Computer Science Department Technical Report
University of California
Los Angeles, CA 90024-1596

NEITHER DOG NOR LOG FITS THE RECEPTIVE FIELD OF A VERTEBRATE CONE

Josef Skrzypek
George Wu

April 1991
CSD-910010

MPL

Machine
Perception
Laboratory

UCLA
Computer Science
Department

Neither DoG nor LoG fits the receptive field of a vertebrate cone

Josef Skrzypek & George Wu

TR 91-9 April1 1991

MPL

Machine
Perception
Laboratory

top-down

bottom-up

UCLA

Neither DoG nor LoG fits the receptive field of a vertebrate cone.

Josef Skrzypek and George Wu

Machine Perception Laboratory
Computer Science Department
UCLA
Los Angeles CA 90024

Keywords: cones, receptive fields, retina, vision, neural networks

Address correspondence to: Prof Josef Skrzypek

Dir. Machine Perception Laboratory
Department of Computer Science
3532 BH
UCLA
Los Angeles CA 90024-1596
Email: skrzypek@cs.ucla.edu
Tel: (213) 825 2381
Fax: (213) UCLA CSD

Neither DoG nor LoG fits the receptive field of the vertebrate cone

Josef Skrzypek and George Wu

Machine Perception Laboratory

Computer Science Department

University of California

Los Angeles, CA 90024

Abstract

What we see depends not only on light intensity falling onto retina but also on intensity changes (Mach1868). For a given light intensity distribution $I = f(x,y)$ representing a scene, the visual system seems to encode the point information in terms of intensity I and in terms of the second derivative of intensity. The question of where in the visual systems and in what form this encoding first takes place and what are the responsible synaptic pathways and mechanisms remains unclear. In this paper we focus on physiological mechanism underlying receptive field of a cone in the vertebrate retina and we test the data with analytical model using UCLA SFINX (Skrzypek & Mesrobian, 1990) simulation environment.

1 Extended summary

Mach was the first to propose that visual receptive fields are responsible for the retinal output that contains second derivative of intensity such as Laplacian of intensity. Kuffler (1953) extended this hypothesis by finding that ganglion cells have antagonistically organized, concentric receptive fields. Ratliff (1965) related Mach spatial derivative with the retinal mechanism of lateral inhibition. At the same time Rodieck and Stone (1965) reported that cats ganglion cells with the center-surround receptive fields can be modeled as a difference of two concentric Gaussian sensitivity profiles;

difference of Gaussians - DoG. Marr and Hildreth (1980) were first to propose Laplacian of a Gaussian (LoG) as a generic analytical model for isotropic receptive fields. They argued that Gaussian is useful in reducing noise and the Laplacian can accurately localize intensity discontinuities. LoG filter, within certain parameter values is a close approximation to a DoG operator.

In the past twenty years, the concentric organization of receptive fields into antagonistic zones was reported in bipolar cells (Werblin & Dowling, 1969), in horizontal cells (Skrzypek, 1980) and in cones (Baylor et al 69). It is now well established that antagonism begins with cones (Skrzypek & Werblin 1983; Baylor et al 1969) but the quantitative test of DoG or LoG formalism with actual physiological data has never been performed. We report here such tests using intracellular data from the cone and horizontal cells in the eyecup preparation of the Tiger salamander retina. The data from physiological experiments is used to build a simulation of the outer retina that is equivalent to 128 by 128 array of cones. Several new findings emerged requiring modification to DoG model of receptive field as applied to retinal cones. The results suggest that a more accurate formulation is expressed by the difference between central Gaussian and the sum of displaced LoGs. The central Gaussian represents the receptive field of a cone and it reflects the coupling between neighboring receptors. The displaced LoG's represent receptive fields of six horizontal cells which are not concentric with the receptive field of a given cone. In fact, our data seems to suggest that a horizontal cell which get direct synaptic input from the cones immediately "above" it, probably does not feedback to the same cones: the feedback comes from horizontal cells which are displaced lateraly.

The retinal outer plexiform layer(OPL) model used in the simulation is shown schematically in attached figure. There are 2 important aspects of the model, its network structures and its receptive field functions. Structurally, the model consists of one 128x128 cone photoreceptor layer and one 42x42 horizontal cell layer. Thus, the cone-horizontal cell coverage ratio is 9. Each cone receives excitatory inputs from incident light and 24(i.e. 5x5 mask) neighboring cones and inhibitory inputs from 6 horizontal cells 'below' it. Each horizontal cell receives excitatory inputs from 9 cones 'above' it and 224(i.e. 25x25 mask) neighboring horizontal cells. The model functionality is determined by its receptive fields' characteristics. All receptive fields(RF) are normalized Gaussian weighted kernels except for the horizontal-horizontal RF, which is either a Gaussian or a Laplacian-of-Gaussian. The respective inputs to a cell are weighted and summed and then normalized to produce the final response. The normalization of response is accomplished via a Sigmoidal squashing function. An explicit list all the modeling parameters will be given in the full paper.

Simulation experiments were conducted to answer 2 questions concerning the steady-state cone response. How is individual cone response modulated by its surrounding cone and horizontal cell activations ? What is the differential effect does Gaussian versus Laplacian-of-Gaussian(LoG) horizontal-horizontal RF have on cone response ? To answer these questions, one general simulation experiment was designed to be conducted in two different contexts. The experiment conducted is as follows, a light spot stimulus of a specified intensity (in this case 2.4 log units above dark-adapted level) and increasing radius(from 0 to 160 μm) is applied to the dark-adapted OPL centered at the cone layer center (referred to as CC from hereon). At each light spot radius, the response of the CC is tracked over a fixed period of time after the stimulus onset. In the experiments conducted, CC response was tracked over a period of 2 seconds, which is presumably long enough to observe the steady-state response. The experiment provides a first order quantitative approximate answer to the first question posed above. The same experiments were conducted on 2 models, one using a Gaussian horizontal-horizontal RF and a LoG RF in the other. The CC response versus time and spot stimulus radius for each of the two models is plotted and shown in attached graphs. The steady-state CC response versus the spot stimulus radius(i.e. response at 2 seconds after stimulus onset) of both models are plotted together for comparison in attached graph. Physiological data will be compared to simulations and the detailed results will be discussed in the full paper.

Fig.1. shows intracellular response recorded from tiger salamander red cone. Two traces are overlaid, representing different diameter of the stimulating spot. Small diameter spot of 0.15 mm causes hyperpolarizing response with sustained level of membrane potential remaining constant for the duration of the stimulus. The large spot 1.0 mm in diameter shows large depolarization from peak response indicating feedback effect.

Fig.2. shows data plotted from intracellular recordings of the narrow field horizontal cell light response. The HC response is plotted as a function of the stimulating spot diameter. Filled symbols represent measurements at the peak of hyperpolarization. Open symbols represent measurements during the plateau of response just before the offset of the stimulus. All "plateu" curves show clear peak and reduction of response with increasing diameter. The reductions is independent of the stimulus intensity and

indicates the effect of feedback pathway mediating lateral effects from the surround. This feedback effect is mediated via cones which drive horizontal cells. This reduction is inconsistent with a DoG model of receptive field in cones. And it suggests that HC themselves have at least DoG or LoG receptive field profile.

Fig.3. shows simulation results, where the normalized response in the "red" cone is plotted against the increasing radius of the stimulating spot. This result is consistent with data in Fig.1.

Fig.4. plot of simulation results from the cone where "light" response amplitude is a function of stimulating spot diameter and the duration of the stimulus. There is clear "feedback" effect with increasing spot diameter and for longer duration small oscilation is possible.

Fig.5. Connectivity pattern between horizontal cells and cones used to generate simulation results. Notice absence of feedback pathway from the central horizontal cell (dark shaded) to the central cone above (dark).

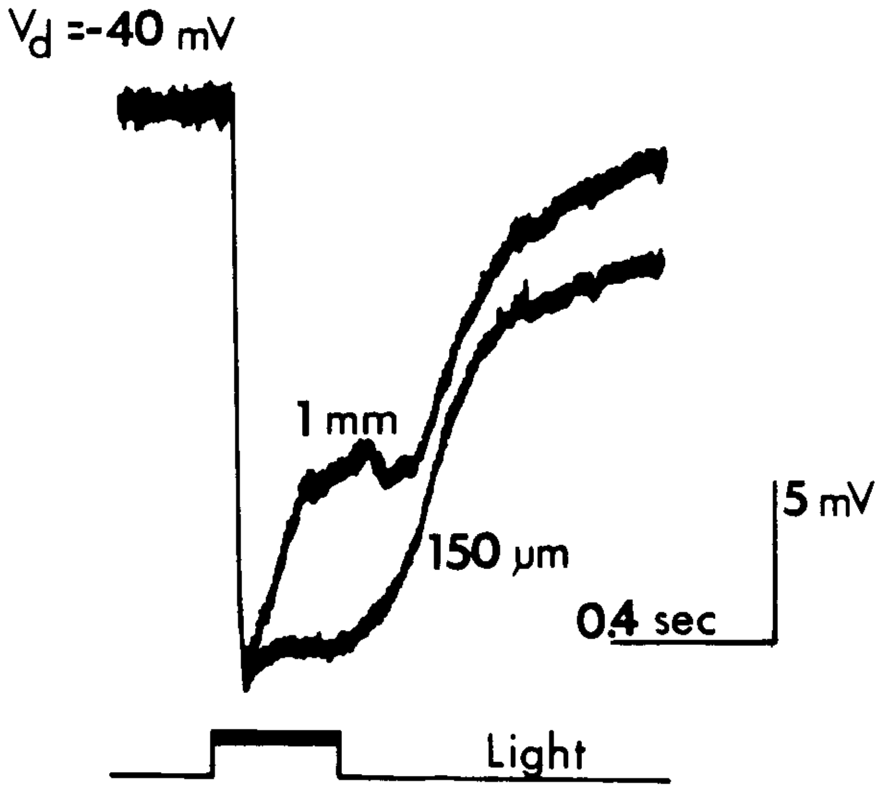

Fig.1. shows intracellular response recorded from tiger salamander red cone. Two traces are overlaid, representing different diameter of the stimulating spot. Small diameter spot of 0.15 mm causes hyperpolarizing response with sustained level of membrane potential remaining constant for the duration of the stimulus. The large spot 1.0 mm in diameter shows large depolarization from peak response indicating feedback effect.

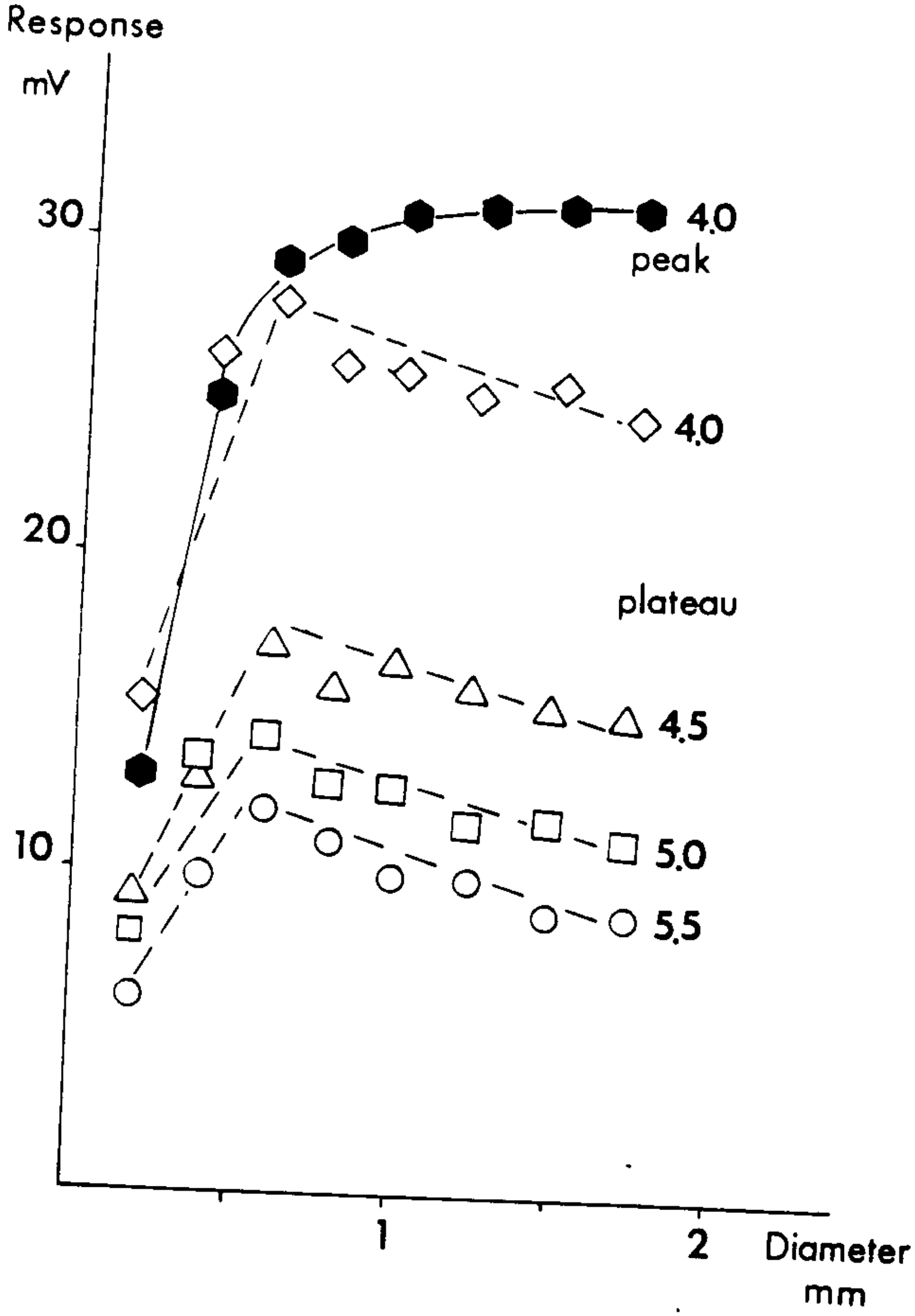

Fig.2. shows data plotted from intracellular recordings of the narrow field horizontal cell light response. The HC response is plotted as a function of the stimulating spot diameter. Filled symbols represent measurements at the peak of hyperpolarization. Open symbols represent measurements during the plateau of response just before the offset of the stimulus. All "plateu" curves show clear peak and reduction of response with increasing diameter. The reductions is independent of the stimulus intensity and indicates the effect of feedback pathway mediating lateral effects from the surround. This feedback effect is mediated via cones which drive horizontal cells. This reduction is inconsistent with a DoG model of receptive field in cones. And it suggests that HC themselves have at least DoG or LoG receptive field profile.

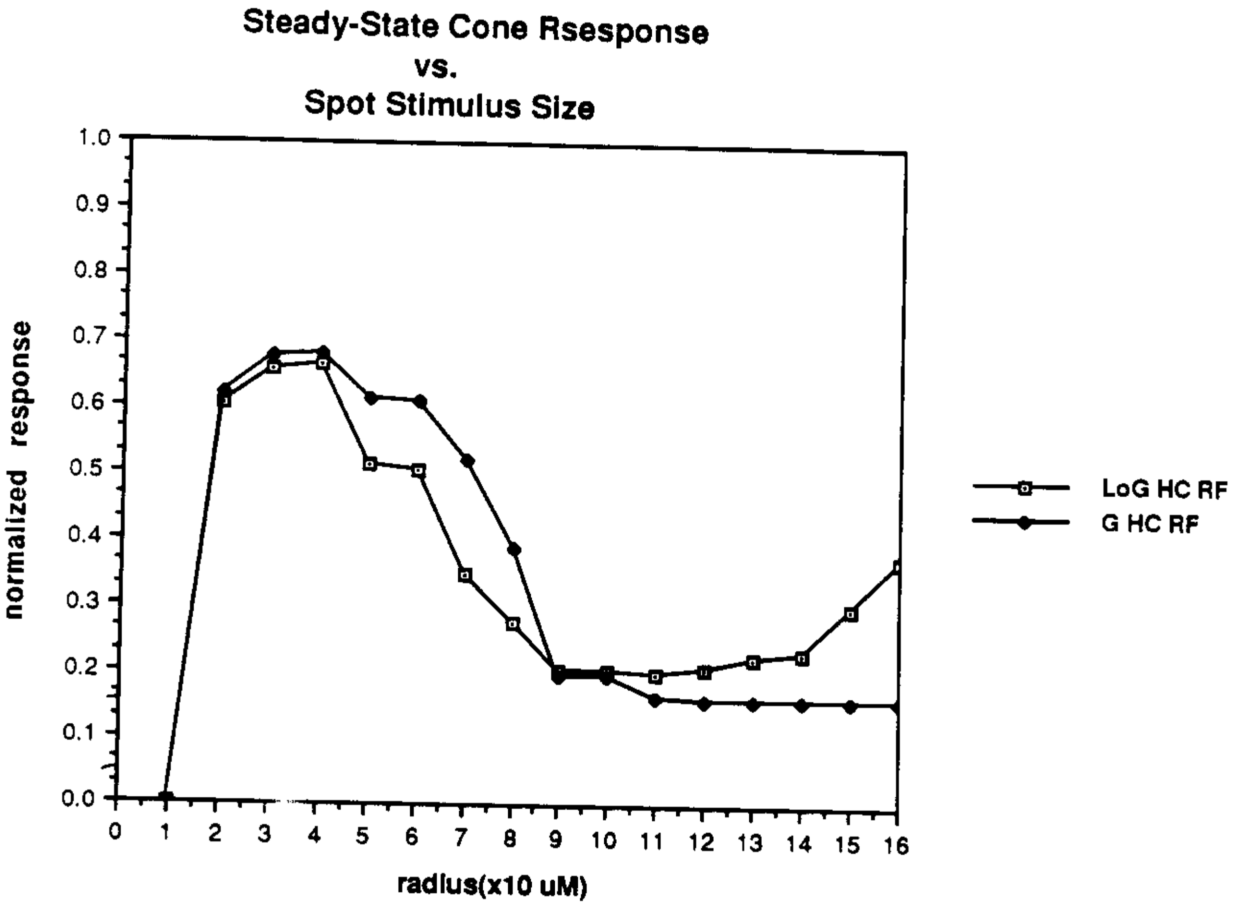

Fig.3. shows simulation results, where the normalized response in the "red" cone is plotted against the increasing radius of the stimulating spot. This result is consistent with data in Fig.1.

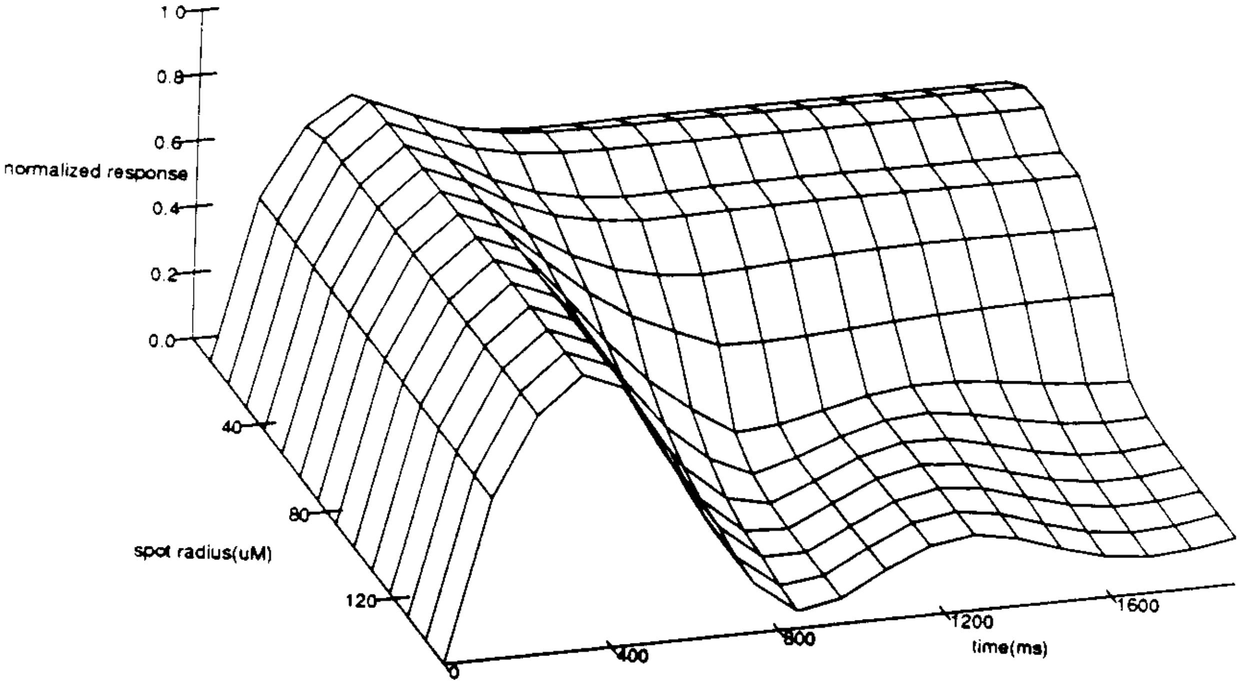

Fig.4. plot of simulation results from the cone where "light" response amplitude is a function of stimulating spot diameter and the duration of the stimulus. There is clear "feedback" effect with increasing spot diameter and for longer duration small oscilation is possible.

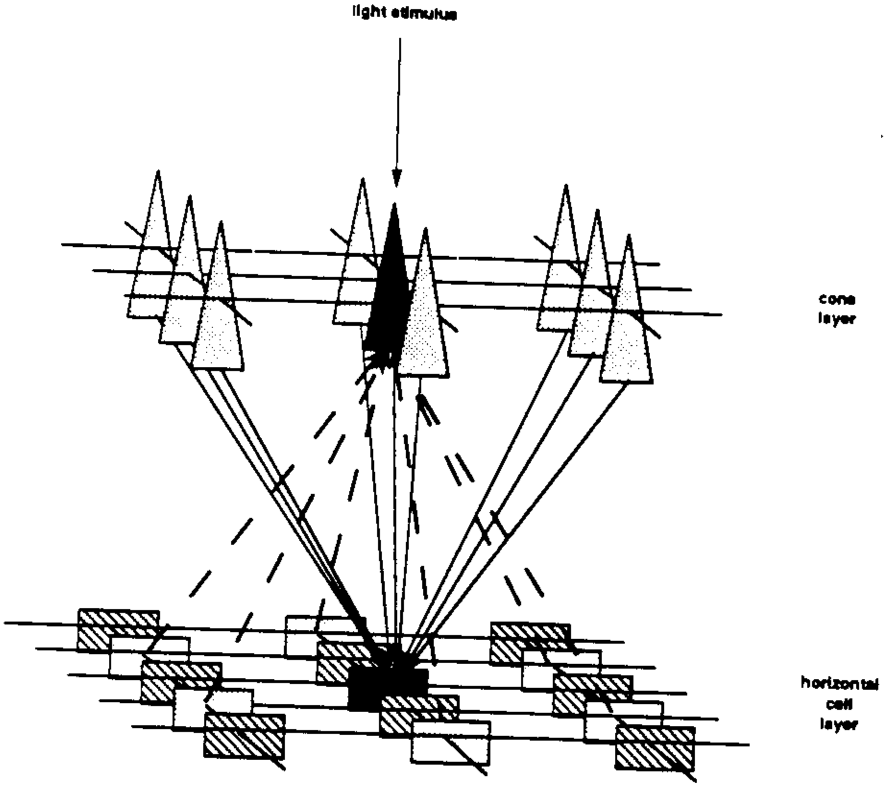

Fig.5. Connectivity pattern between horizontal cells and cones used to generate simulation results. Notice absence of feedback pathway from the central horizontal cell (dark shaded) to the central cone above (dark).