Framework for testing biological utility hypotheses

Nicolai Petkov

Institute for Mathematics and Computing Science,
University of Groningen, PO Box 800, 9700 AV Groningen, The Netherlands
petkov@cs.rug.nl

Introduction

Various aspects of the visual system have been hypothesized to have a certain biological role. The usual argument is that a given neural mechanism would help an animal to perform better a certain task. Such hypotheses are typically not verified by quantitative measurements and statistical studies and remain speculative. For instance, non-classical receptive field (non-CRF) inhibition (Fig. 1) has been hypothesized to have as probable biological utility the detection of texture boundaries [2] and object contours [3].

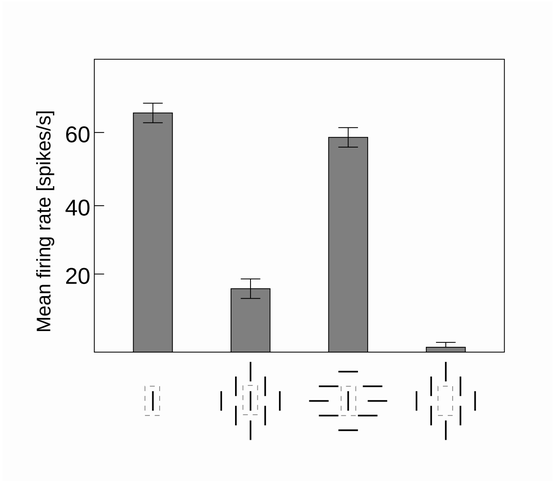


Figure 1: *Responses of a V1 visual neuron to various stimuli (from left to right): a single bar of optimal orientation inside the CRF (delineated by a dotted rectangle), an optimal bar stimulus in the CRF surrounded by other bars of the same orientation outside the CRF, an optimal bar in the CRF surrounded by bars of orthogonal orientation, no stimulus in the CRF (re-drawn from [2]). Surround stimuli of the same orientation as the CRF stimulus have a stronger suppression effect than stimuli of other orientations; 24% of the cells exhibit this type of* anisotropic inhibition*.*

Framework definition

The proposed computational framework for verification of biological utility hypotheses includes the following steps:

1. define a hypothesis for the biological utility of a given neural mechanism,
2. create a computational model of the concerned subsystem, in which the mechanism under investigation can be either included or excluded,
3. define a measure that quantifies the performance of the subsystem in a task related to the hypothesized biological utility,
4. collect statistics on a reasonable number of stimuli (natural images) about the performance improvement/degradation obtained by taking vs. not taking into account the concerned mechanism in the computational model,
5. confirm or reject the hypothesis using the distribution of the performance improvement/degradation values.

A similar approach was previously deployed for the comparison of biologically motivated contour detection algorithms in a computer science context [1].

Step1: Define hypothesis

The biological utility of non-CRF inhibition includes the *improved detection of object contours*.

Step2: Create computational model

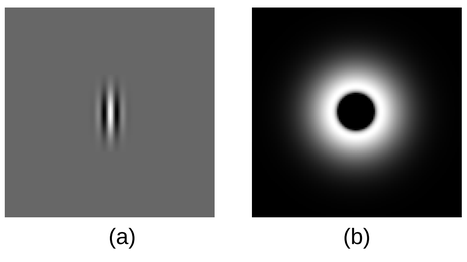
Simple cell

A simple cell CRF is modelled by a Gabor function (Fig. 2a):

$$g_{\lambda,\sigma,\theta,\varphi}(x,y) = e^{-\frac{\tilde{x}^2+\gamma^2\tilde{y}^2}{2\sigma^2}}\cos(2\pi\frac{\tilde{x}}{\lambda}+\varphi)$$
$$\tilde{x} = x\cos\theta + y\sin\theta, \qquad \tilde{y} = -x\sin\theta + y\cos\theta,$$

where γ is the spatial aspect ratio, σ determines the size of the receptive field, λ is the preferred wavelength, θ is the preferred orientation, and φ determines the symmetry.
The response of a simple cell CRF to a stimulus $f(x,y)$ is computed by convolution, i.e. summation of $f(x,y)$ over the CRF, weighted by $g_{\lambda,\sigma,\theta,\varphi}(x,y)$:

$$r_{\lambda,\sigma,\theta,\varphi}(x,y) = (f * g_{\lambda,\sigma,\theta,\varphi})(x,y) \ .$$



(a) (b)

Figure 2: *Intensity maps of (a) a Gabor function $g_{\lambda,\sigma,\theta,\varphi}(x,y)$ modelling a CRF and (b) a weighting function $w_\sigma(x,y)$ modelling the inhibition surround of that CRF.*

Complex cell

The model response of a complex cell is computed from the responses of a pair of simple cells with a phase difference of $\frac{\pi}{2}$:

$$E_{\lambda,\sigma,\theta}(x,y) = \sqrt{r^2_{\lambda,\sigma,\theta,0}(x,y) + r^2_{\lambda,\sigma,\theta,-\frac{\pi}{2}}(x,y)} \ .$$

Non-CRF inhibition

A weighting function $w_\sigma(x,y)$ is defined [3] on an annular surround of the CRF (Fig. 2b),

$$w_\sigma(x,y) = \frac{1}{||H(\mathrm{DoG}_\sigma)||_1} H(\mathrm{DoG}_\sigma(x,y)) \ ,$$
$$H(z) = \begin{cases} 0 & z < 0 \\ z & z \geq 0 \ , \end{cases}$$
$$\mathrm{DoG}_\sigma(x,y) = \frac{1}{2\pi(4\sigma)^2} e^{-\frac{x^2+y^2}{2(4\sigma)^2}} - \frac{1}{2\pi\sigma^2} e^{-\frac{x^2+y^2}{2\sigma^2}} \ ,$$

and an inhibition term is computed by weighted summation (over the annular surround) of the responses of complex cells with a given preferred orientation θ, wavelength λ and CRF size σ:

$$t^A_{\lambda,\sigma,\theta}(x,y) = (E_{\lambda,\sigma,\theta} * w_\sigma)(x,y) \ .$$

The response of a complex cell with anisotropic surround inhibition is computed as the half-wave rectified difference of the response of that cell to the stimulus in the CRF $E_{\lambda,\sigma,\theta}(x,y)$ and the inhibition term $t^A_{\lambda,\sigma,\theta}(x,y)$:

$$\tilde{b}^{A,\alpha}_{\lambda,\sigma,\theta_i}(x,y) = H(E_{\lambda,\sigma,\theta}(x,y) - \alpha t^A_{\lambda,\sigma,\theta}(x,y)) \ .$$

The factor α controls the strength of inhibition.

Binarization

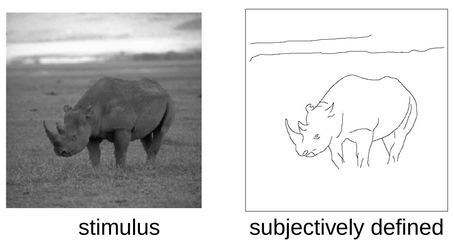
The outputs of the operators for different orientations are superimposed and binarized using non-maxima suppression and hysteresis thresholding (see [1] for details). Typical results are shown in Fig.3.

stimulus CRF responses surround inhibited responses

Figure 3: *(left) Natural image stimulus. Responses of two computational models: (middle) one that does not and (right) another that does include non-CRF inhibition. The operators are available on-line at www.cs.rug.nl/~petkov.*

Step3: Define performance measure

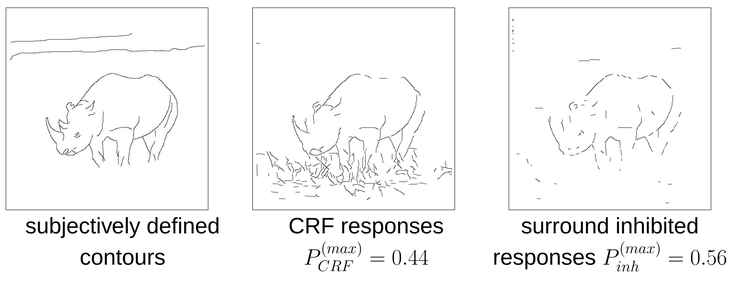
Definition of desired output



stimulus subjectively defined contours

Figure 4: *(left) Natural image stimulus and (right) a corresponding subjectively defined desired output of a contour detection subsystem [1]. A database of such image pairs is available at www.cs.rug.nl/~petkov.*

Comparison of computed and desired output



subjectively defined contours | CRF responses $P^{(max)}_{CRF} = 0.44$ | surround inhibited responses $P^{(max)}_{inh} = 0.56$

Figure 5: *(left) A subjectively defined contour map is compared with (middle and right) the computed contour maps. The degree of coincidence of a computed map with the desired output is quantified by the measure P. The relative performance improvement achieved by the inclusion of non-CRF inhibition is $I = \frac{P^{(max)}_{CRF} - P^{(max)}_{inh}}{P^{(max)}_{CRF}} = \frac{0.56-0.44}{0.44} = 0.27$.*

The performance measure is defined as follows [1]:

$$P = \frac{\mathrm{card}(E)}{\mathrm{card}(E) + \mathrm{card}(E_{\mathrm{FP}}) + \mathrm{card}(E_{\mathrm{FN}})} \ ,$$

where $\mathrm{card}(E)$, $\mathrm{card}(E_{\mathrm{FP}})$ and $\mathrm{card}(E_{\mathrm{FN}})$ are the numbers of points where the computed output correctly indicates, falsely indicates and fails to indicate, respectively, the presence of a contour that is defined in the desired output map. The relative performance improvement/degradation I due to the inclusion of non-CRF inhibition in the model is defined as follows (Fig.6):

$$I = \frac{P^{(max)}_{CRF} - P^{(max)}_{inh}}{P^{(max)}_{CRF}} \ ,$$

where $P^{(max)}$ is the maximum performance value for a given method obtained using an optimal threshold for binarization.

Step 4: Collect statistics

Image database

A sample of 40 natural images (see www.cs.rug.nl/~petkov).

Results

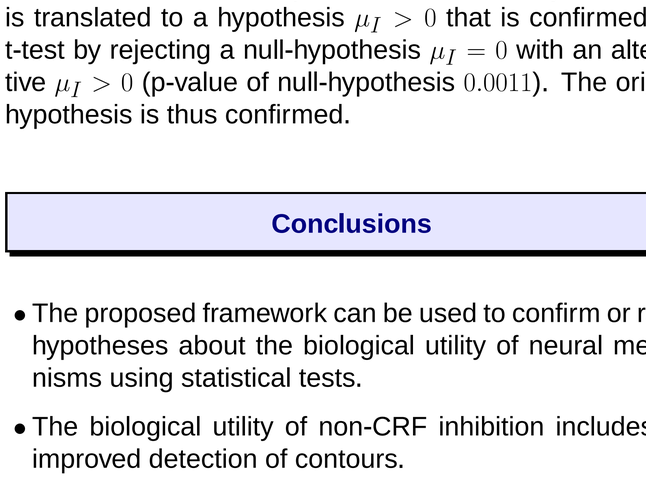


Figure 6: *Box plot of the relative performance improvement due to non-CRF inhibition. Sample size n = 40, $\mu_I = 0.18, \sigma_I = 0.34, P(I > 0) = 0.70, P(\mu_I > 0) = 0.9996$.*

Step 5: Confirm/reject hypothesis

The original hypothesis that the biological utility of non-CRF inhibition includes the improved detection of object contours is translated to a hypothesis $\mu_I > 0$ that is confirmed in a t-test by rejecting a null-hypothesis $\mu_I = 0$ with an alternative $\mu_I > 0$ (p-value of null-hypothesis 0.0011). The original hypothesis is thus confirmed.

Conclusions

- The proposed framework can be used to confirm or reject hypotheses about the biological utility of neural mechanisms using statistical tests.
- The biological utility of non-CRF inhibition includes the improved detection of contours.

References

[1] C. Grigorescu, N. Petkov, and M. A. Westenberg. Contour detection based on nonclassical receptive field inhibition. *IEEE Trans. Image Processing*, 12(7):729–739, 2003.

[2] H. C. Nothdurft, J. L. Gallant, and D. C. van Essen. Response modulation by texture surround in primate area V1: Correlates of "popout" under anesthesia. *Vis. Neurosci.*, 16:15–34, 1999.

[3] N. Petkov and M. A. Westenberg. Suppression of contour perception by band-limited noise and its relation to non-classical receptive field inhibition. *Biological Cybernetics*, 88(3):236–246, 2003.