

Title:

A Possible Mechanism of Curvature Coding in Early Vision.

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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 [7, 8], 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 [6] 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 [16, 4, 5, 18, 19]. Yet these evidences are controversial and point to no final conclusion. Riggs [16] 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. [19] proposed the existence of curvature detectors in a late stage of visual processing. Kramer and Fahle [12] have proposed an orientation-dependent dedicated system for the detection of low-curvature. Heggelund and Hohmann [6] 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. Versavel et al. [18] 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 high

curvature is composed of end-stopped neurons, cells tuned not just to orientation but also to stimulus length. Dobbins et al. [4] have used a combined approach with electrophysiological experiments and computational modeling to investigate Hubel and Wiesel's original suggestion. They have also proposed end-stopped neurons as the basis for curvature estimation and as part of a supplementary system to reinforce orientation [4, 5]. This model proposes that the difference in response of two simple cells with different receptive field sizes (probably located in different cortical layers) converge upon an endstopping cell and varies in proportion to curvature (deviation from straightness) [4, 5]. On the other hand, the model presented here suggests a connection pattern that is capable of detecting low curvature in a geniculate recipient layer (probably layer 4). The circuitry of the model is such that it does not require the existence of curvature-dedicated cells (i.e. endstopped cells). Instead, curvature coding is superimposed to orientation. The biological substrates included in the model are simple cells with oriented receptive fields and short-range connections. 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 [2, 9, 10, 14, 17]. 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 ($0.23 < \sigma_y/\sigma_x < 0.92$) [10]. The number of sub-regions inside the receptive field is determined by the product $f\sigma_x$. This value varies within the ranges 0.5-2.5 for cats [10] and 0.4-2.6 for monkeys [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 0° (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 – differing only in orientation - 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 out of all neurons at the same position tuned to different orientations 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 don't have their activities reinforced. 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 simultaneously the value of σ_x and σ_y , leaving the aspect ratio (σ_y/σ_x) and the bandwidth ($f\sigma_x$) unchanged. By examining Fig. 3 one can see that increasing the size of the receptive field it results in an enhancement of the curvature coding (3A and 3B). However, by increasing only the bandwidth ($f\sigma_x$) it 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 and a clear deterioration of the curvature detection response (Figs. 3C and 3D).

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 [4, 5, 6, 18]. 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 [11; 15]. 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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References

- [1] F.W. Campbell, G.F. Cooper and C. Enroth-Cugell, The spatial selectivity of the visual cells of the cat. J. of Physiology – London, 203 (1969) 223-235.
- [2] P. Dayan and L.F. Abbott, Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems (The MIT Press, Massachusetts, 2001).

- [3] R. L. DeValois, D. G. Albrecht, and L. G. Thorell, Spatial frequency selectivity of cells in macaque visual cortex, *Vision Research*, 22 (1982) 545–559.
- [4] A. Dobbins, S. W. Zucker, M. S. Cynader, Endstopped Neurons in the Visual Cortex as a Substrate for calculating Curvature, *Nature*, 329 (1987) 438-441.
- [5] A. Dobbins, S. W. Zucker, M. S. Cynader, Endstopping and Curvature, *Vision Research*, 29 (1989) 1371-1387.
- [6] P. Heggelund and A. Hohmann, Responses of striate cortical cells to moving edges of different curvatures. *Exp. Brain Research* 23 (1975) 211-216.
- [7] D. H. Hubel and T N. Wiesel, Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Physiology*, 160 (1962)106 - 154.
- [8] D. H. Hubel and T N. Wiesel, Functional architecture of macaque monkey visual cortex (Ferrier Lecture). *Proc. of the R. S. of London B*,198 (1977)1-59.
- [9] J. P. Jones and L. A. Palmer, An evaluation of the two-dimensional gabor filter model of simple receptive-fields in cat striate cortex. *J. of Neurophysiology* 58 (1987) 1233-1258.
- [10] J. P. Jones and L. A. Palmer, The two-dimensional spatial structure of simple receptive-fields in cat striate cortex. *J. of Neurophysiology* 58 (1987) 1187-1211.
- [11] M. K. Kapadia, M. Ito, C. D. Gilbert, G. Westheimer, Improvement in visual sensitivity by changes in local context - parallel studies in human observers and in v1 of alert monkeys. *Neuron*. 15 (1995) 843-856.
- [12] D. Kramer, M. Fahle, A simple mechanism for detecting low curvatures. *Vis. Research*, 36 (1996) 1411-1419.
- [13] G.A. Orban, *Neuronal operations in the visual cortex* (Springer, Berlin, 1984)
- [14] N. Petkov, P. Kruizinga, Computational models of visual neurons specialized in the detection of periodic and aperiodic oriented visual stimuli: bar and grating cells, *Bio. Cybernetics*, 76 (1997) 83-96.

- [15] U. Polat, A.M. Norcia, K. Mizobe, T. Kasamatsu, From neuron to perception: The role of long-range interactions in grouping collinear textures. *Investigative ophthalmology & visual science*, 37 (1996) 2189-2189.
- [16] L. A. Riggs, Curvature as a feature of pattern vision. *Science*, 181 (1973) 1070-1072.
- [17] D.L. Ringach Spatial structure and symmetry of simple-cell receptive fields in macaque primary visual cortex. *J. of Neurophysiology* 88 (2002) 455-463.
- [18] M. Versavel, G.A. Orban, L. Lagae, Responses of visual cortical neurons to curved stimuli and chevrons. *Vision Research* 30 (1990) 235-248.
- [19] J. M. Wolfe, A. Yee, S. R. Friedman-Hill, Curvature is a basic feature for visual search tasks. *Perception*, 21 (1992) 465-480.

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Figures & Legends.

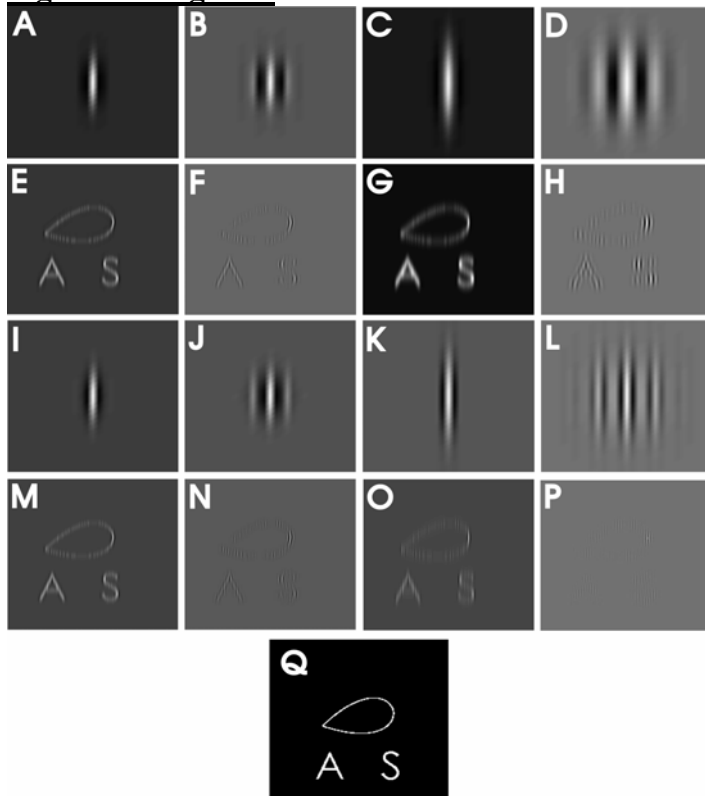


Figure 1. The role of the parameters of the Gabor filter in shaping the receptive field of a simple cell. A) The plot is a plane representing the spatial structure of the receptive field with $\sigma_x = 3, \sigma_y = 1, f = 0.33$ and $\theta = 0^\circ$; B) Same as A with $\sigma_x = 3, \sigma_y = 2$; C) $\sigma_x = 5, \sigma_y = 1, f = 0.2$; D) $\sigma_x = 5, \sigma_y = 4, f = 0.2$; E-H) Activity patterns that result from the convolution with the filters shown in the upper panel; I-L) Same values of σ_x and σ_y used in the panels from A to D but with $f = 0.66$ for I-J and $f = 0.4$ for K-L. M-P) Activity patterns that result from the convolution with the filters shown in the upper panel. Q) The stimulation pattern (A “loop”, an “A” and a “S”).

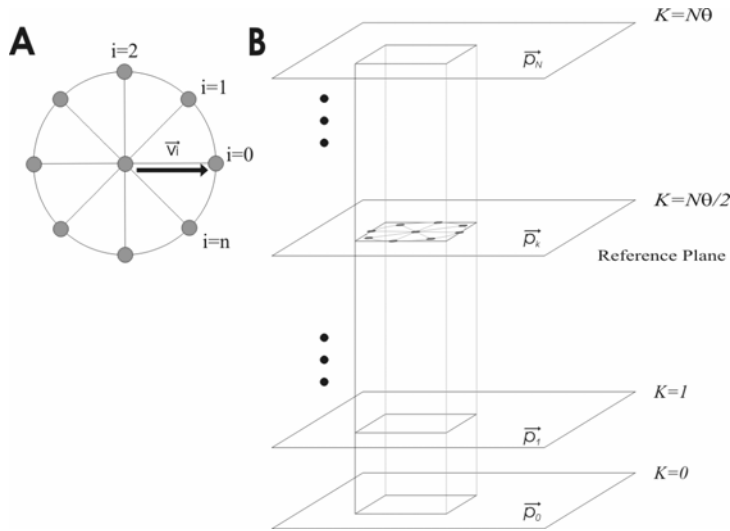


Figure 2. The mask is built using the internal product between $\left| \vec{v}_i \right|$ and $\left| \vec{p}_k \right|$ according to (eq. 3). After this, it is convolved with the volume composed by the orientation planes. The most active cell in each position is detecting not only orientation but also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

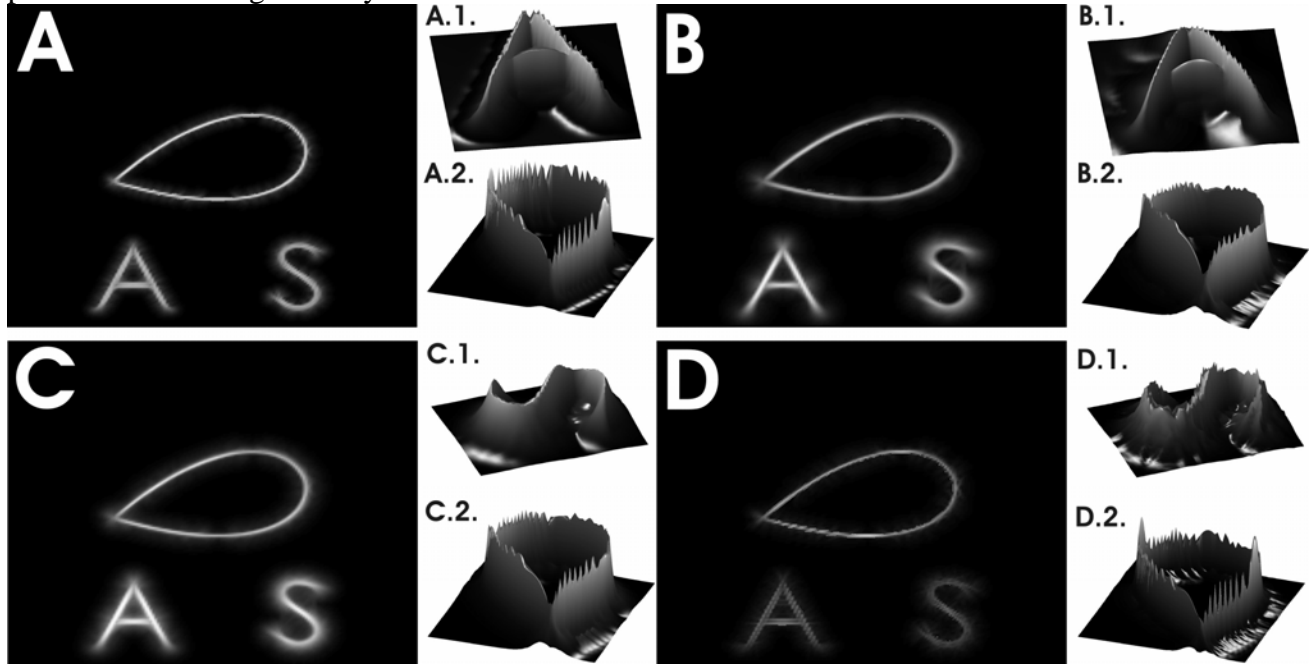


Figure 3. The curvature detection seems not to be too much affected by changes in the size of the oriented receptive field given that the aspect ratio and bandwidth are kept unchanged. In A $\sigma_x = 3, \sigma_y = 1$, and $f = 0.3$ ($\sigma_y / \sigma_x = 0.33; f\sigma_x = 1.0$); while in B $\sigma_x = 6, \sigma_y = 2$, and $f = 0.16$ ($\sigma_y / \sigma_x = 0.33; f\sigma_x = 1.0$). A.1-2 and B.1-2) Surface plots showing in detail the response to parts of the stimulation pattern (“A” and “loop”). C and D) Though all the other values remain unchanged ($\sigma_x = 5, \sigma_y = 1$) the variation in the bandwidth $f\sigma_x$ (from 1 to 2) results in a spread of activity and in a spread of activity and in the deterioration of the curvature dependent response. C.1-2 and D.1-2) Surface plots showing in detail the response to parts of the stimulation pattern (“S” and “loop”).