Modelling and Simulation of Vertebrate Retina: Extended Network*

M. N. Oğuztöreli and K. S. O'Mara

Department of Mathematics, University of Alberta, Edmonton, Alberta, and Department of Computer Science, Concordia University, Montreal, Quebec, Canada

Abstract. In a recent work (Oğuztöreli, 1980) a mathematical model for studying the neural activities in a vertebrate retina has been investigated, where the basic retinal network involves interconnected five neurons of different kind. This model is general enough to cover a great variety of neurons in the same retina as well as in the retinas of different species. In the present work we deal with an extension of the basic network considered in (Oğuztöreli, 1980). This extended model contains interconnected twelve neurons: three receptor cells, two horizontal cells, two bipolar cells, two amacrine cells and three ganglion cells. The performance of the model under different conditions, and, the experimental determination of the system parameters are discussed. The background of the modelling and simulations can be found in (Oğuztöreli, 1979, 1980).

I. Description of the Network

Modelling, analysis and simulations of a vertebrate retina have been studied in (Oğuztöreli, 1980) by making use of some of the results of (Oğuztöreli, 1979). The basic network in (Oğuztöreli, 1980) contains interconnected five neurons: one receptor cell, one horizontal cell, one bipolar cell, one amacrine cell and one ganglion cell. The neural activities in the network are described by the structural and processing characteristics of each of the individual cells and the interactions among the cells.

In the present work we investigate an extended form of the basic network in (Oğuztöreli, 1980). The network which will be studied below is described schematically in Fig. 1, where, as in (Oğuztöreli, 1980), indicates that neuron \( \alpha \) inhibits neuron \( \beta \), while indicates that neuron \( \alpha \) excites neuron \( \beta \), and

1, 2, 3 are receptor cells,
4, 5 are horizontal cells,
6, 7 are bipolar cells,
8, 9 are amacrine cells, and
10, 11, 12 are ganglion cells.

This network has been investigated extensively in the literature (cf. Cervetto and Fuortes, 1978; Dowling, 1970, 1972; Dowling and Werblin, 1969; Michael, 1969; Shepherd, 1974; Werblin, 1970, 1973). In the present work, as in the previous one (Oğuztöreli, 1980), we are motivated mainly by the recent developments reported by Cervetto and Fuortes (1978), Dowling (1970, 1972), Dowling and Werblin (1969), and Werblin (1970, 1973).

Some of the main characteristics of each cell in Fig. 1 are described briefly and the form of the connectivities and interactions among the cells are outlined in (Oğuztöreli, 1980), summarizing the main results of the above mentioned references. We only note here that

1) A receptor cell may interact with neighboring receptor, horizontal cells, and bipolar cells. There is a lateral enhancement among neighboring cones as well as between double cones. Exitatory interactions occur also between rods. A cone input does not significantly affect the peak amplitude of a rod's response.

2) The horizontal cells receive inputs from receptor cells and they exert depolarization on cones. There is a

* This work was supported by grants from the Natural Sciences and Engineering Research Council Canada under Grant NSERC-A-4345 and Grant NSERC-G-0377 to MNO through the University of Alberta
6) The neural pathways described above operate on different time scales. The delays in the paths arise from cell time constants, cable spread, and kinetics of release and of transmitter action. The pathways which relay rod responses are slower than those which relay cone responses.

7) We finally note that the cells of a simple retina, that of the primate, cannot produce periodic oscillations whenever isolated from the network. This fact indicates that the cells in a simple retina are all of the second order at most in the sense of Stein et al. (1974).

8) Only the receptor cells are subjected to external forces (light intensities), denoted by \( f_1, f_2, \) and \( f_3 \), which provide the necessary input for the whole network.

Clearly, the retinal network described in Fig. 1 can be easily adjusted to special conditions of the real situations by adding and or deleting some of the connectivity pathways marked by arrows. For example, if the receptor cell 1 is not excited by the other two receptor cells, and conversely, the feedback pathways between cells 1 and 2, as well as between 2 and 3, should be deleted, but the connectivity 1 --- 2 should be preserved. Similarly, if the bipolar cell 6 receives inputs from the horizontal cell 4 and if it inhibits 4, then the connectivity 4 --- 6 should be added to the Fig. 1.

In the next sections we present a mathematical modelling of the retinal network described in Fig. 1 together with a number of simulations of the dynamics of the neural activities involved under various conditions, and, we discuss the experimentally determination of the system parameters.

Throughout this work we use the terminology, notation and results of Öğuztöreli (1979). The numerical algorithms described in this reference have been implemented in the University of Alberta in the ALGOL W and FORTRAN languages.

II. Mathematical Description of the Retinal Network

The mathematical modelling of the retinal network can be easily achieved by taking into account the form of the connections and interactions in Fig. 1 and by implementing the general rules described in Sect. 1 of our article (Öğuztöreli, 1979). In this way we find the following basic network equations:

\[
\begin{align*}
\frac{1}{a_{10}} \frac{dx_1}{dt} + x_1 &= \mathcal{S} \left\{ f_1 + c_{12} x_2(t - \sigma_{12}) + c_{13} x_3(t - \sigma_{13}) + b_{11} \int_0^t e^{-a_{11}(t-\tau)} x_1(\tau) d\tau \right\}, \\
\frac{1}{a_{20}} \frac{dx_2}{dt} + x_2 &= \mathcal{S} \left\{ f_2 + c_{21} x_1(t - \sigma_{21}) + c_{23} x_3(t - \sigma_{23}) + c_{24} x_2(t - \sigma_{24}) + c_{25} x_3(t - \sigma_{25}) + b_{21} \int_0^t e^{-a_{21}(t-\tau)} x_2(\tau) d\tau \right\}, \\
\frac{1}{a_{30}} \frac{dx_3}{dt} + x_3 &= \mathcal{S} \left\{ f_3 + c_{31} x_1(t - \sigma_{31}) + c_{32} x_2(t - \sigma_{32}) + c_{34} x_2(t - \sigma_{34}) + c_{35} x_3(t - \sigma_{35}) + b_{31} \int_0^t e^{-a_{31}(t-\tau)} x_3(\tau) d\tau \right\},
\end{align*}
\]