An Architectural Model of the Non-linear Subunits of Complex Cells of Visual Cortex Based on Gated Intracortical Interactions[1]

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Abstract— **In this study we propose an architectural model to describe the non-linear effects of intracortical interactions over complex cell receptive fields (RFs). Afferent inputs from lateral geniculate nucleus (LGN) are recurrently combined to form non-linear computational subunits described as 2nd order Volterra integral operators over RFs. Specifically, the feedback path of intracortical interactions is gated by additional LGN afferent projections. The resulting complex cell subunits incorporate summing mechanisms activated by the concomitant stimulation in both central and peripheral parts of the RF. The relation of this type of controlled coordination of sensory information in visual cortex to its signal processing capabilities are considered in perspective.**

I. Introduction

The signal processing capabilities of any cell in the primary visual pathway can be characterized by its receptive field (RF), i.e., by evidencing a functional mapping between the pattern of stimuli over a local portion of the visual field, and the level of activity of the cell. Basically two types of cells can be distinguished in visual cortex: those exhibiting linear spatial summation over their RFs, which are classified as "simple", and those exhibiting non-linear summation, which are classified as "complex" [1]. To understand how, despite the uniform spatial organization of RFs, complex cells exhibit both orientation and spatial frequency tuning, it is necessary to postulate non-linear *subunits* which are the outcome of facilitatory (excitatory) and suppressive (inhibitory) non-linear interactions within the RFs. The precise nature of these non-linearities remains to be determined, notwithstanding many experimental observations [2] [3] [4].

In this paper, guided by functional RF characteristics of complex cells, we intend to develop an architectural model based on simple, non-linear intracortical processing mechanisms. The underlying concepts can guide the specification of structural paradigms for artificial neural visual processors, and are not intended to account for biophysical data in detail.

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II. Methods

Following the standard model of continuum neurodynamics, we regard visual cortex as a continuous distribution of neurons and synapses. Accordingly, the retinocortical pathway can be modeled by two layers interconnected through feed-forward and feedback connections, both inter- and intra-layers. The layers represent the retina ($\mathbf{x}$) and cortical surface ($\mathbf{u}$). The dependence of cortical surface activity $e(\mathbf{u})$ on the visual input $i(\mathbf{x})$ and on the retino-cortical interconnections can be formulated through the following hierarchy of models: (i) feed-forward connections: $e(\mathbf{u}) = (\mathcal{A}i)(\mathbf{u})$; (ii) feed-forward and feedback connections: $e(\mathbf{u}) = (\mathcal{A}_0 i)(\mathbf{u}) + (\mathcal{B}e)(\mathbf{u}) = e_0(\mathbf{u}) + (\mathcal{B}e)(\mathbf{u})$, where $e_0(\mathbf{u})$ is the feed-forward distribution of input cortical excitation; (iii) feed-forward and modulated feedback connections (see Fig. 1):

$$e(\mathbf{u}) = e_0(\mathbf{u}) + (\mathcal{G}i)(\mathbf{u})\ (\mathcal{B}e)(\mathbf{u}). \tag{1}$$

All operators $\mathcal{A}$'s, $\mathcal{B}$, $\mathcal{G}$ can be defined in integral terms. $\mathcal{A}$'s and $\mathcal{G}$ are receptive field operators, typically characterized by elongated kernels $h_{\mathcal{A}}(\mathbf{u};\mathbf{x})$ and $h_{\mathcal{G}}(\mathbf{u};\mathbf{x})$, that make them sentitive to oriented stimuli. $\mathcal{B}$ models inhibitory/excitatory intracortical spatial couplings and can be formulated as

$$(\mathcal{B}e)(\mathbf{u}) = b \int_{\Omega_{\mathbf{u}}} k_{fb}(\mathbf{u};\mathbf{u}')e(\mathbf{u}')d\mathbf{u}', \tag{2}$$

where the kernel $k_{fb}(\mathbf{u};\mathbf{u}')$ specifies the local axonal and dendritic intracortical interaction fields over the spatial neighborhood $\Omega_{\mathbf{u}}$.

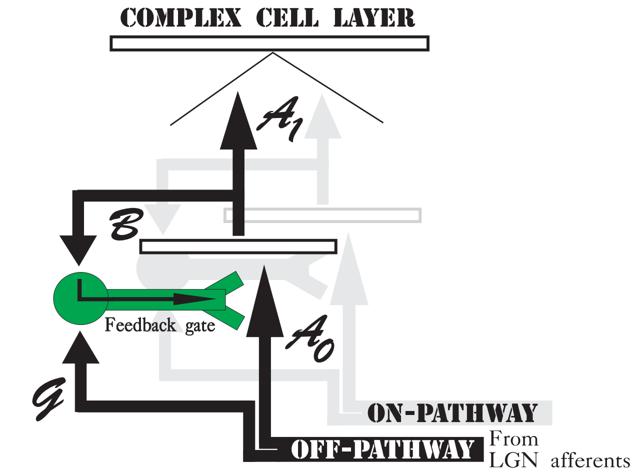


Figure 1: Schematic representation of the architectural model. Two types of processes can be distinguished. The first ($\mathcal{A}_0$) concerns the afferent flow of information from LGN providing a weak bias in orientation. The second ($\mathcal{B}$) concerns efferent projections, or feedback, which recurrently modify and control afferent contributions. Additional feed-forward pathways ($\mathcal{G}$) from the LGN are devoted to tune the efficacy of the recurrent interactions (*gated feedback*). ON and OFF contributions from LGN cells terminate separately into different cortical layers, according to topology-preserving criteria. At complex cell level ON and OFF components are summed up and averaged through a radial symmetric Gaussian kernel ($\mathcal{A}_1$).

The solution of Eq.s (1) and (2) will give $e(\mathbf{u})$, having specified $i(\mathbf{x})$. This is like to define an equivalent feed-forward operator $\mathcal{A}_{eq}$ which acts directly on the input signal, and whose kernel $h_{eq}(\mathbf{u};\mathbf{x})$ summarizes the effect of intracortical gated interconnections ($\mathcal{B}$ and $\mathcal{G}$). To understand what kind of operator $\mathcal{A}_{eq}$ is, we can resort to a Volterra series truncated to its first non-linear term:

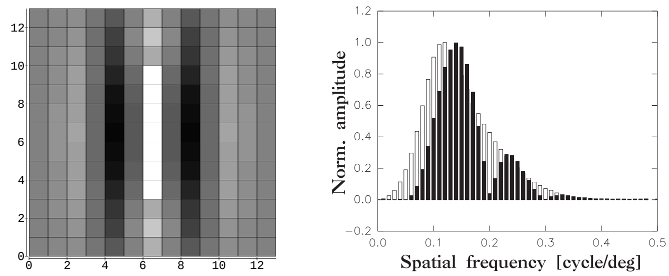
$$e(\mathbf{u}) = \int h^{I}_{eq}(\mathbf{u};\mathbf{x})i(\mathbf{x})d\mathbf{x} + \int h^{II}_{eq}(\mathbf{u};\mathbf{x}_1,\mathbf{x}_2)i(\mathbf{x}_1)i(\mathbf{x}_2)d\mathbf{x}_1 d\mathbf{x}_2$$

The 2nd-order Volterra kernel h^{II}_{eq} can be "measured" by solving numerically Eq.s (1) and (2), when the system is excited with a pair of suitably located impulses [5].

III. Results

- *Spatial kernels* - The spatial profile of h^{II} was analyzed with static activation: the response to a stationary light (*activation stimulus*) is modified by a second stationary stimulus (*test stimulus*). The bi-impulse response is determined and compared with that predicted by linear superposition (see Fig. 2a) [2].

- *Frequency tuning* - The system is excited by sinusoidally modulated gratings oriented along the preferred direction of the feed-forward RF field components. A narrower tuning curve is observed in comparison with the corresponding curve obtained in absence of gated feedback (see Fig. 2b). The frequency selectivity of complex cell



(a) (b)

Figure 2: (a) Spatial profile of the kernel of a 2nd-order subunit: in the elongated central region the response exceeds that predicted by linear superposition, while in the elongated flanking regions the response is less. We observed similar structures both for light-light concomitant stimulation and for dark-dark stimulation, whereas, reversed structures were obtained by stimulations of opposite polarity (e.g., light activation stimulus and dark test stimulus, or *vice versa*). (b) Frequency tuning curve of a complex cell subunit for intracortical interaction with (filled bars) and without (open bars) gated modulation.

subunits is also characterized by the presence of higher-frequency peaks.

In this model, recurrent combination of sensory inflow is mediated by gating circuits controlled by additional feed-forward signals, thus resulting in higher-order neural subunits specifically selective to an event in the visual field and its concomitant circumstances. Thus, the model can be used to investigate also the effects of confluent convergence of ON and OFF pathways as well as the confluence of different temporal channels. Along this line, spatio-temporal interactions across the discharge field of complex cells would be controlled by dynamic non-linearities, whose effect may depend both on the peripheral context and on the recent past of visual stimulation.

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