SIMULATION OF TILT AFTEREFFECT OF VISUAL CELLS IN THE PRIMARY VISUAL CORTEX

M. Ursino, G.E. La Cara, C. Saporetti, E. Magosso

Department of Electronics, Computer Science and Systems, Bologna, Italy

mursino@deis.unibo.it

Abstract: Cells in the primary visual cortex exhibit adaptation to a prolonged stimulus. A typical example of adaptation is the "tilt aftereffect": prolonged viewing of a grating makes a subsequently viewed grating to be perceived as tilted away from the adapting grating. In this work alternative hypotheses on adaptation are tested using two mathematical models of cells in the visual cortex (named the antiphase and in-phase model) developed by the authors recently [10]. The hypotheses assume that adaptation is caused by an increased threshold of neurons during a prolonged stimulus, or by an increase in the strength of inhibitory synapses, or by a decrease in the strength of excitatory synapses. Results show that the in-phase model is able to account for tilt aftereffect, and the associate increase in the minimum perceived contrast of a grating, quite well assuming a change in threshold or in the inhibitory synapses. Changes in excitatory synapses are inadequate. By contrast, the antiphase model produces results compatible with experimental data only in case of an increased threshold. Analysis of results may provide indications to test alternative models of cortical visual cells, and to reach deeper insight into the mechanisms of adaptation in the primary visual cortex.

Introduction

Simple cells in the primary visual cortex of most carnivores and primates respond preferentially to elongated stimuli of a particular orientation [1]. Accordingly, the minimal functional unit of the primary visual cortex is the "hypercolumn": this consists in a set of cells which respond to a stimulus located in the same position of the retina, but with all possible orientations. When a grating or bar is applied at a specific point in the retina, cells in that hypercolumn exhibit a well-defined pattern of activity: activity is maximum for the cell with the same orientation preference as the applied stimulus and progressively decreases for cells with distant orientation. This sensitivity to orientation, however, exhibits a strong phenomenon of adaptation. A typical example of adaptation is named the "tilt aftereffect": prolonged viewing of a grating makes a subsequently viewed grating of similar orientation to appear tilted away from the adapting grating [2-4]. Various hypotheses and alternative mechanisms have been proposed in past years, to explain this phenomenon. Some authors proposed that tilt aftereffect is caused by an increased threshold of neurons during adaptation; others assume that adaptation involves an increase in the strength of inhibitory synapses to the adapting neurons, or a decrease of excitatory synapses [5-7]. The problem is further complicated by the existence of different possible arrangement of intracortical synapses [1]. While it is generally accepted that neurons in the hypercolumn receive excitatory synapses from neurons with similar orientation preference and same polarity (i.e., ON neurons, excited by light, receive excitation by other ON neurons, whereas OFF neurons, excited by darkness, receive excitation by other OFF neurons), the arrangement of intracortical inhibition is still the subject of dispute [1]. Both inhibition with similar phase (ON vs. ON, OFF vs. OFF) or with opposite phase (ON vs. OFF, OFF vs. ON) have been hypothesized [8-10].

Aim of this work is to test the previous hypotheses using two alternative mathematical models of a single hypercolumn (named the in-phase model and anti-phase model) developed by the authors in recent years [10]. Using these models, we will try to simulate tilt aftereffect by ascribing this phenomenon either to an increased threshold of neurons, or to an increased intracortical inhibition or to decreased intracortical excitation. For each hypothesis, the main consequences on neural response (hence, on perception) are examined (amount of deviation from the correct grating, decrease in minimum perceived contrast).

Materials and Methods

Two different mathematical models have been used in this work. Each model includes the thalamic input to a simple cell, feedforward inhibition coming from cortical inhibitory interneurons, and intracortical excitation. The two models differ as to the disposition of feedforward inhibition. In the models the output of the neurons is represented as a continuous quantity describing the firing rate. Both models consider the architecture of a single hypercolumn, composed of 180 excitatory neurons and 45 inhibitory interneurons. Each neuron is parameterized by its preferred orientation, identified by the angle ϑ: two adjacent excitatory neurons differ in their preferred orientation by just 1°, while inhibitory interneurons differ by 4°. The ratio between the number of excitatory cells and inhibitory interneurons (180/45 = 4) agrees with the literature [8,

ISSN: 1727-1983

9]. The angle ϑ determines the preferred orientation for each neuron.

The activity of neurons in an hypercolumn, in response to a grating with given orientation, is the result of the following contributions: i) a description of the receptive fields of thalamic cells, including both ON-center and OFF-center cells. ii) a description of the receptive fields of simple cells in the cortex. This is constructed using afferent inputs from 15 thalamic cells, oriented along the preferred orientation of the cell and sampled by means of a Gabor function; iii) the presence of excitatory connections between simple cells; iv) the presence of inhibitory connections between interneurons in the visual cortex and the simple cells. In the in-phase model inhibition has the same phase as excitation, but a wider orientation tuning. In the anti-phase model, inhibition has opposite polarity than excitation (OFF vs. ON) and similar orientation tuning. Details on the models, with equations and parameter numerical values can be found in our previous paper [10].

In order to simulate adaptation, we assumed that the subject observes a grating with an orientation slightly modified compared with the vertical one (in the following 80°). This is named the "adaptation phase" of the experiment. Adaptation implies that all neurons stimulated by this grating modify the adaptation parameter (either the threshold, the inhibitory synapses or the excitatory synapses) according to their level of activity. Since, as shown in Ursino and La Cara [10], the width of the orientation tuning curve is ±40°, with an half width at half height as great as 20-25°, we assumed that adaptation modifies the parameter with the following law:

i) change in excitatory synapses which target to a neuron with optimal orientation ϑ (see Eq. 15 in paper [10])

$$\Delta a(\vartheta) = \Delta a_0 \cdot exp\left(-(\vartheta - \vartheta_0)^2 / (2\sigma^2)\right) \qquad (1)$$

ii) change in inhibitory synapses which target to a neuron with optimal orientation ϑ (see Eq. 16 in paper [10])

$$\Delta c(\vartheta) = \Delta c_0 \cdot exp\left(-(\vartheta - \vartheta_0)^2 / (2\sigma^2)\right) \qquad (2)$$

iii) change in threshold for a neuron with optimal orientation ϑ (see Eq. 11 in paper [10])

$$\Delta v(\vartheta) = \Delta v_0 \cdot exp\left(-(\vartheta - \vartheta_0)^2 / (2\sigma^2)\right) \qquad (3)$$

where ϑ_0 is the orientation of the grating used during the adaptation phase, and σ is a standard deviation. In this paper we used $\vartheta_0 = 80°$ and $\sigma = 20°$.

Eqs. 1-3 mean that the neuron which signals the orientation ϑ_0 exhibits maximal adaptation; adaptation progressively decreases for proximal neurons in the hypercolumn, and falls to zero (i.e., neurons exhibit no adaptation) for an orientation difference of $\pm 2\sigma$.

In the following we will refer to three parameters to quantify adaptation: $\Delta v_0 \geq 0$ (maximal change in threshold); $\Delta a_0 \leq 0$ (maximal change of excitatory synapses); $\Delta c_0 \geq 0$ (maximal change of inhibitory synapses).

Results

Simulations have been performed by separately testing the effect of the three adjustments delineated above, i.e., that aftereffect is due to: i) a decrease in the strength of excitatory synapses (Eq. 1); ii) an increase in the strength of inhibitory synapses (Eq. 2); iii) an increase in the activation threshold (Eq. 3); These hypotheses have been tested for each of the two models, with antiphase and in-phase synapses.

Fig. 1 shows how the orientation tuning curve, obtained in response to presentation of a vertical grating (orientation 90°) changes as a consequence of the adaptation in the threshold (in-phase model). Two main effects can be observed: a progressive decrease in the maximal response of neurons, consequence of the adaptation, and a shift of the position of the optimal response with respect to 90°. The applied grating, which before adaptation produces maximal activation at the neuron with optimal orientation 90°, causes maximal activity at about 95° and 100° after small and severe adaptation, respectively.

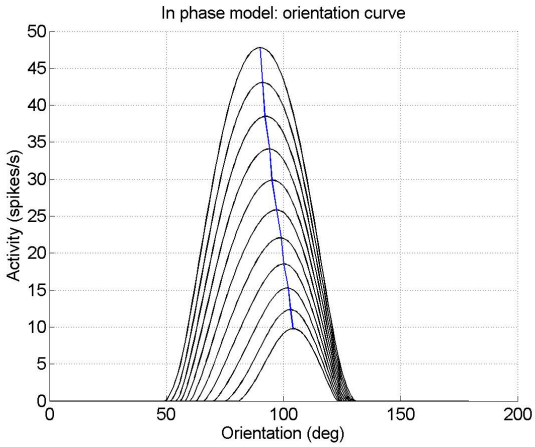


Figure 1: Orientation curve obtained in response to a vertical grating (orientation 90°) in basal conditions, and after different levels of adaptation to a grating with 80° orientation. Simulations have been obtained with the in-phase model, by assuming different increasing changes in the threshold (Eq. 3 in the text). The curve represents the activity of all neurons in the hypercolumn. It is worth noting that, after adaptation, the maximum of the curve shifts to the right (blue line), i.e., a vertical grating is perceived as a grating rotated clockwise.

ISSN: 1727-1983

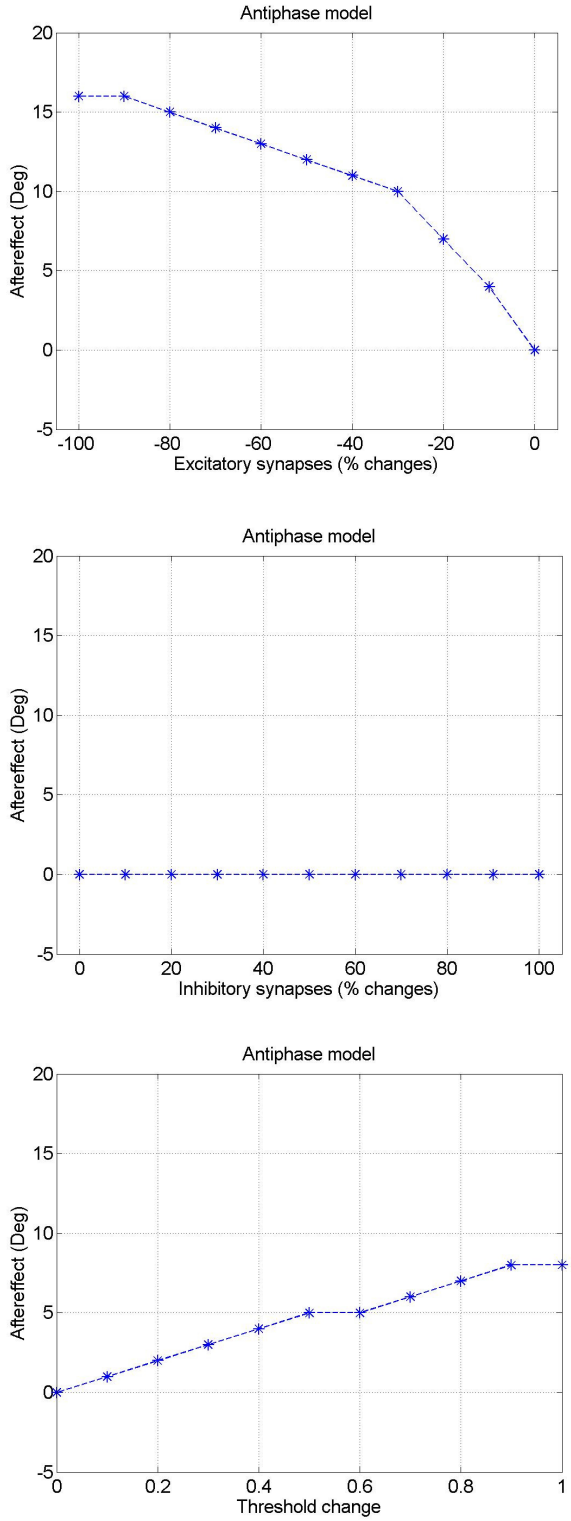


Figure 2: Changes in the perceived orientation (aftereffect) evaluated with the antiphase model by assuming a change in excitatory synapses (Eq. 1, upper panel) a change in inhibitory synapses (Eq. 2, middle panel) and a change in the threshold for neuron activation (Eq. 3, bottom panel).

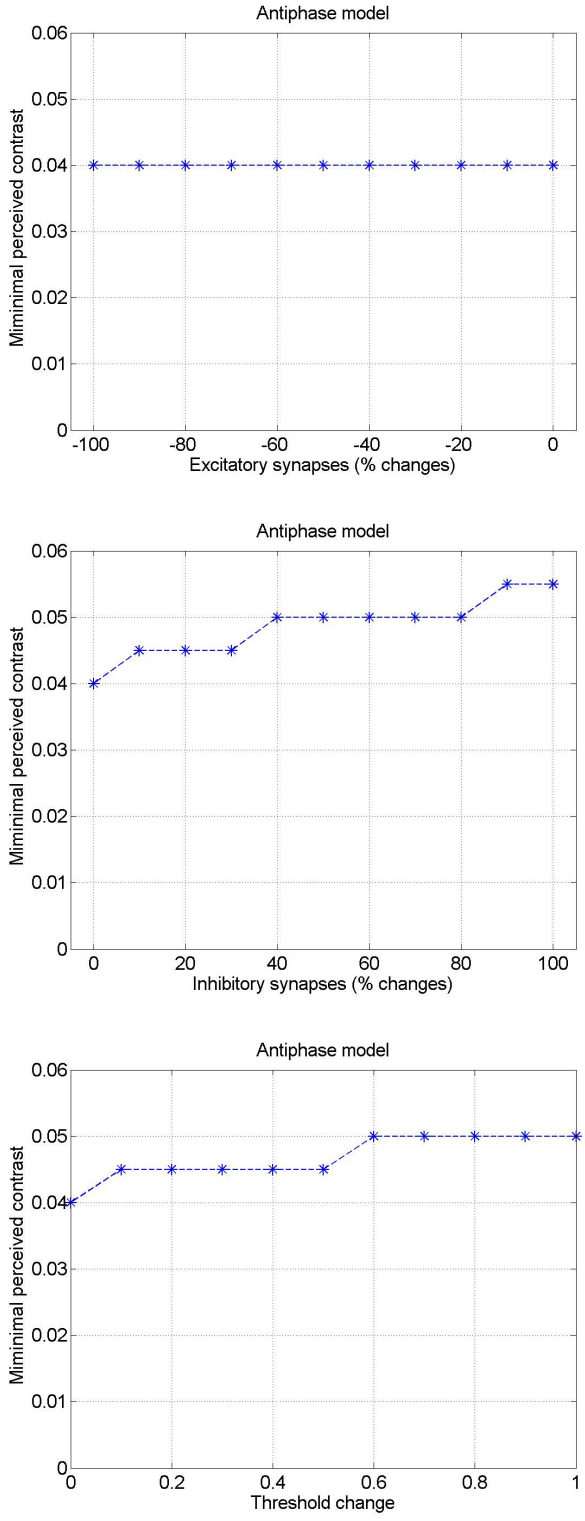
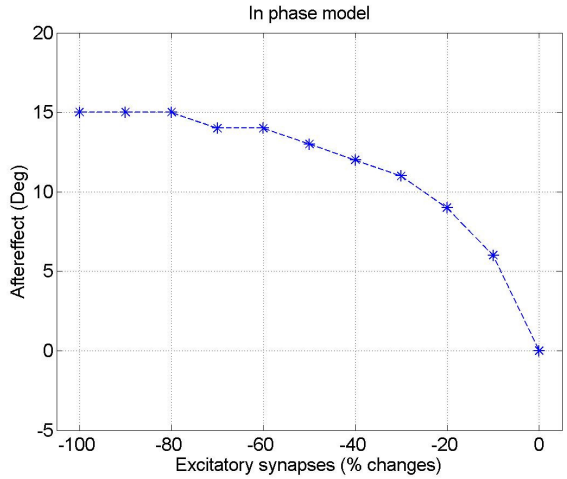
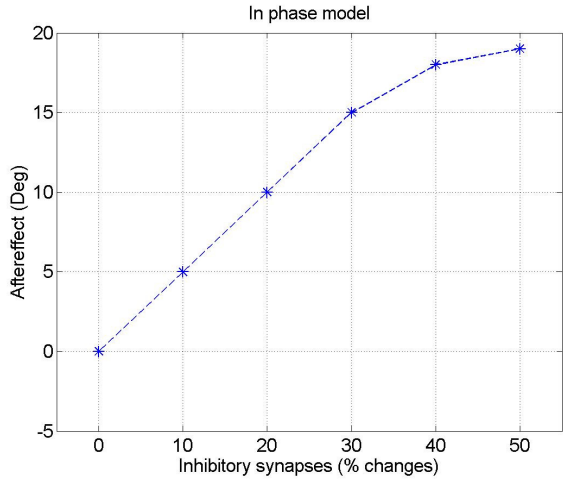


Figure 3: Changes in the minimal perceived contrast evaluated with the antiphase model by assuming a change in excitatory synapses (Eq. 1, upper panel) a change in inhibitory synapses (Eq. 2, middle panel) and a change in the threshold for neuron activation (Eq. 3, bottom panel).

ISSN: 1727-1983





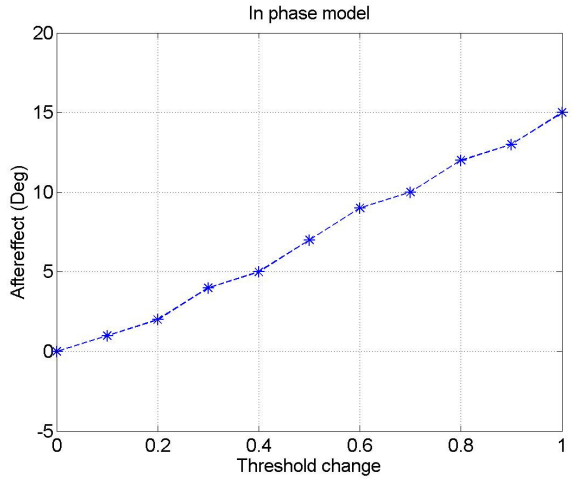
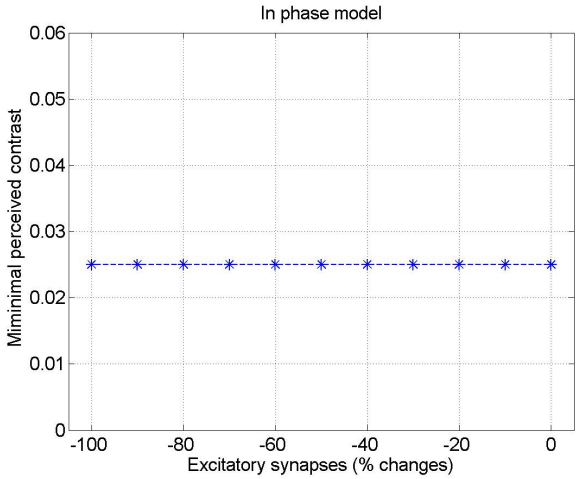
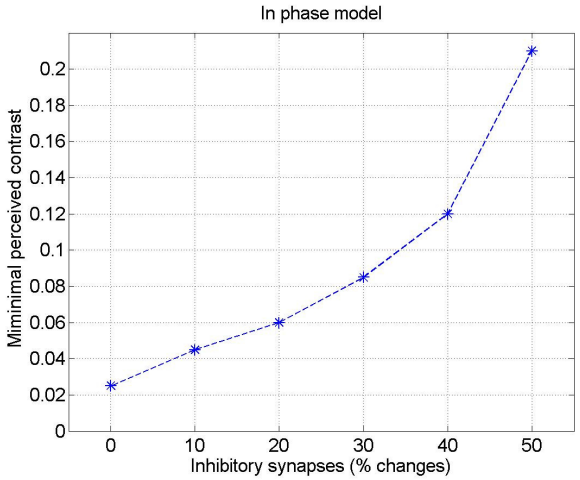


Figure 4: Changes in the perceived orientation (aftereffect) evaluated with the in-phase model by assuming a change in excitatory synapses (Eq. 1, upper panel) a change in inhibitory synapses (Eq. 2, middle panel) and a change in the threshold for neuron activation (Eq. 3, bottom panel).





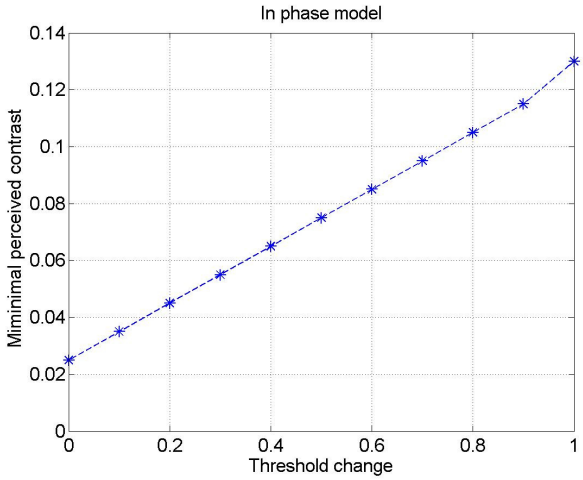


Figure 5: Changes in the minimal perceived contrast evaluated with the in-phase model by assuming a change in excitatory synapses (Eq. 1, upper panel) a change in inhibitory synapses (Eq. 2, middle panel) and a change in the threshold for neuron activation (Eq. 3, bottom panel).

ISSN: 1727-1983

The aftereffect (i.e., the shift in the position of the maximal response compared with the "true" one) is summarized in Figs. 2 (antiphase model) and 4 (in-phase model), as a function of the modified parameter, for the three simulations performed separately. The change in threshold is shown as its absolute value (the normal threshold was 0.2). By contrast, since the values of synapses are strongly different in the in-phase and antiphase models, their changes are expressed as percentage of the normal value.

Since adaptation reduces the response of neurons to a grating, a phenomenon strictly associated with it is a decrease in detection sensitivity [11]. This means that the minimal contrast for detecting gratings increases with adaptation. In order to test this aspect, we simulated the activity of all neurons in the hypercolumn, in response to a vertical grating, with different values of contrast, in order to detect the minimal contrast which evokes a positive response. These simulations were performed in basal condition (i.e., in the absence of adaptation) and after various levels of adaptation. Figs. 3 (antiphase model) and 5 (in-phase model) show how the minimal perceived contrast changes as a function of the modified parameter, for the three simulations performed separately.

Figs. 2 and 3 show that the antiphase model is able to produce values of aftereffect in the range reported in the literature (between 3 and 10 deg, see [2-4, 11]) after a moderate change in excitatory synapses and in neuron threshold. By contrast, a change in inhibitory synapses does not induce appreciable aftereffect in this model. Concerning the change in the minimum perceived contrast, a change in excitatory synapses in this model does not have any effect. Changing inhibitory synapses and neuron threshold produces just a moderate increase in the minimum perceived contrast, from 4% to 5-6%.

Figs. 4 and 5 show that the in-phase model is able to produce reliable values of aftereffect by changing each parameter in the model (both excitatory and inhibitory synapses as well as threshold). However, a change in excitatory synapses has no effect in the minimal perceived contrast. The minimum perceived contrast increases significantly after a change in inhibitory synapses and threshold.

Discussion

Adaptation to a prolonged grating is a well-known phenomenon, which has detectable experimental consequences: among the others, tilt aftereffect, and a reduced contrast sensitivity. Alternative mechanisms may be responsible for adaptation in the cortex [5, 6, 7]. First, a neuron may show a fatigue after prolonged activity, i.e., it requires greater positive input to be excited. This phenomenon may be easily simulated by increasing the threshold of the neuron. Alternatively, adaptation may involve synaptic plasticity within the cortex, either a decrease in excitatory synapses or an increase in the inhibitory ones. Furthermore, different arrangements of synapses can be postulated within the cortex [1].

Aim of this work was to analyze, by means of mathematical models and computer simulations, whether detectable changes in behaviour (which can be investigated via psychophysical experiments) may occur assuming different kinds of adaptation, and/or different synaptic arrangements.

The obtained results (Figs. 2-5) underline the existence of profound differences in the tilt aftereffect and in detection sensitivity, depending on the arrangement of intracortical synapses and on the parameters on which adaptation works. In general, our results suggest that the in-phase model can simulate tilt aftereffect and reduced contrast sensitivity very well, either by assuming a fatigue for the neurons, or by assuming an increased intracortical inhibition. An increase in excitation is also able to explain tilt aftereffect, but without a clear decrease in detection sensitivity (the minimal perceived contrast remains unaffected).

The anti-phase model seems less able to explain the experimental data. An increase in cortical inhibition induces no aftereffect in this model. An increase in threshold (i.e., neuron fatigue) is able to explain aftereffect, with a moderate lost of sensitivity. Finally, decreasing excitation in the anti-phase model has similar results as in the in-phase model: aftereffect is obtained but without any lost of sensitivity.

We propose that, according to the previous results, either the in-phase model, with a change in threshold and/or inhibitory synapses, or the anti-phase model, with a change in threshold, may account for data on adaptation to a grating. Of course, it is also possible that adaptation involves a change in several parameters simultaneously (for instance, both neuron fatigue and a change in intracortical synapses, or simultaneous excitation and inhibition plasticity). This multifactorial aspect may be analyzed in subsequent works, but will probably require more complex psychophysical experiments to discriminate among the various parameter changes.

Conclusions

The in-phase model is able to account for tilt aftereffect quite well by assuming an increase in threshold (neuron fatigue) and/or an increase in inhibitory synapses. Both simulated mechanisms can explain the same phenomenon, without significant differences. The values of tilting (from 3-4° to 10°) and contrast threshold elevation (0.5-1%) agree with those reported in psychophysical experiments. An increase in excitation strength is unable to explain a fall in sensitivity. The anti-phase model can explain data only with a threshold increase. Analysis of results, at different contrast for the gratings and with different levels of adaptation, may provide indications to test alternative models of intracortical connectivity.

ISSN: 1727-1983

References

[1] FERSTER D., MILLER K.D. (2000): 'Neural mechanisms of orientation selectivity in the visual cortex', Annual Review of Neuroscience, 23, pp. 441-471.

[2] DRAGOI V., SHARMA J., SUR M. (2000): 'Adaptation induced plasticity of orientation tuning in adult visual cortex', *Neuron*, **28**, pp. 287-298.

[3] HE S., MACLEOD D.I. (2001): 'Orientation selective adaptation and tilt after-effect from invisible patterns', *Nature*, **411**, pp. 473-476.

[4] FESTMAN Y., AHISSAR M. (2004): 'Attentional states and the degree of visual adaptation to gratings', *Neural Network*, **17**, pp. 849-860.

[5] HUBEL D.H., WIESEL, T.N. (1968): 'Receptive fields and functional architecture of monkey striate cortex', J. Physiol., **195**, pp. 215-243.

[6] TOLHURST D.J., THOMPSON P.G. (1975): 'Orientation illusion and aftereffects: Inhibition between channels', *Vision Research*, **15**, pp. 967-972.

[7] BARLOW H. B. (1990): 'A theory about the functional role and synaptic mechanism of visual after-effects', in BLAKEMORE C. (Ed.): 'Vision: Coding and efficiency', (Cambridge University Press, New York), pp. 363-375.

[8] TROYER T.W., KRUKOWSKI A.E., PRIEBE N.J., MILLER K.D. (1998): 'Contrast-invariant orientation tuning in cat visual cortex: thalamocortical input tuning and correlation-based intracortical connectivity', *J Neurosci.*, **18**, pp. 5908-5927.

[9] SOMERS D.C., NELSON S.B., SUR M. (1995): 'An emergent model of orientation selectivity in cat visual cortical simple cells', *J Neurosc*i., **15**, pp. 5448-5465.

[10] URSINO M., LA CARA G.E. (2004): 'Comparison of different models of orientation selectivity based on distinct intracortical inhibition rules'. *Vision Res.*, **44**, pp. 1641-1658.

[11] BLAKEMORE C., CAMPBELL F. W. (1969): 'On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images', *J. Physiol.*, **210**, pp. 237-260.

ISSN: 1727-1983