

Title:

A Possible Mechanism of Curvature Coding in Early Vision.

Authors:

Rodrigo F. Oliveira ^a, Luciano da Fontoura Costa ^b, Antonio C. Roque ^c

^a Departamento de Psicologia e Educação, FFCLRP, Universidade de São Paulo,

Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto- SP, Brazil

phone: +55 16 6023859,

e-mail: rodrigo@neuron.ffclrp.usp.br

^b Instituto de Física de São Carlos, Universidade de São Paulo,

Av. Trabalhador São Carlense, 369, 13560-970, São Carlos- SP, Brazil

phone: +55 162 739858, FAX +55 162 71 3616,

e-mail: luciano@if.sc.usp.br

^c Departamento de Física e Matemática, FFCLRP, Universidade de São Paulo,

Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto- SP, Brazil

phone: +55 16 6023768.

e-mail: antonior@neuron.ffclrp.usp.br

Abstract:

This paper addresses the issue of curvature coding in the mammalian visual system. Considering the successful account of cortical neurons as detectors of features of visual stimuli like orientation, spatial frequency among others, we discuss the role of curvature in visual processes, review some previous investigations on curvature and present a possible biologically plausible model of curvature detection. This model requires only orientation selective neurons (simple cells) and short-range connections, both known and well documented features of the mammalian primary visual cortex. The dependence of the model on different parameters is explored and discussed.

Keywords: curvature detection; orientation selectivity; visual system; contextual effects; short-range connections.

Introduction

Neurons in the visual cortex are known as feature detectors. They typically respond to ocularity, orientation [6,7], spatial frequency [1], direction of movement [13] etc. These responses are typically thought to provide information about properties of the visual stimuli. This concept has fostered exhaustive descriptions of visual cortex neurons and their receptive field organization. The basic idea behind it is that by increasing the complexity of connections along the visual pathway a progressive complexity is achieved in the properties of the receptive fields. Besides, this increase in the complexity of the receptive fields leads to an enhancement of information compression. Hubel and Wiesel [7] also proposed that at some point this strategy could promote the occurrence of curvature tuned neurons in the visual cortex. However, this hypothesis has not received enough attention. Some evidence has been gathered to support the existence of curvature detection neurons in the visual cortex [15, 4, 17]. Yet these evidences are controversial and point to no final conclusion. Riggs [15] used curved stimuli to investigate the existence of color adaptation in cortical edge-detectors and found that this phenomenon could also be observed with curved lines. He suggested the existence of curvature detecting neurons whose properties would be orientation independent. Observing the role of curvature selectivity in natural perception, Wolfe et al. [18] proposed the existence of curvature detectors in a late stage of visual processing. Kramer and Fahle [11] have proposed an orientation-dependent dedicated system for the detection of low-curvature. Heggelund and Hohmann [5] investigated the existence of curvature selective cells in area 17 of cats and found high variability in responses of simple cells to curvature and no response at all from complex cells. Their findings did not support the existence of curvature detectors in the visual cortex. Later, electrophysiological experiments and computational modeling approaches have been carried on to investigate Hubel and Wiesel's original suggestion. They have proposed end-stopped neurons, cells

tuned not just to orientation but also to stimulus length as the basis for curvature estimation and as part of a supplementary system to reinforce orientation [4]. Versavel et al. [17] have proposed the existence of 3 distinct classes of cells related with an orientation-dependent system of curvature detection. Their class III set of cells responsive to curvature is composed of end-stopped cells.

The model presented here suggests a connection pattern that is capable of detecting low curvature in the early visual system. The biological substrates included in the model are simple cells with oriented receptive fields and short-range connections. The orientation selectivity of the model is such that it does not require the existence of curvature-dedicated cells. Instead, curvature coding is superimposed to orientation. According to this model curvature is not a global feature but is viewed as the variation in local orientation.

In the following sections we give details of the model's implementation, its results and explore its dependency on parameters. We finish with a discussion of its plausibility in terms of what is known about the mammalian visual cortex.

Model

According to our model the coding of curvature is dependent on orientation. Therefore, this section is divided into two sub-sections: Orientation and Curvature.

Orientation. The spatial structure of a simple cell's receptive field can be well described by a two-dimensional Gabor filter [8, 9, 2, 16]. This filter is the product of a Gaussian envelope and a sinusoidal function (eq.1).

$$RF(x, y) = \frac{1}{2\pi\sigma_x\sigma_y} \exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right) \cos(2\pi fx - \phi) \quad (1)$$

Here we use a 31x31 matrix to build this filter as a mask that will be convolved with the stimulation matrix (200x200). The parameters of this filter determine the spatial properties of the receptive field as follows: σ_x and σ_y correspond to its extent in the x and y directions respectively; f is the preferred spatial frequency; and ϕ determines its spatial phase or symmetry. The spatial aspect ratio has been found to vary within a limited range ($0.23 < \sigma_y/\sigma_x < 0.92$) [9]. The number of sub-regions inside the

receptive field is determined by the product $f\sigma_x$. This value varies within the ranges 1.7–6.9 for cats (weighted mean 2.75) [9] and 1.6–8.5 for monkeys (median 2.61) [3].

This filter can be centered at any point with an arbitrary orientation by a simultaneous translation and rotation (eq.2):

$$\begin{cases} x = (x - x_0) \cos \theta + (y - y_0) \sin \theta \\ y = (x - x_0) \sin \theta + (y - y_0) \cos \theta \end{cases} \quad (2)$$

Fig. 1 shows how the parameters of the Gabor function shape the activity of the neurons. Different masks were built with orientation of 90° (1A to 1D and 1I to 1L) and the resulting activity patterns are shown in (1E to 1H and 1M to 1P).

INSERT FIGURE 1.

By changing the orientation of the Gabor function, a set of 32 masks was built and convolved with the stimulation pattern (Fig. 1Q). This results in a volume (200x200x32). Each plane of this volume corresponds to the activity pattern of a population of neurons tuned to a specific orientation ranging from 0° to 180°. Though we refer to this as planes they are actually representing populations of neurons in the same cortical layer, a geniculate recipient layer.

Curvature. The pattern of connections that gives rise to the curvature detection system involves strong connections among neurons that respond to similar orientations and are assigned to the processing of adjacent areas of the visual field (they are in neighboring positions regarding retinotopy). In the model, this pattern profile is given by a Gaussian $G(\theta)$ where θ is the orientation angle. Therefore, neurons that are in near planes of the volume defined previously have stronger connections than those located in far planes, as given by (eq.3):

$$W_{i,k} = G(\theta) \langle \vec{v}_i, \vec{p}_k \rangle = G(\theta) \cos(\alpha) \quad (3)$$

where \vec{v}_i and \vec{p}_k are unit vectors representing a direction in the mask and the orientation of a plane, respectively; and $\langle \vec{v}_i, \vec{p}_k \rangle$ is the internal product between them and α is the smallest angle between them.

The mask is built for a reference plane (see Fig. 2) and is applied to all planes by a convolution with the volume defined by the orientation planes. The toroidal periodicity of the 3-d Fourier transform appropriately matches all the other orientations. After this, for each position in the volume composed by the planes, the most active cell is acting as a curvature detector. These are the cells whose activity is plotted in Fig. 3.

INSERT FIGURE 2.

Results

Since this pattern of connections mutually reinforces the activities of neighboring neurons with similar orientation-selectivity profiles, it acts as a low curvature coding mechanism whereby neurons located in regions with high curvature or very different orientations have a decrease in their activities. The same stimulus used to test orientation has been used to investigate curvature (Fig. 1Q). We have investigated the increase in the size of the receptive field (by increasing σ_x and consequently σ_x/σ_y) and also by increasing simultaneously the value of σ_x and σ_y , leaving the aspect ratio almost unchanged. By examining Fig. 3 one can see that increasing the aspect ratio does not result in great loss of precision in the curvature coding (3A and 3B). However, by increasing only σ_x this results in a direct increase in the number of sub-regions and, therefore, in an increase of the spatial frequency to which the neuron is tuned accompanied by a spreading of activity beyond the regions excited in the previous situations (Figs. 3C and 3D).

This happens because the tuning to a spatial frequency of the receptive field is determined by the product $f\sigma_x$. Figs. 3E and 3F show what happens when both f and σ_x are increased. There is a spreading of activity and a clear deterioration of the curvature detection response.

INSERT FIGURE 3.

Discussion and Conclusion

A system of curvature might show its highest activity at points of low curvature instead of high, besides its coding might be superimposed to orientation. The model presented here is capable of showing orientation-dependent curvature detection without the requirement of curvature-dedicated

cells. Many electrophysiological investigations have searched for curvature-dedicated cells and end-stopped cells have been a major research topic [5, 4, 17]. Indeed, these investigations point to the existence of cells well tuned to straight lines or with zero curvature for simple cells.

Moreover, neurons in V1 are capable of integrating information from outside of their classic receptive fields in such a way that facilitation can be shown in orientation selectivity cells when a collinear stimulation is placed along their receptive fields [10; 14].

This evidence might be re-interpreted as a particular instance of a system for curvature detection wired up in the early visual system. Curvature coding may be dependent on orientation and even superimposed to it. A possible pattern of connection responsible for such system has been proposed and it is in good agreement with reported data.

In future works, we will be exploring extensively the role of the parameters and the temporal dynamics related to curvature detection.

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Biosketch: Rodrigo Freire Oliveira was born in Salvador, BA, Brazil, where he received his B.S. in Psychology from the Universidade Federal da Bahia in 1998. He received his M.Sc. degree in Psychobiology from the University of São Paulo in Ribeirão Preto, SP, Brazil, in 2001. His research interests are computational neuroscience and connectionist modeling of psychological phenomena.

Biosketch: Luciano da F. Costa was born in São Carlos, Brazil. He received a B.Sc. degree in Electronic Engineering (University of São Paulo), a B.Sc. in Computer Science (Federal University of São Carlos, Brazil) and a Specialization in Computer Science (University of São Paulo). He also received a M.Sc. in Applied Physics (University of São Paulo) and a Ph.D degree in Electronic Engineering (King's College, University of London, 1992). He is currently an Associate Professor and researcher at the Institute of Physics, University of São Paulo at São Carlos, Brazil, and his principal interests include cybernetic vision (i.e. artificial + natural vision), shape analysis, visual inspection, pattern recognition, datamining, visual quality control, computational neuroscience, neuromorphometry, neuromorphic modeling, concurrent computer architectures, differential geometry, graphic design, neural networks, simulation and digital signal processing. Luciano was the idealizer and founder of the Cybernetic Vision Research Group (<http://cyvision.if.sc.usp.br/>) at the University of São Paulo.

Biosketch: Antonio Carlos Roque was born in São Paulo, SP, Brazil. He received his B.Sc. and M.Sc. in Physics from the State University of Campinas, Brazil, in 1985 and 1987, respectively. He received his Ph.D. in Computer Science and Artificial Intelligence from the University of Sussex, UK, in 1992. In 1993 he joined the faculty of the Department of Physics and Mathematics of the University of São Paulo at Ribeirão Preto, SP, Brazil, where he founded and is the present coordinator of the Laboratory of Neural Systems (SisNe) (<http://neuron.ffclrp.usp.br/>). His research interests are computational neuroscience and medical applications of neural networks.

Figures & Legends.

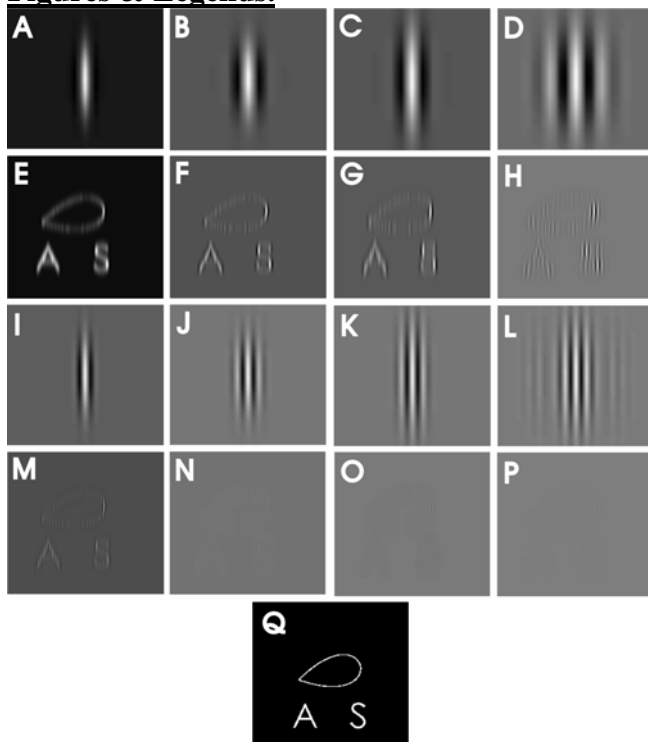


Figure 1. The role of the parameters of the Gabor filter in shaping the receptive field of a simple cell. A) The plot is a plane representing the spatial structure of the receptive field with $\sigma_x = 5, \sigma_y = 1, f = 0.2$ and $\theta = 90^\circ$; B) Same as A with $\sigma_x = 5, \sigma_y = 2$; C) $\sigma_x = 7, \sigma_y = 2$; D) $\sigma_x = 7, \sigma_y = 2$; E-H) Activity pattern that results from the convolution with the filter shown in the upper panel; I-L) Same values of $\sigma_x = 5, \sigma_y =$ used in the panels from A to D but with $f = 0.55$. M-P) Activity pattern that results from the convolution with the filter shown in the upper panel. Q) The stimulation pattern.

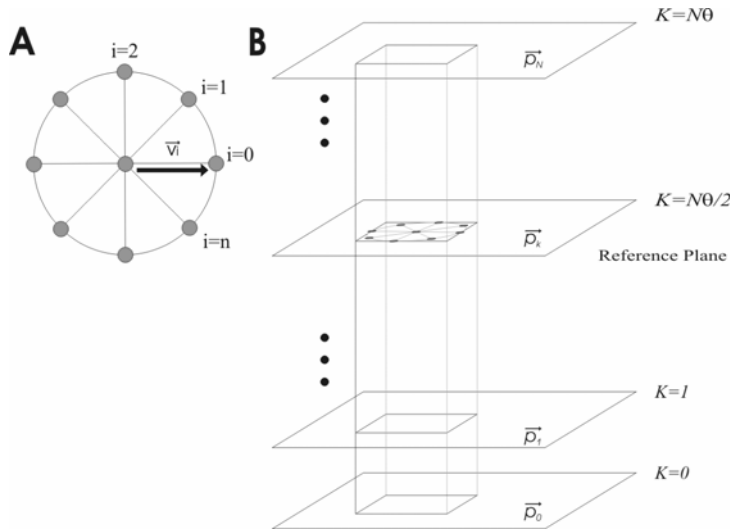


Figure 2. The mask is built using the internal product between $\left| \vec{v}_i \right|$ and $\left| \vec{p}_k \right|$ according to (eq. 3). After this, it is convolved with the volume composed by the orientation planes. The most active cell in each position is detecting not only orientation but also curvature.

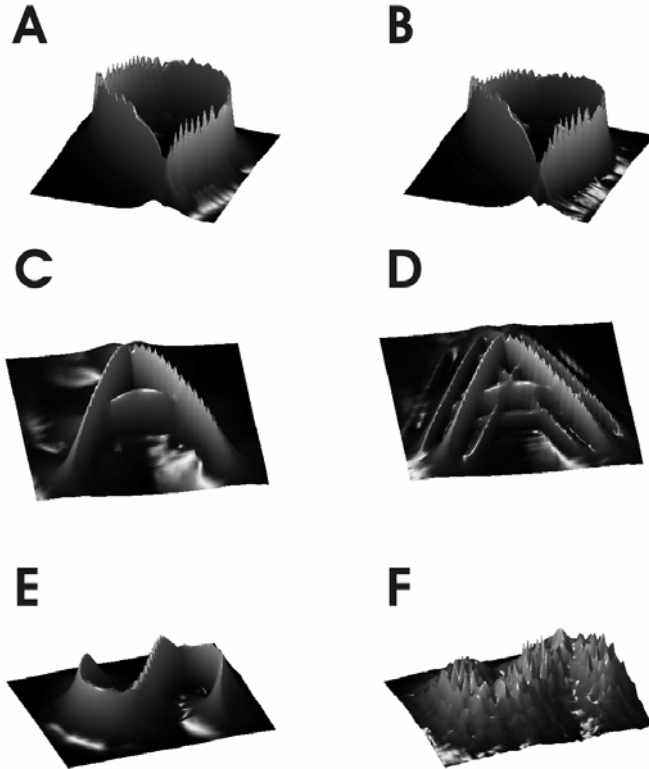


Figure 3. The curvature detection seems not to be affected by changes in the size of the oriented receptive field given that the aspect ratio is kept. In A $\sigma_x = 5, \sigma_y = 1$, and $f = 0.2$ ($\sigma_y / \sigma_x = 0.2$); while in B $\sigma_x = 7, \sigma_y = 2$, and $f = 0.2$ ($\sigma_y / \sigma_x = 0.28$). But in C and D though all the other values remain unchanged ($\sigma_x = 7$ and $f = 0.2$) the variation in σ_y (from 2 to 4) results in a large spread of activity. The panels E and F show the effect of increasing σ_y and f at the same time. Not just the spread of activity was even higher but also the curvature dependent response has been severely disturbed.