Available online at www.sciencedirect.com
SCIENCE DIRECT®
ELSEVIER
Neurocomputing 69 (2006) 1020–1024
NEUROCOMPUTING
www.elsevier.com/locate/neucom

A realistic model of rod photoreceptor for use in a retina network model

Rodrigo Publio[a,*], Rodrigo F. Oliveira[b], Antonio C. Roque[a]

[a]*Departamento de Física e Matemática, FFCLRP, Universidade de São Paulo, Av. Bandeirantes, 3900, Ribeirão Preto 14040-901, SP, Brazil*
[b]*Departamento de Psicologia e Educação, FFCLRP, Universidade de São Paulo, Av. Bandeirantes, 3900, Ribeirão Preto 14040-901, SP, Brazil*

Available online 15 February 2006

Abstract

We propose a conductance-based model of a rod photoreceptor cell based on experimental data and other modeling works. In this model we use four types of ionic channels identified in the inner segment of the rod: nonselective cation channel (h), delayed rectifying potassium channel (K_v), noninactivating potassium channel (K_x) and calcium channel (Ca). The model accurately reproduces the rod response when fed with a simulated photocurrent signal. The results show that the initial transient in the voltage response is generated by the h channel. They also show that the h channel has a role in increasing the dynamic range of rod response to light intensity. Since we used a single compartment model and directly injected the photocurrent in this compartment instead of simulating the phototransduction process we produced a model with low computational cost to be used in large-scale retina models.

Keywords: Retina; Rod photoreceptor; Realistic modeling; Dynamic range; Ion channels

1. Introduction

Recent studies have shown the existence of a complex arrangement of rod signaling pathways across the retina in which there are at least three different circuits responsible for the transmission of rod signals to ganglion cells [5,13]. Evidence also indicates that each pathway serves a nonoverlapping range of stimulus intensities, with ganglion cells receiving either segregated or convergent inputs.

The functional significance of having multiple rod pathways is unclear and computational modeling can offer some aid in the effort to understand it. The first step in the construction of a large-scale realistic model of the retina to study rod pathways is the construction of a model of the rod photoreceptor itself, which is presented in this work. Photoreceptors respond to light with graded membrane hyperpolarization produced by voltage-gated channels in their inner segment. The objective of this work is to develop a rod model based on a variety of experimental results from cat and larval tiger salamanders (*Ambystoma tigrinum*) and some theoretical models [2,3,8,9,11], capable of reproducing light response properties at a low computational cost.

2. The rod model

The model was created using NEURON [6] and consists of a single compartment with passive properties and four voltage-gated channels. The outer and inner segments in real cells were collapsed in the model to produce a single compartment. The simulations show that there is no significant difference between a model with a compartment for each segment or a collapsed compartment. Fig. 1 shows a picture of the compartment where simulated stimuli were injected and voltage responses were measured. Instead of simulating the phototransduction process we used as stimulus a simulated photocurrent waveform [9].

2.1. Ionic currents in the compartment model

The single compartment model has four voltage-gated channels, where each ionic current was modeled according to Hodgkin–Huxley-like equations. Parameters and equations of the model are given in Tables 1 and 2.

*Corresponding author.
E-mail address: publio@neuron.ffclrp.usp.br (R. Publio).

0925-2312/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.neucom.2005.12.037

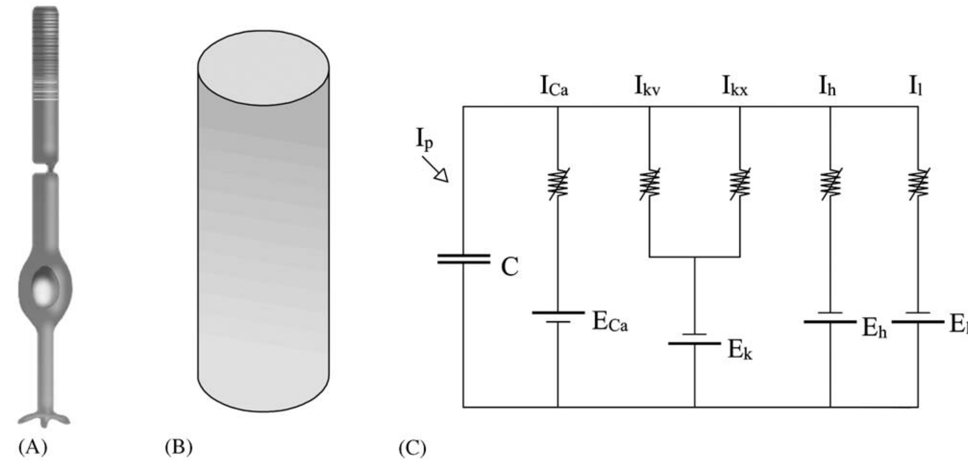

Fig. 1. (A) The rod photoreceptor is composed of an inner segment containing the normal cell organelles, and an outer segment composed of a stack of about a thousand membranous disks. (B) Single compartment rod model. (C) Equivalent circuit.

Table 1
Passive properties of the compartment model

Diameter (μm)	*Rm* ($\Omega\,cm^2$)	*Cm* ($\mu F/cm^2$)	*Ra* (Ω cm)	Leak conductance (S/cm^2)
8 [12]	6000 [12]	1 [12]	200 [7]	4.97×10^{-6} [8]

The references from where the parameters were taken are shown within brackets.

Table 2
Parameters and equations of the ionic currents

Ionic current	Reversal potential (mV)	Maximum conductance (S/cm^2)	Current equation
I_h [1,8]	−32	9.1×10^{-3}	$I_h=\overline{g_h}n(V-E_h)$
I_{K_v} [8,9,10]	−74	1×10^{-3}	$I_{K_v}=\overline{g_{K_v}}m^3h(V-E_k)$
I_{K_x} [4,9,10]	−74	4×10^{-4}	$I_{K_x}=\overline{g_{K_x}}n(V-E_k)$
I_{Ca} [1]	40	5×10^{-4}	$I_{Ca}=\overline{g_{Ca}}n(V-E_{Ca})$

2.1.1. Hyperpolarization activated current (I_h)

We used the five state kinetic model proposed by Barnes and Hille [1] to describe the inward current produced by hyperpolarization. This model is described by two closed and three open states with voltage dependent rate constants α and β,

$$C_1 \underset{\beta}{\overset{4\alpha}{\leftrightarrow}} C_2 \underset{2\beta}{\overset{3\alpha}{\leftrightarrow}} O_1 \underset{3\beta}{\overset{2\alpha}{\leftrightarrow}} O_2 \underset{4\beta}{\overset{\alpha}{\leftrightarrow}} O_3, \tag{1}$$

where the rates α and β can be described by [1]

$$\alpha=\frac{a_1}{(1+\exp((V+b_1)/c_1))},$$
$$\beta=\frac{a_2}{(1+\exp(-(V+b_2)/c_2))}$$

and

$$a_1=0.3\,\mathrm{m\,s^{-1}},\quad b_1=98\,\mathrm{mV},\quad c_1=10\,\mathrm{mV},$$
$$a_2=0.3\,\mathrm{m\,s^{-1}},\quad b_2=30\,\mathrm{mV},\quad c_2=20\,\mathrm{mV}.$$

The channel open probability is calculated by $n=1-(1+3r)(1-r)^2$.

2.1.2. Noninactivating K current (I_{K_x})

The voltage-dependent current, I_{K_x}, has slow kinetics of activation and deactivation. This current participates in setting the rod resting potential in darkness and in accelerating the response to dim light [3].

2.1.3. Delayed rectifying K current (I_{K_v})

Experimental evidence [2] shows that rod photoreceptors have a voltage-dependent current with characteristics of a delayed rectifier.

2.1.4. Calcium current (I_{Ca})

Evidence shows that vertebrate rod photoreceptors express a noninactivating, high-voltage-activated L-type calcium channel [9].

2.2. Photocurrent

The photocurrent waveform was reconstructed from bright light [2,9] and has the form

$$I=I_{dark}+A\left[(1-e^{-t/\tau_1})-\left(\frac{1}{1+e^{-(t-b)/\tau_2}}\right)+(1-e^{-t/\tau_3})\right], \tag{3}$$

where I_{dark} represents the dark current, A is the photocurrent amplitude and τ_1, τ_2, τ_3 and b are time constants. The values of the parameters are [2,9]: $I_{dark}=-0.04\,\mathrm{nA}$, $\tau_1=50\,\mathrm{ms}$, $\tau_2=450\,\mathrm{ms}$, $\tau_3=800\,\mathrm{ms}$, $b=3800\,\mathrm{ms}$.

The dark-adapted rod photoreceptor responds to the absorption of individual photons and produces a