

**MEAN FIELD APPROACHES TO THE  
PRIMATE VISUAL CORTEX**

by

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**ABSTRACT**

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Mathematical models of large neural networks are notorious for being computationally intensive, cumbersome, and difficult to analyze. Smaller networks are more easily manageable and offer greater insight into underlying mechanisms, yet they tend to lack the large-scale interaction between neurons required to manifest the phenomena scientist are most interested in studying. A prime example of a biological system with features requiring substantial networks to describe properly is the primate visual cortex. In this study, we examine a technique for constructing models of neural networks. While Mean Field networks demonstrate some of the salient characteristics of a cortical network at a significant discount in computational cost, it has also been recognized that properly identified individual nerve cells are fundamental to correctly describe biological networks and their properties, a feature that Mean Field networks lack by definition. Ideally, this network might be utilized to formulate a model retaining a certain degree of intuitive transparency, while also incorporating single neural elements for detailed analysis. Using numerical analysis to compare and evaluate such hybrid networks, the author hopes to ascertain their feasibility, and to propose a cortical model exploiting these advantages for the study of visual phenomena.

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## GLOSSARY

**Action Potential.** A cellular event where a stereotypical voltage change propagates through the cell, causing the release of certain chemicals at junctures with other cells. These chemicals in turn alters the membrane conductances of those other cells.

**Coarse Grain.** A technique that groups elements of a network by certain parameters, greatly reducing the number of equations and calculations needed.

**Excitatory Cell.** A cell which, when activated, releases a neurotransmitter which depolarizes its target cells, increasing the probability of their activation.

**Excitatory Post Synaptic Potential, E.P.S.P.** The change in membrane potential a cell undergoes when stimulated by an excitatory cell.

**Inhibitory Post Synaptic Potential, I.P.S.P.** The change in membrane potential a cell undergoes when stimulated by an inhibitory cell.

**Inhibitory Cell.** A cell which, when activated, releases a neurotransmitter which hyperpolarizes its target cells, decreasing the probability of their activation.

**Lateral Geniculate Nucleus, LGN.** A thalamic nucleus that serves as a relay for incoming visual information from the retina, via retinal ganglion cells, transmitting it in an organized fashion to layers IV C and VI of the primary visual cortex.

**Mean Field.** A neural network representation where individual elements encode an average firing rate, instead of a membrane potential.

**Membrane Equation.** An equation used to model the behavior of a neuron, often utilizing a system of differential equations.

**Primary Visual Cortex, V1.** An area of the brain in the anterior portion of the occipital lobe of the brain, where visual input from the retina is first processed. See Figure 1.

## INTRODUCTION

Vision Research is a cornerstone field in the discipline of neural science. Understanding the functional anatomy, the correlation between spatial organization of cells in a network and its emergent properties, is a critical step towards unlocking the mysteries of the brain. For example, some neurons of the visual cortex respond preferentially to stimulus oriented in a particular direction when projected upon a screen. How does such a preference arise, and how do these preferences manifest in perception and behavior?

Theoretical Neuroscience provides a fundamental approach to understanding these complexities of the nervous system. It incorporates mathematical models to explain phenomena by utilizing the physiology underlying the network. Neural network models are a popular and powerful tool for investigating theories of the visual system. A vast array of physiological studies found the basis of many mathematical models useful for investigating of certain important properties of the visual cortex. These properties include not only orientation selectivity, but also “perceptual grouping,” contour

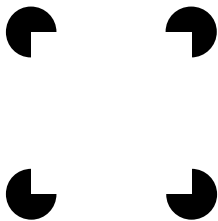


Figure 1: A Kanizsa<sup>1</sup> square.

completion, and surface representation. Many scientists now believe that initial processing of information responsible for the manifestation of such phenomena occurs within V1. Large networks of cells are necessary to reproduce recorded physiological data, and to generate the phenomena scientists are interested in studying. They allow the investigation of proposed mechanisms underlying the phenomena. However, large networks of individual cells are computationally expensive, often unwieldy, and generally obfuscate how these properties arise.

This study will focus on a point-neuron model developed by McLaughlin et al.<sup>2</sup>, which was reduced to a Mean Field neural network. This reduction yielded significant discount and has also lead to a theory addressing orientation selectivity.

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<sup>1</sup> Kanizsa, G. (1979). Normal viewers perceive the outline of a square circumscribed by the circles. While a uniform background exists across the figure, a viewer perceives contrast between the ‘inside’ and ‘outside’ of the square.

The author hopes to determine if and how a multi-layer model of the visual cortex might incorporate mean field networks. The assumptions underlying a Mean Field reduction of an point neuron model will be tested for validity. If successful, the study will not only support some of the assumptions made, but may raise new questions about the conceptual framework upon which cortical models are built. Ultimately, a Mean Field network would be used to represent background stimulation within a cortical layer, which represents long-range excitation/inhibition, as well as the inclusion of noise into the system.

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<sup>2</sup> See McLaughlin, D., Shapley, R., Shelley, M., Wielaard, D.J. (2000) & Shelley, M., McLaughlin, D. *Unpublished*.

## REVIEW OF THE LITERATURE

Understanding the mechanism of vision has been the goal of many scientists. Nobel Prize winning studies by Hubel and Wiesel in the 1960s showed that the primary visual cortex is organized relative to features in the visual field of the retinas. The primary visual cortex, like the other parts of the cortex, is composed of a two-dimensional, slightly folded sheet of neurons. If flattened, human V1 would cover an area of nearly four square inches<sup>3</sup>. It contains at least 150 million neurons<sup>3</sup>, each making many hundreds of specific connections with other neurons. The primary visual cortex is divided into six layers, or laminae, each with different anatomical characteristics. The physical architecture and connectivity between layers is generally well understood; for a complete treatment, the reader should refer to studies of cellular projections between layers performed by J.S. Lund and E.M. Callaway.



Figure 2: Human brain with occipital lobe highlighted.

LGN: Two distinct pathways segregate retinal information relayed through the LGN. These functionally different pathways, labeled *Magni* and *Parvi* influence cells of the cortex to various degrees.

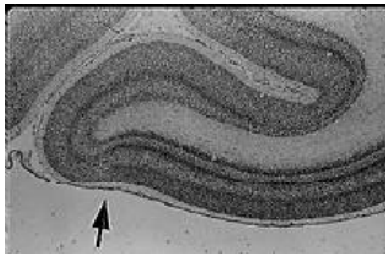


Figure 3: Horizontal section through the striate cortex, showing distinct cellular layers.

Though all neurons receive information from each pathway, cells influenced primarily by the *M* pathway differ in their response to certain stimuli from cells influenced primarily by the *P* pathway. This segregation of information is preserved in the LGN through a stratification of the nucleus, separating cells with similar input. Table 1 summarizes the information transmitted through each pathway. A third pathway has been proposed, named the *Intralaminar* or *Konicocellular* pathway; little is understood except that axons

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<sup>3</sup> Wandell, B.A. (1995).

originating between LGN layers terminate in lamina 2/3A of V1. Input from the thalamus (the *afferent* input) typically targets layer IV<sup>4,5</sup>, with some axon collaterals projecting minor inputs to layers 6.

Layer IV C is the initial target for visual input, and is a subdivision of layer 4. As such, its cells have

Stimulus:	PREFERENCE	
	M cells	P cells
Color	No	Yes
Contrast	Great	Small
Spatial Frequency	Low	High
Temporal Frequency	High	Low

Table 1: Excitation of the *Magni* and *Parvi* cellular pathways<sup>6</sup>.

receptive fields that more closely match retinal fields than any other cells in V1. The layer is further subdivided into an  $\alpha$  and  $\beta$  sub lamina. Sub lamina 4C $\alpha$  principally receives input from *M* cells of the LGN; most LGN *P* cells terminate axons in sub lamina 4C $\beta$ . Layer 4C is the first place in the visual pathway where cells can exhibit receptive field quite different from the center-surround fields of the retina; in 4C  $\alpha$  some cells are orientation-specific, with simple receptive fields. Excitatory cells called Spiny Stellate neurons

inhabit the layer, one of the two major classes of neurons that comprise the cerebral cortex. Spiny Stellates residing in the  $\alpha$  division of 4C project axons primarily to layer 4B, while those residing in the  $\beta$  division project to layer 2/3A. The inhibitory circuitry in layer 4C is usually consistent with the lateral. Above and below 4C, the visual cortex is divided into narrow columns of cells, from 30 to 100  $\mu\text{m}$  wide. Cells in a column have receptive fields that nearly identical retinal positions, as well as identical orientation preference.

Layer 2/3A: This superficial layer is quite thick, and contains many processes projecting to extra-striate regions of the cortex (such as V2). Layer 2/3A features another regular spatial organization besides a vertical stratification. This lateral organization is apparent in a slice of tissue histochemically prepared to reveal the density of cytochrome oxidase, a mitochondrial enzyme involved in cellular respiration. The columnar organization of cells by orientation is evident in the surrounding lattice of lower cytochrome oxidase density. These regions of high C.O. density appears to correspond to the specificity of feed-forward connections from layer 4.

<sup>4</sup> Lund, J.S. (1983).

<sup>5</sup> Fitzpatrick et al. (1985).

<sup>6</sup> Adapted from Kandel et al. (2000).

Layer V houses many pyramidal neurons which project out of the cortex. Most of the pyramidal cells have extensive dendritic and axonal arborization in layer 2/3A. This widespread connectivity does not appear to have any relation to the C.O. Blob organization of layer 2/3A. The functionality of the layer seems to parallel the relationship between layer 6 and 4C; in that it seems to serve primarily as a feed-back circuit comparing the input and output of layers 2/3A and modulating them accordingly.

Both stellate and pyramidal cell types inhabit layer 6, the deepest layer of the cortex. Principal stimulation of layer 6 arrives through axonal projections originating in layer 4C. Similarly, most layer 6 efferent axons terminate back in layer 4C, with occasional collaterals branching off into layer 5. Recent studies advocate the vitality of feedback circuitry, as well as feed-forward, to the functionality of the striate cortex. Studies by Fitzpatrick et al., as well as many others support the theory that various cell groups of layer 6 target not only the input layer of 4C, but also project back to the white matter.

Connections such as these, and in layer 5 most likely serve to modulate the response of each layer in the feed-forward circuit by suppressing neural activity at a distance from the activated patch.

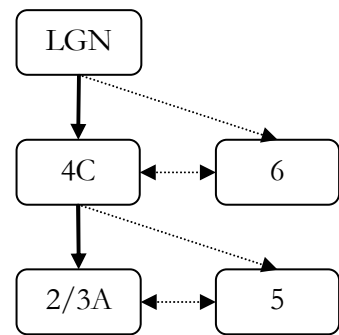


Figure 4: A schema of visual processing in V1. The primary flow of information is illustrated in bold, while dotted lines indicate modulatory and feedback circuitry<sup>7</sup>.

In addition to feedback modulation, physiological studies furnish a role to feed-forward inhibition. J.S. Lund has observed an inhibitory circuit of inter-laminar projections by smooth stellate neurons. This circuit seems to parallel the feed-forward flow of excitation in the 4C to 2/3A pathway, in that the action of the rinsing connections serves to inhibit the inhibitory cells in the target layer, thereby leaving excitatory pyramids to respond to rising feed-forward excitation.

The approaches to modeling this area are also extensive. A simple, yet quite powerful model of a spiking neuron, first investigated in 1907, *integrate-and-fire* models reflect two key aspects of neuronal excitability: passive, sub-threshold integration of an input, and regular, stereotypical behavior once threshold is exceeded. Treating the cellular membrane of a neuron as a capacitor, Ohm's law can

<sup>7</sup> Adapted from Callaway, E.M. (1998).

predict the voltage of a cell across its membrane. Differentiating this equation yields an expression relating the change in voltage due to cellular currents, typically called the *Membrane Equation*. In a model where neural units encode an instantaneous firing rate, the generation of each voltage spike is independent of the preceding spikes. Only a single number, firing rate, matters.

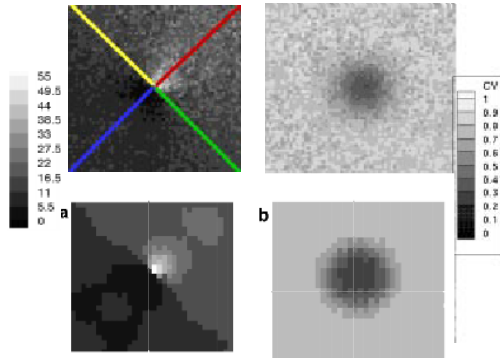


Figure 5: A top-to-bottom comparison between point-neuron and Mean Field cortical response. The left column gives time-averaged firing rates due to a grating stimulus. The right column shows the distribution of circular variance<sup>8</sup>.

model, developed by A. Treves approaches cortical dynamics using an all-to-all coupled system, similar to models by D. Nykamp and D. Tranchina in its use of population density theory. A model by Somers et al. examines feline visual cortex using a one-dimensional system organized with respect to orientation.

It is rare that a model accurately describes both the behavior and the physiological organization of the cortex. Reviews of contemporary cortical models reveal several that are germane in scope and motivation to that developed by McLaughlin et al<sup>2</sup>. Studies by Troyer et al. and D. Hansel and H. Sompolinsky are notable examples in their investigation of the local interaction in the cortex. A series of studies by S. Grossberg seek to understand the relationships between behavior and perception using idealized models that do not always account for the anatomical architecture observed. Another mean rate

<sup>8</sup> Reproduced with permission from Shelly, M., McLaughlin, D. (2001).

## METHODOLOGY

The each step of the study hopes to affirm the suitability of a mean field for physiological modeling. These experiments are designed to determine under what circumstances may a Mean Field network safely replace a group of Integrate-and-Fire neurons.

The analysis will follow three steps:

1. A small but complete Mean Field network will be compared to an integrate and fire network. The networks will not be spatially organized; all-to-all coupling will exist between each unit.
2. A model will be derived combining a single Integrate-and-Fire neuron into a Mean Field network, to compare the actual firing rate to the rate predicted by the Mean Field.
3. A small point neuron network will be constructed with background and long range stimulation provided by a Mean Field network. Firing properties of the point neuron network will be compared to firing properties predicted by a full Mean Field.

All networks will be encoded and run using MATLAB® visualization software. The basic model equations may be found in the Appendix, and a complete reduction to mean field will be given in the analysis.

The author will conduct these studies keeping in mind the goal of constructing a multi-layer representation of the cortex.

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## APPENDIX: MODEL EQUATIONS

The Mean Field network is derived from an Integrate and Fire network, and follows from the treatment McLaughlin et al. used for the development of the model. The network is represented by a two-dimensional coupled system of Membrane equations, each defined as:

$$C \frac{dV}{dt} = -g_L(t)(V - V_L) - g_E(t)(V - V_E) - g_I(t)(V - V_I)$$

The capacitance  $C$  is set to a standard value of  $10^{-6}$  F/cm<sup>2</sup>. The membrane leakage conductance,  $g_L$ , is set to  $5 \cdot 10^{-7}$   $\Omega^{-1}$ cm<sup>2</sup>. The excitatory reversal potential  $V_E$  and inhibitory potential  $V_I$  are normalized respectively to 14/3 and -2/3. The time dependent conductances,  $g_E$  and  $g_I$ , are described as:

EXCITATORY POPULATION	INHIBITORY POPULATION
$g_E(t) = F(t) + S_{EE} \sum_{k \in E} K_E \sum_{\substack{\text{Spike} \\ \text{times}}} G(t - t_k)$	$g_E(t) = S_{IE} \sum_{k \in E} K_E \sum_{\substack{\text{Spike} \\ \text{times}}} G(t - t_k)$
$g_I(t) = S_{EI} \sum_{j \in I} K_I \sum_{\substack{\text{Spike} \\ \text{times}}} G(t - t_j)$	$g_I(t) = S_{II} \sum_{j \in I} K_I \sum_{\substack{\text{Spike} \\ \text{times}}} G(t - t_j)$

The functions  $F(t)$  on the right-hand-sides represent extra-cortical input, as well as a stochastic conductance due to cortical noise. Those cells representing the excitatory population of layer IV  $C\alpha$  will also receive an excitatory conductance from the LGN. The term  $K_{E,I}$  designates the spatial coupling strength between the neurons; it is a function of their spatial distance, a Gaussian falloff of the form:

$$K(i, j) = \frac{C^2}{\pi L^2} e^{-\frac{\|i-j\|}{L}}$$

where constants  $L$  and  $C$  are exclusive properties of each specific cell population. The time course of the changes in conductance from incoming action potentials is modeled with an  $\alpha$ -function:

$$G(t) = C \frac{t^n}{\tau^n} e^{-\frac{t}{\tau}}$$

with a peak time  $\tau$  of 3 ms for E.P.S.P.'s, and 5 ms for I.P.S.P.'s. The constant  $C$  is determined such that  $\int_0^{\infty} G(t) dt = 1$ . The strength coupling parameters  $S_{E,I}$  will be chosen such that the model remains stable and exhibits normal cortical response.