-cell variability and loss of spatial resolution across the human visual field can be reproduced using the topological functions provided by the simulation platform.

Regarding the transformation of the input visual stimuli to the cone responses we use the Hunt-Pointer-Estevez (HPE) matrix [16] to get the different L-, M-, and S-cone values.

3 Overview of the Platform

The basic structure implemented in the platform is a neural layer of cells of the same type, such as horizontal or bipolar cells present in the retina. Spatiotemporal equations of neural layers are updated using an image-based processing approach that benefits from the fact that cells in the retina are arranged in planar maps. A time-driven simulation core is responsible for modifying the membrane potential and synaptic currents associated to each neuron in every discrete time step. When interfacing the platform with models of higher brain areas the neural network simulator integrates our software efficiently and the retina module can be easily loaded in the neural network script. A scheme of the platform connected to a neural network simulator can be seen in figure 1.

The software, which is implemented in C++, has been optimized to run on CPU-based architectures. Space-variant filters are based on the Deriche's recursive approach [12–14,32,34]. The main advantage of these filters is that the number of operations per pixel is constant and does not depend on the size of the kernel. Moreover, kernel coefficients can be modified at every pixel to simulate a foveated retina [32]. The performance of the spatial filtering has been significantly improved in a multi-core processor that takes advantage of the fact that every row and every column of the image are processed independently according to the Deriche's recursive algorithm and can be executed in different threads.

Temporal equations are also updated recursively. Linear filter implementation, i.e. exponential and gamma functions, has been adapted from the IIR

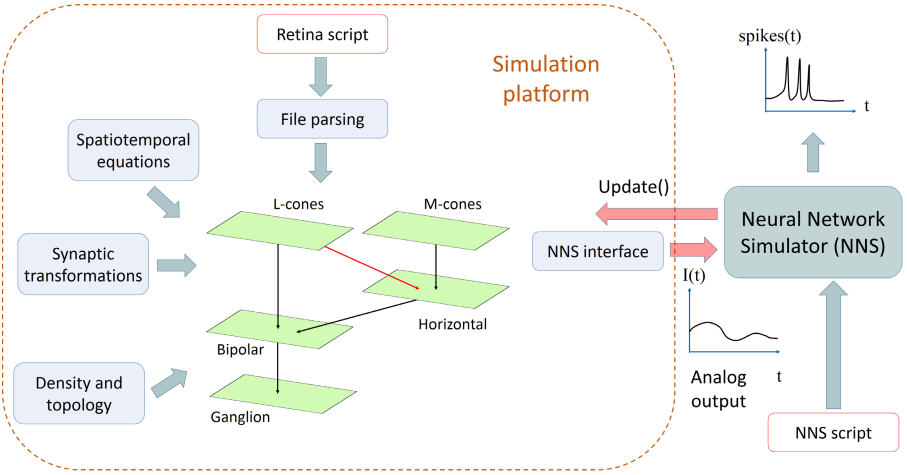

Fig. 1. Scheme of the simulation platform connected to a neural network simulator. The analog outputs of the platform correspond to the ganglion synaptic currents, which are processed by the neural network simulator to produce the spiking output. The neural network simulator drives the simulation time and synchronizes the update process of spatiotemporal equations in the retina model. In the figure we show simultaneously two possible retina configurations where the only difference is the red arrow that links L-cones and horizontal cells. For example, when this link is considered the surround of the receptive field, via horizontal cells, is fed by both M- and L-cones. Other different retina architectures can be easily configured by creating new neural layers and modifying the connection scheme among them.

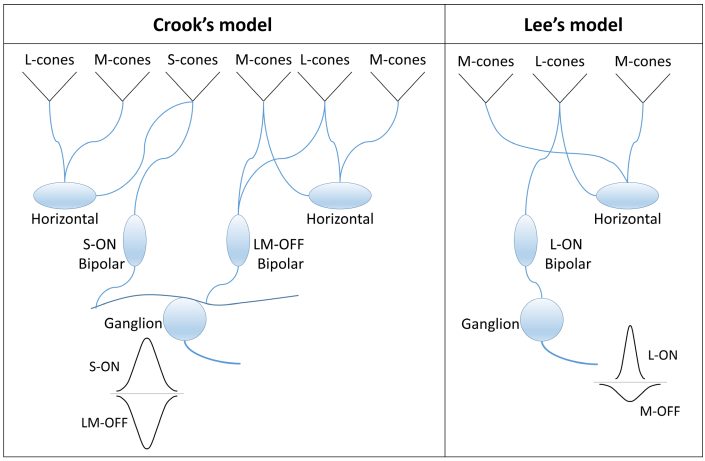

Fig. 2. Outline of two of the retinal circuits simulated by the platform. These retina models have been proposed by Crook et al. [7] and Lee et al. [25] to explain the physiological behavior observed in the blue-yellow and red-green pathways, respectively. The structure of the ganglion receptive field is depicted at the bottom of each circuit.

(Infinite Impulse Response) implementation of Virtual Retina [39] and single-compartment equations are integrated by the so-called Euler method [10]. Provided that the temporal step is sufficiently small, repeated application of these updating methods provides an accurate way of determining the membrane potential.

The platform has been tested under a Linux operating system and connected to the NEST simulator. The processed output of our software can be also adapted to feed other computer vision applications that require a retina input. The source code of this simulator will be open source, following the roadmap of the Human Brain Project [1], and available for download from [2].

4 Evaluation

A set of electrophysiological experiments that reproduce the red-green and blue-yellow opponent pathways in the retina have been simulated to evaluate the capability of the platform to adapt to different retina models. We compare our software with other retina simulators in terms of configurability and scalability. To the best of our knowledge, this is the first simulator that can reproduce retinal circuits as different as those shown in figure 2.

We have simulated two different retina models of the red-green pathway, proposed by Lee et al. [25] and Crook et al. [8] respectively, and one model of the blue-yellow pathway, whose retina circuitry was proposed by Crook et al. [7]. Simulated models are tuned by exhaustive search of parameters that best fit the available published data. There are two different theories explaining the physiological recordings obtained in the red-green pathway: the cone-type selective surround [23–25,31] and the random-wiring or mixed surround [8,35]. While supporters of the cone-type selective surround argue that there is a single cone that feeds the periphery of the receptive field, some research groups proposed that both type of cones, L and M, connect to the surround and this fact could be enough to generate a cone-opponent signal.

With the mixed surround model, a bandpass tuning curve is obtained for a cone-isolating grating targeting the center cone class (see blue graph in figure 2). With the cone-selective surround circuit, the platform reproduces the low-pass shape of the contrast sensitivity function for a cone-isolating grating targeting the center cone class alone (red graph in figure 3). In this figure, the response of the Lee's model for the M-cone isolating grating is also plotted in green to compare the different high-frequency cutoffs of the center, connected to a L-cone, and the periphery, connected to a M-cone, of an L-ON receptive field. Considering there is a 180 deg out of phase between the center and the periphery, which is not represented in this figure, the resulting spatial filtering profile of this cell resembles the typical DoG model.

Some examples of intermediate images produced by the platform and the spiking output generated by the neural network simulator are shown in figures 4 and 5, respectively. A retina density scheme has been configured in the simulation of figure 4 so that the receptive field size of cells is increased with eccentricity.

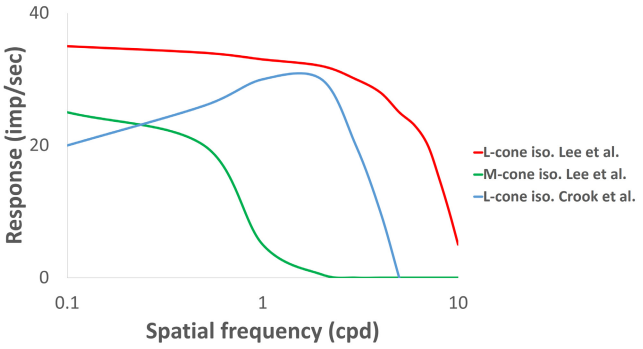

Fig. 3. Contrast sensitivity functions computed from simulation of the retina models proposed for the red-green pathway by Lee et al. [25] and Crook et al. [8]. With the mixed surround model, a bandpass tuning curve is obtained for a cone-isolating grating targeting the center cone class (blue graph). With the cone-selective surround circuit, the platform reproduces the low-pass shape of the contrast sensitivity function for a cone-isolating grating targeting the center cone class alone (red graph). The absolute response of the Lee's model for the M-cone isolating grating is also plotted in green to compare the different high-frequency cutoffs of the center, connected to a L-cone, and the periphery, connected to a M-cone, of an L-ON receptive field.

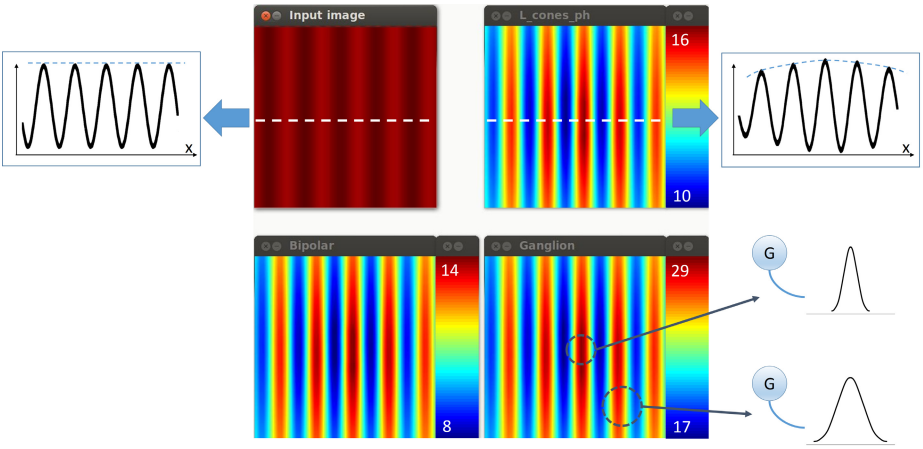

Fig. 4. Example of intermediate outputs generated by the software for a L-cone isolating grating of 5 cpd. The simulated model corresponds to the Lee's retina architecture. It is shown: the input image, membrane potential of L-cones and bipolar cells and input synaptic current of ganglion cells. A retina density scheme has been configured in the simulation so that the receptive field size of cells is increased with eccentricity. This phenomenon produces a decrease of sensitivity in the peripheral area of the simulated retina compared to the center. The horizontal intensity profile of the input image is compared with the profile of the L-cones to further explain this phenomenon.

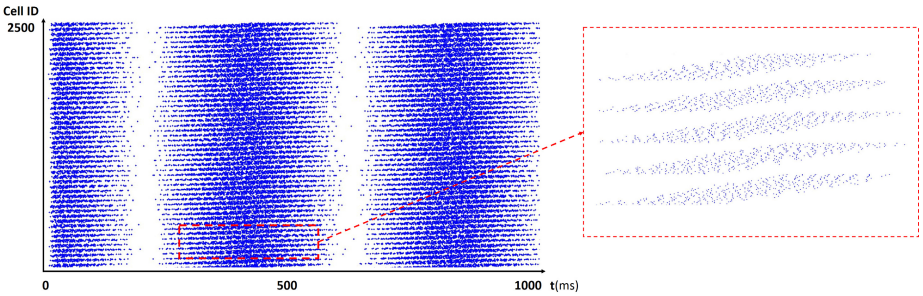

Fig. 5. Raster plot of the spiking outputs generated by NEST [18] for a population of 2500 ganglion cells. The simulation time considered is 1000 ms and the spatial frequency of the input pattern is 0.5 cpd. Every blue spot corresponds to the time a neuron fire a spike. Cell IDs are numbered by rows so that the first 25 cell IDs correspond to cells situated in the top first 25-pixel row. A zoomed area of the raster plot is shown on the right to better visualize the spiking pattern resulting from the input grating.

This phenomenon produces a decrease of sensitivity in the peripheral area of the simulated retina compared to the center.

5 Conclusions and Future Work

A general-purpose simulation environment of the first stages in the visual system is presented. The main contribution is that it can reproduce efficiently the analog neural response of different retina models by modifying not only the model parameters but also its architecture and interconnections of neural layers. The software can be easily used as an efficient benchmark to simulate and understand the visual processing at low-level. Our software can simulate many of the biological mechanisms found in retina cells, such as signal gathering through chemical synapses and gap junctions or variations in the neuron density and the receptive field size with eccentricity. Based on an image-processing approach, simulated neurons perform spatiotemporal and color processing of the input visual stimuli generating the visual maps of every intermediate stage, which correspond to membrane potentials and synaptic currents. An interface with neural network simulators has been implemented, which allows to reproduce the spiking output of some specific cells, such as ganglion cells, and integrate the platform with models of higher brain areas.

The platform has been evaluated based on simulations of different retina models that reproduce the red-green and blue-yellow opponency obtained in electrophysiological experiments. The neural behavior of three retina architectures has been reproduced, the cone-type selective surround and the mixed surround of the red-green pathway and the coextensive receptive field in the blue-yellow pathway, approximating the experimental curves. Simulations of other retina models, concerning contrast and mean luminance adaptation mechanisms in the retina, are being configured to complement the evaluation of the platform.

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