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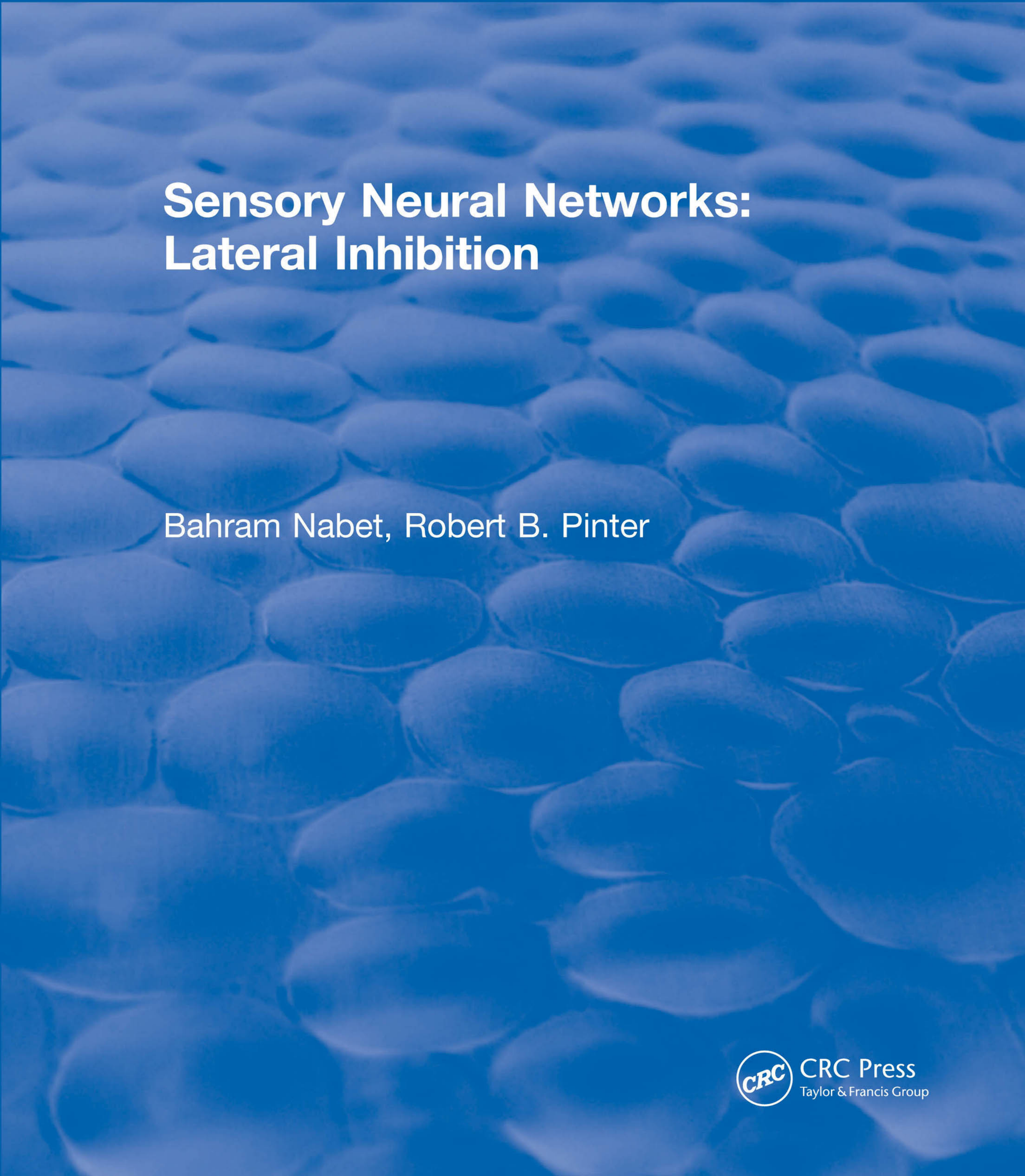

Sensory Neural Networks: Lateral Inhibition

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To you, Behrooz.

B. N.

To Marie.

R. B. P.

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Contents

Abstract

Sensory information is detected and transformed by sensory neural networks before reaching higher levels of processing. These networks need to perform significant processing tasks while being compatible with the following levels. Lateral inhibition is a mechanism of local neuronal interaction that gives rise to significant global properties. This book studies visual sensory neural networks whose activity is governed by nonlinear lateral inhibition. It studies biological bases of models of lateral inhibition, computational properties of these models stressing their short term adaptive behavior, their relation to recent activity in neural networks and connectionist systems, their use for image processing applications, and their application to motion detection. Analog hardware implementation of these classes of networks are described in different technologies and results of implementation which corroborate theoretical analysis and show technologically desirable applications are presented.

Finally, nonlinear mathematical techniques are used to analyze temporal and spatial behavior of these models with the latter showing high order classification properties of the networks. As an interdisciplinary work, this book provides a consistent but multifaceted view which is useful for neural network theorists, biologists, circuit designers, and vision scientists.

1

Introduction

This work is part of a general research effort whose final goals were aptly described by one of the most eloquent researchers of the field, Warren S. McCulloch (1961),[1] as

> "The inquiry into the physiological substrate of knowledge which is here to stay until it is solved thoroughly, that is until we have a satisfactory explanation of how we know what we know stated in terms of the physics and chemistry, the anatomy and physiology, of the biological system."

In pursuing such an aim, Seymour Pappert (McCulloch, 1965) cautioned that:

> "We must, so to speak, maintain a dialectical balance between evading the problem of knowledge by declaring that it is *"nothing but"* an affair of simple neurons, without postulating *"anything but"* neurons in the brain."

This manuscript has the modest goal of presenting a *coherent* view of one of the simplest, and most fundamental, mechanisms that connect simple neurons into *networks*. In doing so Pappert's dictum was adhered to and, it is hoped, a contribution made to the field of neural networks as defined by McCulloch.

As a reflection of the field it is describing, this work has to make several *connections:*

- It has to be related to what has re-evolved into the *field of neural networks*, keeping both its new computational and biological trends in perspective.

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[1] This paper has the intriguing title: "What is a number, that a man may know it, and a man, that he may know a number?"

- It has to be based on a solid mathematical foundation, and contribute to the understanding of these networks.
- It has to keep abreast of technological advances in materials, devices, and circuits in general and progress in the implementations of neural networks in particular.

This book is organized as a merger of these aspects. Chapter 2 describes the biological bases and historical background of the network of neurons related by lateral inhibition. Chapter 3 relates the described models to recent efforts in neural network modeling, stressing the properties that are suitable for processing of sensory visual information. Chapter 4 reports on the application of models of nonlinear lateral inhibition to image processing. Chapter 5 studies preferential directional and motion selectivity properties of these networks.

Chapter 6 discusses a general framework for electronic, and optoelectronic implementation of nonlinear lateral inhibition. This topic is further elaborated in the next chapter where choice of different technologies is detailed. Chapter 8 reports the results of actual electronic realization of a prototype model that although very simple, corroborates the theoretical results of the previous chapters. The implementation results prove that networks of nonlinear lateral inhibition, and implementations with *few* transistors, are indeed capable of capturing some of the most salient features of peripheral vision which also have direct technological application. Among these are edge enhancement, dynamic range compression, feature extraction, adaptation to mean input intensity, tuning of the receptive field and modulation transfer function, tunability of the sensitivity, directional selectivity, and coding of the intensity.

Chapter 9 explores the mathematical "connection" by first describing the stability of the network and then using the Volterra-Wiener series expansion to determine its temporal and steady-state spatial behavior. The results of spatial expansion are shown to be directly related to classification properties of the network.

Given the plurality of aspects, each chapter is written to be self-consistent and independent, hence some introductory parts of the chapters may slightly overlap, but this was deemed necessary for readers of different backgrounds and interests. Each chapter also includes a "discussion," or "conclusions" section that highlights the important results and establishes the continuity of the topics.

Preparation of this manuscript, of course, far exceeded the initial estimates of the required time and effort. This work would not have been completed without the support of Zohreh Nabet and Marie Harrington. The work of H. K. Hartline and F. Ratliff encouraged a fascination of biological visual systems for R. B. Pinter which now spans three decades; this book is also a tribute to Floyd Ratliff. The authors have benefited from numerous discussions with colleagues and are especially indebted to those who agreed to contribute to this volume for a broader and more detailed coverage. The wit, wisdom, and encouragements of Professor David L. Johnson are greatly appreciated. Mr. Russ Hall of CRC Press suggested the publication of this monograph and patiently supported and guided its preperation. This work was supported by the National Science Foundation through grants MIP8822121 and BNS8510888. B. Nabet gratefully acknowledges the support provided by Drexel University's Research Scholar Award.

2

Biological Bases

2.1 A BRIEF HISTORY OF LATERAL INHIBITION

The concept of lateral inhibition arose in the extensive experimental research of H. K. Hartline and colleagues on the facetted compound eye of the familiar "Horseshoe crab" *Limulus* (Xiphosura). This research occupied a period of over fifty years and is an outstanding example of bringing quantitative mathematical methods of signal transmission to bear on a biological preparation (Hartline and Ratliff, 1974). The *Limulus* is an animal which appears not to have evolved further from its form in the time of the trilobites (Middle Paleozoic era). This animal is thus among the most primitive living. Yet, we can most easily describe the operations of lateral inhibition in mathematical terms. It is a quantitative, precise mechanism which was synthesized by evolution of this organism, very early in geologic time. Lateral inhibition is simultaneously a biological principle and a mathematical description of a biological neural network. Currently an electronic synthesis of lateral inhibition would be termed a sensory neural network.

The facets of the compound eye of *Limulus* are the largest found, approximately 100 micrometers (microns) in diameter, and the photoreceptor cells are quite accessible to electrophysiological-experiment methods. The structure behind (proximal to) the clear facets, and which includes them as the crystalline cones, is termed the ommatidium (from the Greek for "little-eye"). The ommatidium contains the primary photoreceptor cells termed retinular cells; and the secondary cell, the eccentric cell, which sends nerve impulses (spikes) to the brain of the animal along an axon in the optic nerve. The retinular cells are arranged about the central axis (dendrite) of the eccentric cell in the manner of the slices in an orange. The visual pigment (rhodopsin) is within the retinular cells, which signal light via a slow, or generator, potential which is communicated to the eccentric cells. Proximal to the retina and its layer of ommatidia is the neural plexus, which contains the cross-connections among the eccentric cells that mediate the lateral inhibition. These connections lie in several levels, each of a different dominant neighbor extent, and have been extensively documented by Fahrenbach (1985). From visual neurophysiological experimental analyses, the dominant lateral inhibition is very weak beyond approximately eight facets, having a maximum effect at the third facet or neighbor. This is true for the horizontal (anterior-posterior axis) and scaled somewhat smaller for the vertical (dorsal-ventral axis). From such considerations the Hartline-Ratliff equations have been synthesized, and these are:

$$r_i = e_i(I_i) - \sum_{j=1}^{n} k_{pj}\left(r_j - r_{pj}^0\right), \tag{2.1}$$

where

$$k_{pj} = 0 \text{ if } \left(r_j - r_{pj}^0\right) < 0.$$

This is a system of linear algebraic equations when each response r_i is positive and above threshold. The response is the spike firing rate of the ith eccentric cell, which receives excitation e_i from the retinular cells as a result of generator or slow potential responses to the facet's incident light I_i . The transformation $e_i(I_i)$ is nonlinear both in steady-state and time-dependent dynamics (Fuortes and Hodgkin, 1964; Pinter, 1966): the output is a compressed version of the input, similar to a logarithmic relationship, often designated a Weber-Fechner law. The time dynamics have a leftward pole migration as a function of the mean input light intensity or flux (Pinter, 1966). The Hartline-Ratliff equations (2.1) are feedback or recurrent and can often be approximated by a small number of iterated levels of feedforward or nonrecurrent equations (Varju 1962; for a concise development see Ch. 3, Ratliff 1965).

Because of the nonlinear transformation $e_i(I_i)$ and the thresholds, these equations are not linear, but often the experimental parameter set or theoretical analysis is operating in the linear range, where all responses are suprathreshold and the light flux variations in time and space are of low contrast at some given mean level I_0. In this case (2.1) are simply spatially discrete linear filters. The coefficient sets of the k_{pj} generally do not depend on the absolute values p, j but only on the difference function over space, $|p–j|$, and approach zero for $|p - j| > 10$ (Finite impulse response discrete spatial filter "FIR") with a maximum at $|p - j| = 5$. The coefficient set can be approximated with a continuous function which is the spatial impulse response of the system (2.1) (Ratliff et al. 1969).

For spatial impulse response functions possessing at least one maximum, the system (2.1) processes the input e_i across spatial dimension i into an output r_i. The discontinuities and near-discontinuities in e_i are accentuated in response space r_i by the appearance of overshoots and undershoots, or ringing, which is termed the "Mach band." Originally the Mach bands referred to the visual perception of darkening near the dim side and lightening near the bright side of a gradual or ramped edge. This was discovered in a long series of perceptual experiments by the physicist Ernst Mach and described in a series of papers on the interdependence of retinal points (1865–1906), available in English translation by Ratliff (1965). However, the perceptual phenomena are altered for a discontinuous step (sharp edge) such that another "edge detector" selective for that step discontinuity predominates or supplants the Mach band perception (Ratliff 1984). Mach sought to explain these perceptual "illusions" in the function of a neural network that was known, anatomically, to exist in the retina and the brain. In the early studies he proposed a model for the response r to the luminance distribution $I(x)$:

$$r = a \log \left\{ \frac{I(x)}{b} \pm k \frac{d^2 I(x)/dx^2}{I(x)} \right\}. \tag{2.2}$$

There are suitable upper and lower bounds on the value of $I(x)$, such that $I(x)$ is not zero and its range of values is limited, relative to two decades. The positive sign applies for a negative second derivative of $I(x)$, and a, b and k are constants. In the later studies Mach proposed a reciprocal inhibition model which resembles shunting or multiplicative lateral inhibition:

$$r_p = I_p \frac{I_p \sum_j \Phi(x_{jp}) \Delta a_j}{\sum_j I_j \Phi(x_{jp}) \Delta a_j}. \tag{2.3}$$

The inhibition function $\Phi(x_{jp})$ is a positive, monotonic decreasing function of the distance $|p{-}j|$ between retinal points.

The most obvious effect of the lateral inhibition operations (2.1), (2.2), or (2.3) is to produce a response of enhanced contrast relative to the input. At regions of high contrast this result takes the form of Mach bands. The accentuation of edges, which is the differentiating nature of lateral inhibition can be considered a deblurring operation, an attempt to restore contrast information lost by blurring. Blurring is necessarily the physical result of the non-infinitesmal width of the central maximum of the spatial impulse response. Another function of lateral inhibition may be to reduce redundancy. The inhibitory connections collect information from a wider area than the excitatory, so that the inhibitory receptive field region may be viewed as an estimator of a central local luminance level, and only deviation from that estimation, as signalled by a difference between excitation and inhibition, is transmitted. This hypothesis leads to a quite interesting theory of adaptation of form of receptive fields (Srinivasan, Laughlin, and Dubs 1982). Thus a further concomitant function is likely to be the limitation of the dynamic range which must be utilized by the nervous system in signalling luminance distribution, and functions thereof, from the visual space. Since the variation, or contrast, of the luminance distribution often carries the salient information for an organism, only the difference from the mean need be transmitted. This difference distribution has a more limited dynamic range than the luminance distribution (Laughlin 1989). While these effects, and the neural network Equations (2.1), (2.2), and (2.3) may appear on first sight as simple and straightforward, the overall visual impact in simulations of the lateral inhibition processing can be complex and dramatic (see for example, Ratliff 1965; Stockham 1972; Jernigan et al. 1989; Belshaw, this volume).

It is not only the visual system which contains clearly proven lateral inhibition, but also tactile and auditory systems (Bekesy 1967; Ratliff 1965; Moller 1987). The function of lateral inhibition may exist well beyond sensory systems, and into the central nervous system. Its functions may be not only those discussed above, but also a means of an organism's synthesis of nonlinear adaptive filtering of information from the sensory system.

2.2 CENTER-SURROUND ORGANIZATION AND RECEPTIVE FIELDS

The receptive field of a visual cell is defined as the region of visual space over which any response of the cell is obtained. The visual stimuli used to make this observation initially would be points or bars, of positive (brightening) or negative (dimming) contrast. It is often the case that there are antagonistic responses due to a given visual stimulus presented in the surround of the receptive field as opposed to the center of the receptive field. A pattern of organization of inhibitory surround concentric with or adjacent to the excitatory center, or region, resembles the lateral inhibition discussed above. The measures of cell response are several: various aspects of the often complicated response of the cell, for example, the peak response, the time-integrated area of response, or short-term or long-term steady state response.

The linear lateral inhibition discussed is a statement of connections, and requires a solution (by, e.g., matrix inversion; see Chapter 9) to define a receptive field. The linear receptive field is the output of the discrete spatial lateral inhibitory filter for a Dirac delta function (impulse function) visual space input. The linear receptive field is the spatial impulse response, weighting function or first order kernel in a Volterra or Wiener series (see Chapter 9). In Marr's classic treatment (1982) the $\nabla^2 G$ operator is the receptive field. However, when the lateral inhibition or the receptive field are not linear (e.g., the receptive fields of retinal ganglion Y-cells, or cortical complex cells) there is no known, closed form transformation from the lateral inhibition connection scheme to the receptive field, and vice versa (Pinter 1987a; Pinter and Nabet 1990). Only the linearization process will allow applications of matrix algebra and linear systems theory to the transformation of the lateral inhibition to the receptive field and vice versa. Furthermore, beyond the purely spatial considerations there is often great complexity in the temporal relationships of higher order visual interneurons, far beyond that found for *Limulus* compound eye eccentric cells. Useful descriptions of the activity of the cell then require a complete spatio-temporal analysis (Yasui et al. 1979; Curlander and Marmarelis, 1987).

An early quantitative experimental and theoretical analysis of cat retinal ganglion cells by Enroth-Cugell and Robson (1966) demonstrates clearly such complexities in the spatio-temporal response for the retinal X- and Y-type cells. That the often assumed linearity of the X-type cell is not precise can clearly be seen along with the decidedly stronger rectification properties of the Y-type cells (Enroth-Cugell and Robson 1966). There are many very nonlinear retinal ganglion cells (Troy et al. 1989). Motion analysis by cortical visual interneurons requires strong nonlinearity in spatio-temporal receptive fields (Emerson et al. 1987; Chen et al. 1989).

It is the thesis of this book that the nonlinear aspects of vision are the most interesting, useful for visual analysis and potentially the most productive for engineering visual systems design.

2.3 ADAPTIVE LATERAL INHIBITION

A long tradition of psychophysical investigation of linear filtering of images by the human visual system was established following the pioneering work of Ernst Mach (Ratliff 1965). Some of this approach is reflected in the linear operators and analysis discussed by David Marr in his book *Vision* (1982) and by Martin Levine in his book *Vision in Man and Machine* (1985). However, it is clear that there are significant nonlinearities and adaptive filtering in the visual system.

The perceptual spatio-temporal frequency response, known also as a Contrast Sensitivity Function (CSF), is obtained by subjects' adjustment or choice of threshold contrast at a set of points on the frequency plane. This is a linear model of the filtering properties of the visual system. However, it is found that as the mean luminance level of the stimulus is raised, the frequency response changes from low pass to band-pass, the upper band-limit increases, and the low frequency gain decreases. What are the causes of this distinctive adaptation? There is of course the primary effect of the lower information capacity at lower luminance levels, because there are fewer photon absorption events to signal the different parts of a given visual pattern. This might be evident as shot noise, or lower relative signal levels. Yet we do not see a pointillist or patchy pattern as luminance is lowered. There may be many reasons for this, but the visual system is without question low pass and low bandwidth at low luminance levels. (This is discussed further in Section 6 below.) Adaptive nonlinear filtering, via nonlinear lateral inhibitory networks and receptive fields may be another important mechanism in these adaptive visual changes (Pinter 1985). Preceding this primarily spatial adaptive filtering, it is well known that the photoreceptors themselves adapt temporally such that they become significantly slower at low luminance (Pinter 1966; Wong and Knight 1980).

Conversely, at higher luminance levels, visual systems become stronger differentiators. This adaptive differentiation was best described for human visual perception by Kelly (1975) in a study where the perceptual experiment gave a family of contrast sensitivity functions each taken at a different mean luminance (see Fig. 2.1). Thus for a given mean luminance, a model of the contrast sensitivity function is a linear Modulation Transfer Function (MTF) followed by a fixed level threshold. To obtain a prediction of the receptive field in this case, one then takes the inverse Fourier transform of the MTF with the assumption that the MTF is a real, even function. The predictive power of this receptive field is substantial (Kelly 1975). A key point in Fig. 2.1 is the adaptation of the MTFs to mean luminance levels. Since the spatial differentiation in the spatial domain is given as ∇^2, this accounts for the decrease of the MTF at low frequencies. The mean luminance controls this spatial differentiation. The model for the adaptive control of spatial differentiation adopted by Kelly (1975) is to replace the ∇^2 operator with $(1 - a(L_0)\nabla^2)$, where $a(L_0)$ is a monotonic increasing function of mean luminance L_0. Lateral inhibition in this context can be shown to be related to this adaptive differentiation simply by