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A network view of the structure of center/surround modulations of V1 receptive field properties in visual and cortical spaces

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Abstract

Firing of V1 cells in response to test stimuli shown in the classical discharge field is highly dependent on the spatial context (orientation/contrast center-surround gradients) in which they are embedded. Here, we present a preliminary study of a large-scale detailed model constrained by physiological and psychophysical data which accounts for the modulatory effects induced by the concomitant stimulation of the “silent” surround. Numerical simulations were used to predict the changes produced at the firing level as a function of the neighborhood relationship imposed by the location of the cell in the orientation map. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Primary visual cortex; Contextual modulations; Long-range horizontal connectivity; Cortical orientation maps

1. Introduction

The responses of neurons in primary visual cortex (V1) to stimuli presented within their receptive field (RF) can be markedly modulated by stimuli falling in surroundings regions which by themselves fail to activate the cell (reviewed in [4]). Whether this contextual influence is facilitatory or suppressive is known to depend at the cortical level on the contrast and on the spatial configuration of the pattern elements

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inside and outside the RF. Long-range interactions are thought to be mediated by cortico-cortical feedback from higher cortical areas, but also by long-range horizontal connections within V1. The functional role of this latter network, intrinsic to V1, may represent an early mechanism for visual segmentation and spatial integration. However, although center/surround modulations have been thoroughly investigated both experimentally and theoretically, it is still unclear whether the various perceptual phenomena such as pop-out, contour linking and orientation contrast discrimination rely or not on the same cortical mechanisms. At the cellular level, only few studies have tried to quantitatively vary center/surround stimulus configurations. Similarly, limited attention has been given to the dependency of the effectiveness of center-surround effects on the local characteristics of the intracortical network in which the recorded cell is embedded. We present here a large-scale detailed model of V1 intracortical connectivity in superficial layers. Our aim is to: (i) reproduce and discuss previously proposed contextual modulation mechanisms (in particular [13,14]); (ii) explore within the same framework the coherence of the network's behavior under a wide range of paradigms that have been used in physiology and psychophysics; (iii) by using an idealized orientation cortical map, allow a systematic exploration of the possible influence of the position of the recorded cell in the orientation map on its ability to differentially discriminate what belongs to the discharge field from its immediate periphery.

2. Model

The model represents a 4.2 mm by 4.2 mm region of V1 layers 2/3 receiving the feedforward projection of a 4.2° by 4.2° patch in retinal space. When possible, model parameters were constrained by physiological data obtained in cat V1. The model contains 18 000 spiking cortical neurons and 1.2 million synapses. Neurons are organized into a 6 by 6 grid of hypercolumns, each of which contain 400 excitatory and 100 inhibitory neurons modelled as integrate-and-fire neurons with realistic firing characteristics (gain: 50, 70 sp/s/nA). Preferred orientations are determined according to an idealized crystal-like orientation map inspired from [8] (Fig. 1A). The map is radially organized: orientation centers are distributed evenly across the map, and linear sequences of orientation run in between the horizontal and vertical lines along which the singularities are distributed [11]. Model cells receive two types of external inputs: random background bombardment of excitatory (E) and inhibitory (I) synaptic inputs, and selective visual inputs. Feedforward inputs are assumed to originate from retinotopic locations distributed over the visual field and to include an orientation bias ($\sigma = 20^\circ$) processed by the intracortical network to build the map of preferred orientations. Afferent spike trains are modelled as Poisson processes. For every cell, their mean rate is a function of the log-contrast, the orientation and the position of the stimulus relative to the cell's RF location. Cortical magnification is $1 \text{ mm}/^\circ$. RF positions are assumed to move uniformly across the cortical map. RF diameters are 0.7° . The architecture of intracortical connexions is illustrated in Fig. 1B. Intracortical connexions provide local short-range excitation ($< 200 \mu\text{m}$),

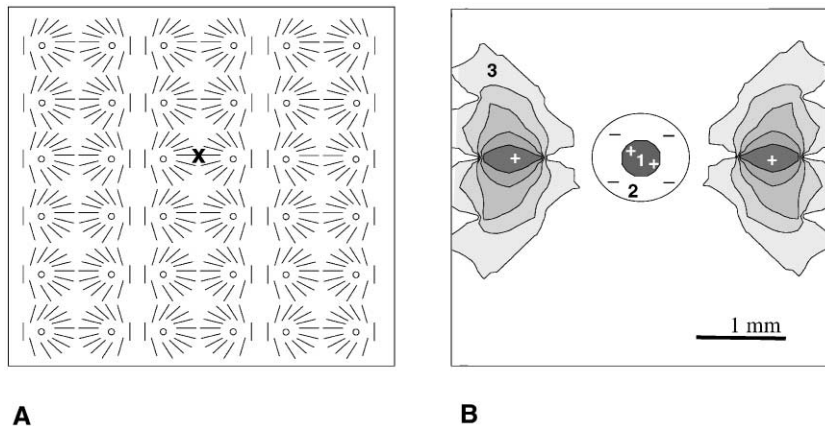


Fig. 1. (A). Schematic representation of the idealized orientation map (6×6 hypercolumns). Open circles indicate orientation singularities and oriented bars indicate preferred orientations, ranging from 0° to 180° . (B). Example of the localization of the E and I afferents targeting a neuron with a preferred orientation equal to 0° (with location indicated by a cross in A). In region (1) and (2), E and I connection densities decrease with distance from 100% (center) to 0%, and from 24% to 12% respectively. In region (3), long-range E connection density ranges from 1% (dark gray) to 0.1% (light gray).

short-range inhibition ($< 500 \mu\text{m}$) and long-range horizontal excitation ($< 500 \mu\text{m}$). Consistent with anatomical data, the density of all types of connections decreases with intracortical distance, but while local connections are radially symmetrical and independent on orientation [3], long-range connections show a moderate preference ($\sigma = 40^\circ$) for iso-orientation of the pre- and post-synaptic cells [6], and a preference ($\sigma = 20^\circ$) for receptive fields co-alignment [10]. The onset latency of synaptic depolarizing responses to stimuli flashed at increasing distances from the RF increase linearly with distance, with low apparent speed of horizontal propagation (0.1 m/s) [1]. The possible consequences of this temporal property of the horizontal network are studied elsewhere [7].

3. Results

3.1. Simulation of classical RF properties

When tested with a unique focal oriented stimulus, the model accounts for orientation-selective supra-threshold responses, contrast saturation and contrast-dependent length-tuning (Fig. 2A).

3.2. Influence of contrast and orientation on center/surround modulations

Center/surround interactions were first tested with a bipartite stimulus composed of an optimally oriented central grating placed inside the RF and flanked by an

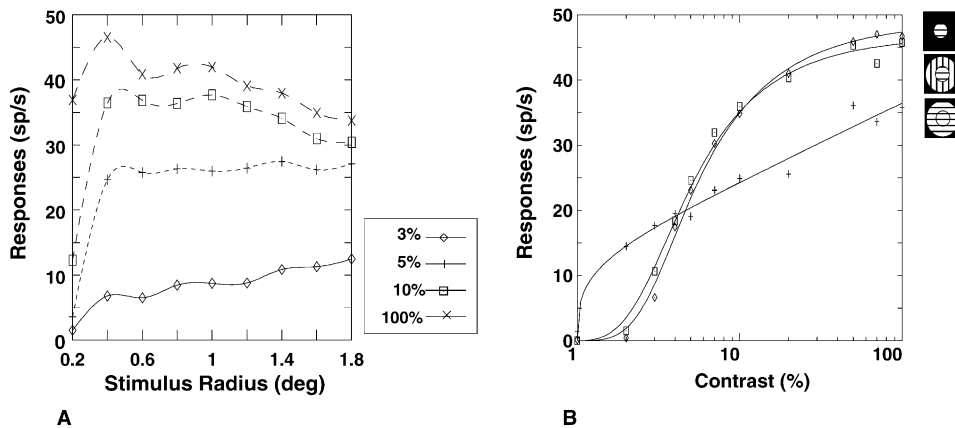


Fig. 2. (A). Response as a function of stimulus radius. Optimal stimulus radius increases with decreasing stimulus contrast. (B). Mean firing rate of 36 excitatory neurons in the central 3×3 column (iso-oriented domain), to varying contrast levels of a center circular stimulus (radius: 0.35°) under 3 fixed conditions: no surround, high-contrast (100%) cross-oriented or iso-oriented surround (internal and external radii: 0.7° , 2.1°) respectively.

annular surround outside the RF. The model accounts for the fact that the contrast of the center stimulus regulates whether surround interactions are facilitative or suppressive [9,15]. In the presence of an iso-oriented surround, responses are facilitated at low center stimulus contrast and suppressed at high contrast (Fig. 2B). The mechanism underlying this biphasic behavior and the parameter regime where the network is studied are similar to that proposed by earlier studies (in particular [13,14]). It is based on an asymmetry between excitatory and inhibitory local circuit responses: for low contrast levels only the excitatory population is active and acts as a linear amplifier, while for higher contrasts, high-threshold inhibitory neurons become active, inhibit the postsynaptic excitatory population and cause their saturation.

3.3. Influence of the spatial retinal configuration

Three parametric studies of the geometry of these center-surround interactions, similar to that performed by [5] in monkey V1 and human, are illustrated in Fig. 3. We used 2 oriented circular patches, one of variable contrast presented within the RF (“test”), and a high contrast (100%) additional patch (“flank”) in the RF surround. We systematically varied: (i) the separation between the test and the flank along the axis of colinearity of the test stimulus; (ii) the lateral offset and (iii) the relative angle between the two stimuli. A first striking finding is that, whatever the configuration, suppressive modulations are very weak with such stimuli, indicating a strong influence of the stimulus size on these effects. Facilitatory effects are still observed at low test contrasts and 2 to 3-fold enhancement is found for iso-oriented,

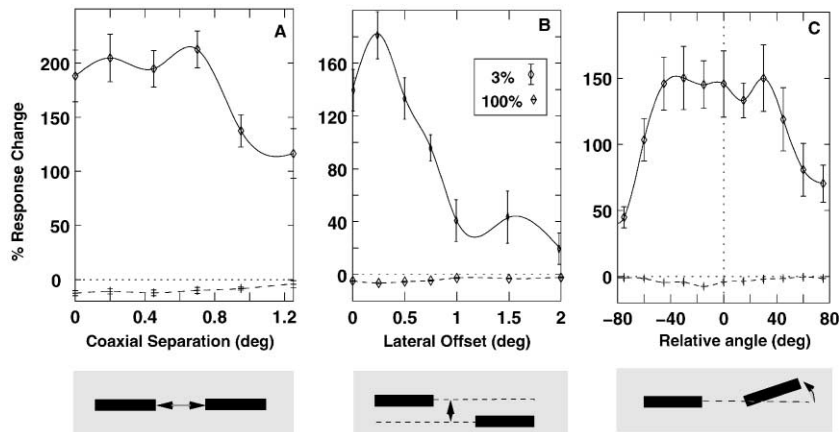


Fig. 3. Dependence of test response on test-to-flank co-axial separation, lateral offset and relative orientation. Response modulation change is defined relatively to the response of the test alone ($R_{[test + flank]} - R_{test}/R_{test}$). Flank and test stimuli are circular gratings of radii 0.7° and 0.35° , respectively. 5 trials.

co-aligned configurations. The decrease of the facilitatory interaction when the two stimuli are separated along their axis of orientation, are displaced from colinearity, and have their orientation changed is qualitatively similar to that described by [5]. The tuning of these effects is a bit broader than that observed by [5], which might be explained by differences in the stimuli that were used. It would alternatively suggest that the dependency of the horizontal network architecture on orientation and alignment is more specific in monkey V1 than assumed here in cat.

3.4. Influence of the position in the orientation map

For every position in two central hypercolumns (200 sites), we studied the responses to a bipartite stimulus centered at this location. Results indicate that: (i) The behaviors exhibited by the network population are globally homogeneous and of the biphasic type; (ii) Some variability is found in the magnitude of these effects, with smooth variations across the cortical map; (ii) At pinwheel centers, in particular, large facilitations are observed at low contrast, while no effect of the periphery is found at high contrast (due to a weaker amplification of center responses by the local circuit, resulting in a lower recruitment of local inhibition). Fig. 4 illustrates the distribution of response changes in the population, and how pinwheel centers compare with the rest of the population.

4. Conclusion

We have shown that the model accounts for a dependence of center/surround modulations on the relative contrast, separation, orientation, and alignment of

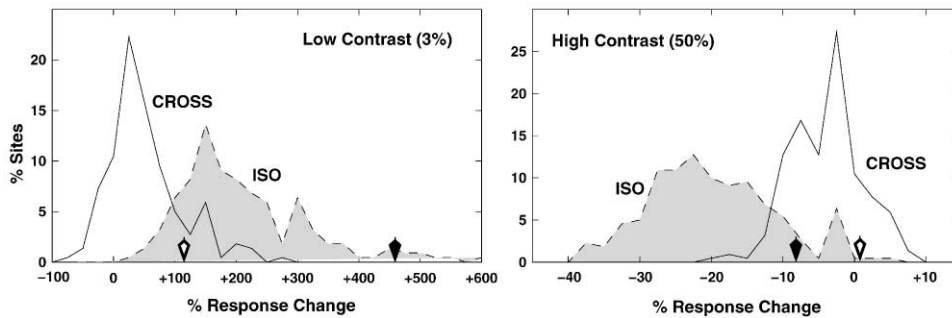


Fig. 4. Distribution of the response changes for a population of 1000 neurons (2 hypercolumns). The arrows indicate the mean response change at pinwheel centers for cross-oriented (white) and iso-oriented bipartite stimulus (black).

the stimuli presented within and outside the RF. These effects are consistent with experimental results which indicate that contextual influences are highly structured in visual space. Although the model exhibits some variability of center/surround modulations as a function of cells' positions in the orientation map, simulations show that these effects are globally homogeneous. In particular, the model does not exhibit strong boosting of the test response when center and surround are cross-oriented [12]. Our model architecture, and specifically the assumptions made concerning contrast gain control, and the existence of a unique high-threshold population of inhibitory neurons, might be too simplistic to account for a possible diversity of coexisting regimes and excitation/inhibition balances in the network. Further extensions in this direction and a more systematic exploration of the effect of neighborhood connectivity in the cortical map will aim at evaluating the potential diversity of the characteristics of center/surround modulations. Moreover, further experimental quantification of the anisotropy of the local movement of the RF location (e.g. [2]) in the cortical map may be used to feed the present model, and may conciliate apparently contradictory observations made by electrophysiologists at a time when the position of the recorded cell was ignored. Finally, preliminary results indicate that RF properties can be influenced by contextual information that was present a few tens of milliseconds earlier in its periphery. The dynamical characteristics of center/surround modulations will be explored in further studies.

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