A model of binocular rivalry based on competition in IT

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Abstract

Binocular rivalry is observed when the stimuli presented to both eyes are incongruent and cannot be fused together into a single percept. In such a situation the brain perceives an alternation of the two images, with the mean duration of the dominant perception being a few seconds. We propose a computational model of competition with spiking frequency adaptation in the inferotemporal cortex (IT) that is able to reproduce the experimental distributions of the dominant phase durations. We also include top–down connections from IT to earlier visual areas (V4) that generate the observed perception-modulated response of some neurons in these areas. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Binocular rivalry; Competition; Frequency adaptation

1. Introduction

The phenomenon of binocular rivalry occurs when the images perceived by the two eyes are conflicting and cannot be fused into a single coherent percept. Then, both images compete for dominance, giving rise to a perceptual oscillation in which only one image is seen at a time. For some time it was argued that binocular rivalry arises from a competition between monocular neurons in primary visual cortex [2], but many experimental results in the last years discard this hypothesis. For instance, Leopold and Logothetis [7], in experiments with trained monkeys, reported that only a small percentage of neurons in V1 correlate with the monkey perception. This percentage is higher in V4 and increases as we go further in the visual pathway, reaching a 90% in the inferotemporal cortex and the superior temporal sulcus [12]. Furthermore, when the

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images presented to both eyes are interchanged with a frequency of 3 Hz, no differences are observed with respect to the stationary case [8]. A single image is perceived for several seconds independent of the eye to which it is presented, which is clearly in contrast to a monocular competition model. Also psychophysical studies seem to be inconsistent with this view: the Diaz-Caneja phenomenon [4,11] shows that the brain organizes the visual stimuli presented to each eye into coherent perceptions taking, if necessary, elements from both monocular channels. This effect cannot be explained if we assume the total suppression of the input from one eye. A general conclusion from all these works is that the competition leading to binocular rivalry must be placed at high visual areas. The competition between stimulus representations, and not between both eyes, seems to be the last responsible for binocular rivalry, and so it is feasible that its underlying mechanisms are the same that produce other multistable phenomena, such as reversible figures.

2. The model

In this work, we present a computational model for binocular rivalry that is able to reproduce most of the experimental findings described above. We propose the existence of competition mechanisms between pools of neurons that respond to complex stimuli representations in a high visual area (such as the inferotemporal cortex, IT). This competition, along with firing rate adaptation dynamics, produces an oscillatory alternation of the dominant pool. The distributions of the dominant phase durations are well fitted by a gamma function with parameters close to those found in experimental conditions. Top–down connections to primary visual areas allow for the existence of neurons in these areas whose activity is modulated by the perceptual report.

We use population equations that describe the mean activity of a group of neurons with common functional and dynamical properties. These groups of neurons are constituted by a large and homogeneous population of identical spiking neurons which receive the same external input and are mutually coupled by synapses of uniform strength. Here, we describe the mean activity of such a pool of neurons in the framework of the mean field theory [1,15], with the following equation relating the input current for pool i to the input currents in other pools:

$$\tau^s \frac{\mathrm{d}I_i(t)}{\mathrm{d}t} = -I_i(t) + \sum_j w_{ij} F(I_j(t)) + I_{\text{noise}} + I_0, \tag{1}$$

where $\tau^s = 6.0$, I_{noise} is a Gaussian noise term of amplitude 0.01 and $I_0 = 0.025$ is a diffuse spontaneous background input current. An extra input current, $I_{\text{input}} = 0.05$, is added to the input pools. The sum on the right-hand side extends to all the pools that synaptically influence pool i; w_{ij} is the synaptic strength of the connection; and F is the activation function, that relates the input current to the mean pool activity. Usually, F is a non-negative function that takes the value 0 below a certain activation threshold and saturates to a maximum value due to refractoriness. We assume the following
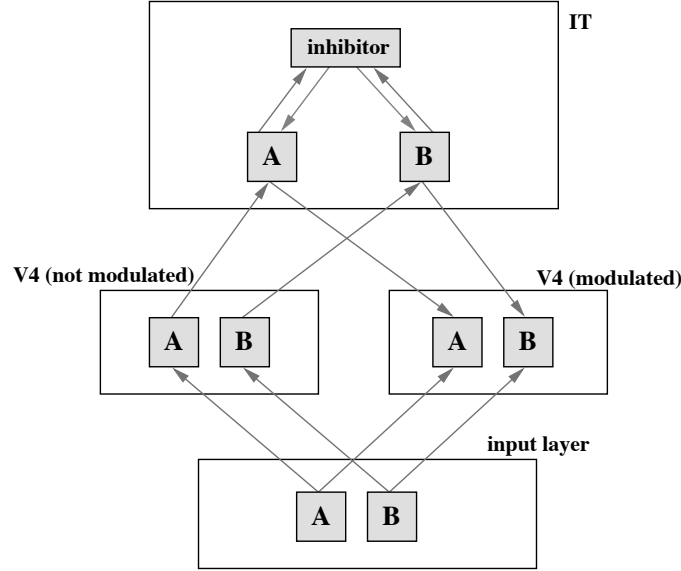
Fig. 1. Network architecture. The connection weights are $w^{I-V4\text{not}} = 0.85$ and $w^{I-V4\text{mod}} = 0.2$ for connections between the input layer and V4; $w^{V4\text{not}-\text{IT}} = 0.7$ and $w^{\text{IT}-V4\text{mod}} = 0.2$ for the connections between V4 and IT; and $w^{\text{IT}-\text{INH}} = 1.8$ and $w^{\text{INH}-\text{IT}} = -1.2$ for the connections between IT pools and the inhibitor. Self-connection weights are $w^{\text{EXC}} = 0.95$ for excitatory pools and $w^{\text{INH}} = -0.1$ for the inhibitor.

activation function:

$$F(I_j(t)) = \frac{1}{T - (\tau + a_j(t))\log(1 - 1/\tau I_j(t))}, \tag{2}$$

where $T = 1.0$, $\tau = 20.0$, and $a_j(t)$ is a frequency adaptation parameter that is described below.

The model architecture includes an input layer, a middle layer that could be identified with V4, and a complex stimuli processing layer that we will refer to as IT. The connection schema is shown in Fig. 1. Populations in IT responding to conflicting stimuli compete for perceptual dominance through a common inhibitory pool. This kind of competition has been used by Deco and Zihl [3] in a model of visual attention. Here, we use the same competition mechanisms, but also include activity adaptation to achieve oscillatory activation of the competing pools. The adaptation parameter has the following dynamics:

$$\tau_a \frac{\mathrm{d}a_j(t)}{\mathrm{d}t} = -a_j(t) + \alpha I_j(t), \tag{3}$$

where $\tau_a = 400.0$ and $\alpha = 95.0$. This mechanism is similar to that proposed in [14]. As a result of competition and firing rate adaptation, we obtain that dominant perceptions alternate in the same way as observed in experiments, and that the relative distributions of phase duration are satisfactorily reproduced (Fig. 2).

Most of the physiological experiments related to binocular rivalry have shown that some neurons in early visual areas modulate their activity according to the reported
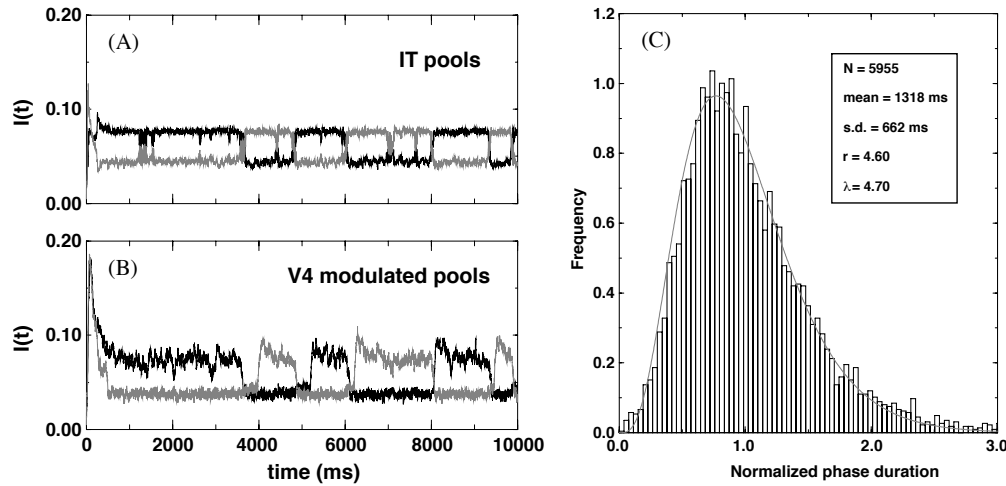
Fig. 2. (a) Input current for IT pools when both stimuli are presented. The two pools compete for dominance and an alternation of the winning perception is observed. (b) Input current for V4 modulated pools. Note the correlation with pools in IT, achieved through the top–down connections. (c) Distribution of relative phase durations (dominant phase durations as a fraction of the mean phase duration). It has been fitted with a gamma function ($f(x) = \lambda^r/\Gamma(r)x^{r-1}\exp(-\lambda x)$) with parameters $r = 4.60$ and $\lambda = 4.70$.

perception. Here, we propose that this modulation is attained by backpropagating connections that come from high visual areas where the competition takes place. Including connections from IT to some V4 populations in the model (see Fig. 1) produces the related modulation. The rest of V4 neurons show no dependence with the winning perception. So the model we postulate includes two kinds of neurons in V4. The first type is composed by neurons which act as input for IT, or other higher processing areas, and their activity is uncorrelated with the dominant representation. The second type is composed by neurons which receive top–down connections from IT, and their activity is modulated. This group of neurons could serve as a synchronizing link to other regions such as posterior parietal cortex (PP), which is known to process object positions. Such a schema would allow to have correlated activity between neurons in IT responding to an object and neurons in PP responding to its position, and would provide a way to solve the problem of binding by means of temporal correlations [13,5].

3. Discussion

The assumption that competition for perceptual dominance is occurring in IT is based on two facts: First, Sheinberg and Logothetis [12] found that 90% of the neurons in IT are correlated with the perception. Second, the current theories assume that the competition that leads to binocular rivalry takes place at the stimulus level, and IT is known to respond to complex stimuli [9,6]. However, this competition could be occurring in other areas or even could be a competition between cerebral hemispheres

for visual awareness [10]. In any case the model of competition at a high level with top–down connections to V4 is perfectly extensible to any area and our results remain valid even for inter-hemisphere competition.

Finally, we have made no assumption on the monocular or binocular nature of the input neurons. We only require that the two presented stimuli be sufficiently different so that they cannot be fused together into a single percept. Under these circumstances we observe a competition in IT between pools responding to each of the stimuli (note that there is no pool that responds to the combination of both). So our model can also be applied to situations of monocular rivalry or reversible figures. As stated in [8], binocular rivalry is just an easy way to obtain the sufficient discordance between the two alternative images.

Acknowledgements

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