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# A UNIFIED AND QUANTITATIVE NETWORK MODEL TO DESCRIBE SPATIAL ATTENTION IN AREA V4

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## ABSTRACT

Electrophysiological experiments in V4 visual area have shown that spatial attention induces a number of neural activity modulations. Depending on the stimulus characteristics, neuronal firing rates either increase or decrease. At the network level, the oscillatory activity in the gamma frequency range (30-70 Hz) is enhanced by attention. Recently, pyramidal neurons and interneurons have been surmised to respond differently, but have been shown to have both a high firing variability. These results raise the question of the nature of the modulatory attentional input to V4 and of the network mechanisms that lead to the emergence of these different modulations. Here, we propose a biophysical network model of V4. We first reproduce the neural activity observed in response to different stimulus configurations. We found that different forms of the attentional input are possible, and that this fact can explain the observed multiplicity of modulations when stimulus contrast is varied. Our model offers a unified and quantitative picture, from which the cognitive roles played by these attentional modulations can be investigated.

## KEY WORDS

Attention, vision, modeling, spiking neurons, network and simulation.

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Electrophysiological experiments in V4 visual area have shown that spatial attention induces a number of neural activity modulations. Depending on the stimulus characteristics, neuronal firing rates either increase or decrease. At the network level, the oscillatory activity in the gamma frequency range (30-70 Hz) is enhanced by attention. Recently, pyramidal neurons and interneurons have been surmised to respond differently, but have been shown to have both a high firing variability. These results raise the question of the nature of the modulatory attentional input to V4 and of the network mechanisms that lead to the emergence of these different modulations. Here, we propose a biophysical network model of V4. We first reproduce the neural activity observed in response to different stimulus configurations. We found that different forms of the attentional input are possible, and that this fact can explain the observed multiplicity of modulations when stimulus contrast is varied. Our model offers a unified and quantitative picture, from which the cognitive roles played by these attentional modulations can be investigated.

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## 1. Introduction

Spatial attention is the ability to selectively focus attention to a particular location in the visual field. The effects of this kind of attention on the neural activity are best studied in visual area V4, where the modulations are found to be important. In the last decade, electrophysiological experiments in behaving macaque monkeys have revealed a number of neural activity modulations [1-7]. When one stimulus is presented, responding neurons increase their firing rate and their tuning curve is modulated multiplicatively [1]. When the stimulus contrast was varied, several types of gain responses were found for the contrast response function (CRF) [2-3]. When two stimuli are presented simultaneously, the neuronal firing rate response is in between those when each stimulus is presented separately (stimulus competition) and when one stimulus is attended the neuronal response is closer to the response when it is presented alone (biased competition) [4]. At the network level, the oscillatory activity in the gamma frequency range (30-70 Hz) and the related coherence of the neuronal firing are enhanced by attention [5], and has been found to correlate positively with behavioral performance [6]. Recently, from the extracellularly recorded spike waveforms, two different classes of neurons have been distinguished, which are thought to correspond to pyramidal neurons (PNs) and interneurons (INs) [7]. INs respond with higher firing rates than PNs. For both neuronal types, the response variability characterized by the Fano factor (FF) is high, independently of their firing rate. With attention, firing rates increase and the FF decreases for both neuronal types.

Attention in V4 is believed to be conveyed by a feedback input to this area, originating from another brain area, presumably in the prefrontal cortex. From

the experimental results, we don't know the nature of the attentional input, neither we know how the diversity of the attentional modulations can be explained in a unified way. To address these questions, we have proposed a biophysical network model of V4. We first constrain the model to reproduce the neural activity observed in response to different stimulus configurations. Response variability is reproduced when neurons receive nearly balanced inputs at high frequency rates. We found that different forms of the attentional input can induce the observed attentional modulations. This input multiplicity leads to multiple modulations when contrast is varied and we predict their dependence on the neuronal type.

## 2. Model

We consider a network of PNs and INs, with the topology of a ring (see Fig. 1): each neuron has a stimulus preference, indexed by  $x$ , which varies monotonically from 0 and 1 along the ring. The network should in fact consider at least two dimensions, at least one for the spatial dimension and one for the orientation of the stimulus. However, for simulation purposes, we have only considered this simplified one-dimensional network. We assume that this approximation will lead to correct qualitative results. Below, we describe the main features of the model, For further details, the reader is directed to [8,9].

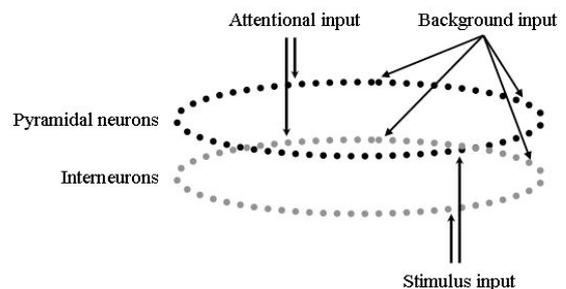


Fig. 1: Sketch of the network model.

**The network.** It is composed of  $N_E$  PNs and  $N_I$  INs, with  $N_E = 4N_I$  ( $N_E = 400$  here), similar to the proportions found in the cortex. To help reproduce the experimental results quantitatively, we consider biophysical models to describe neurons and synapses. PNs are represented by the Ermentrout-Kopell model [10] and INs by the Wang-Buzsaki model [11]. For both models, the membrane potential  $V$  obeys the following differential equation:

$$C \frac{dV}{dt} = -g_L(V - V_L) - g_{Na}m^3h(V - V_{Na}) - g_Kn^4(V - V_K) + I_{syn}$$

$C$  is the membrane capacitance. The three first terms on the right are the membrane currents: the leak ( $L$ ), the sodium ( $Na$ ) and the potassium ( $K$ ) currents. The synaptic current,  $I_{syn}$ , is the sum of all currents received at the neuron's synapses, which are either input synapses or network synapses. For the membrane current  $X$  ( $X = L, Na, K$ ),  $g_X$  is the maximal conductance and  $V_{syn}$  is the reverse potential.  $m$  and  $h$

are, respectively, the activation and inactivation sodium current variables, and  $n$  is the activation variable of the potassium current.

The synaptic current entering a neuron via synaptic receptors is given by

$$I_{syn} = -g_{syn}s(t)(V - V_{syn}),$$

where  $g_{syn}$  is the maximal synaptic conductance and  $s(t)$  is the gating variable;  $V_{syn}$  is the reverse potential of the synapse ( $V_{syn} = 0 mV$  for excitatory synapses and  $V_{syn} = -70 mV$  for inhibitory synapses). For AMPA and GABA<sub>A</sub> receptors, the gating variable is given by

$$s(t) = \sum_k H(t - t_k)(e^{-(t-t_k)/\tau_d} - e^{-(t-t_k)/\tau_r})$$

where the sum is over all incoming spikes.  $H$  is the Heaviside step function. For an AMPA receptor, the decay time is  $\tau_d = 2 ms$  and the rise time is  $\tau_r = 1 ms$ . For a GABA<sub>A</sub> receptor,  $\tau_d = 10 ms$  and  $\tau_r = 1 ms$ . For an NMDA receptor, the current has the voltage dependence  $1/\{1 + [Mg^{2+}]e^{-0.062V}/3.57\}$ , which is controlled by the external magnesium concentration ( $[Mg^{2+}] = 1 mM$ ). The gating variable is obtained by solving the following equations:

$$\frac{ds}{dt} = -\frac{s}{\tau_d} + \alpha x(1 - s)$$

$$\frac{dx}{dt} = -\frac{x}{\tau_r} + \sum_k \delta(t - t_k),$$

where  $\delta$  is the Dirac-delta function,  $\tau_d = 100 ms$ ,  $\alpha = 0.5 ms^{-1}$  and  $\tau_r = 2 ms$ .

A neuron at position  $x$  in the population  $X$  is connected to a neuron at position  $y$  in the population  $Y$  with probability

$$P_{XY}(x, y) = \frac{P_{XY}}{\sqrt{2\pi}\sigma_{XY}} e^{-d^2/2\sigma_{XY}^2}.$$

$d$  is the minimum distance between the neurons on the ring. The width of the connectivity profile  $\sigma_{XY}$  is chosen to be small compared to 1 ( $\sigma_{XY} \leq 0.15$ ), so that  $P_{XY}$  is almost the mean connection probability between populations  $X$  and  $Y$ . The connectivity is chosen to be sparse ( $P_{XY} \leq 0.1$ ).

**Neuronal inputs.** V4 receives inputs from different parts of the brain: the visual input, the attentional input, and a background input originating from other brain areas whose activity is unrelated to the tasks considered here. The visual input predominantly originates from area V2. This input is localized around  $x_s$ , with a Gaussian shape and width  $\sigma_s$ . The feedback attentional input, including only excitatory inputs, is localized around a location  $x_a$  [12]. Its other properties are not known from experiments, and one of the goals of this study is to determine the possible forms of this input. In the absence of stimulus presentation or attention, the background input induces in V4 a spontaneous activity at low firing rates. All external inputs are modeled as Poisson spike trains, characterized by their frequency.

### 3. Results

In a first step, adjusting the network parameters, we show that the network quantitatively reproduces the experimentally observed responses to different stimulus presentations without attention. Then, we propose feedback inputs that reproduce the observed attentional modulations.

#### 3.1 Stimulus response

When one stimulus is presented at network location  $x_s$ , a local hill of activity is induced in the network. Although the firing rates can be reproduced quantitatively for a number of network parameters, this is not the case for the firing variability. Based on the study of the response of single neurons to excitatory and inhibitory Poisson spike trains, we found that the FF factor is high, and independent of the neuronal firing rate only when the rates of the input spike trains are high, as seen *in vivo*. The other condition is that the excitatory and inhibitory inputs should be almost balanced, the only region where the FF is high. When these conditions are fulfilled, we find also that the network results reproduce the experimental results (see Fig. 2).

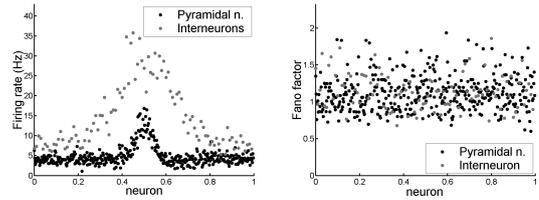


Fig. 2: Network response to the presentation of one stimulus at  $x_s=0.5$ . *Left*: Firing rates for PNs (black dots) and INs (grey dots). *Right*: FF for PNs and INs.

When two stimuli are simultaneously presented, the firing rate of responding V2 neurons has been found to be in between the ones elicited by each of the two stimuli presented separately [4]. As shown in Fig. 3, this is what occurs in the model. Stimulus competition in V4 is found to be the consequence of the sub-linear sum of the V2 inputs.

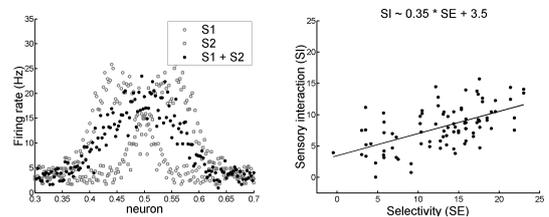


Fig. 3: Network response to the presentation of two stimuli at  $x_s=0.45$  and  $0.55$ . *Left*: PNs firing rates for one (open dots) and two stimuli (black dots). *Right*: sensory interaction ( $f(S1+S2)-f(S1)$ ) as a function of selectivity ( $f(S2)-f(S1)$ ) for responding PNs. S1 and S2 compete when the slope of the best line-fit (line and equation) is between 0 and 1.

### 3.2 Attentional input and modulations

In the one stimulus case, attention increases the neuronal firing rates. From this, we can infer that an increase of the mean excitatory level of the feedback input to V4 may be a candidate for the attentional input. However, as excitation and inhibition compete in the network, this has to be verified, as well as the occurrence of the other attentional modulations. In a recent experiment, and during attention, an increased coherence of the network oscillation and of the neuronal firing has been found in the gamma frequency range between a prefrontal area, the frontal eye field, and V4 [13]. Even if this area is not proved to be the source of the attentional input to V4, this suggests that the attentional input may oscillate in the gamma frequency range.

We have tested these two different forms of feedback inputs: (1) one which oscillates in the gamma frequency range, and (2) one whose mean increases with attention.

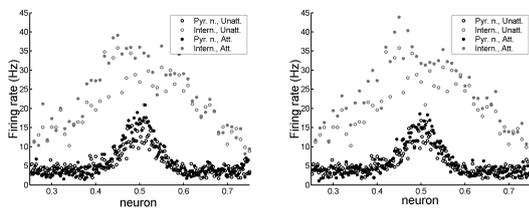


Fig. 4: Network response (PNs: black circles, INs: grey circles) when attention is directed to the stimulus location at  $x_s=0.5$ . The attentional input oscillates in the gamma frequency range -50 Hz here- (left), or its mean increases (right). Compared to the unattended condition (open circles), the firing rate attentional modulation appears around the attended location (filled circles). Between the two different attentional inputs, the firing rate modulations are undistinguishable.

We found that these two qualitatively different inputs lead to undistinguishable local firing rate increases (see Fig. 4). In both cases, locally, the Fano factor generally decreases slightly. The neuronal tuning curves are found to be multiplicatively modulated. When two stimuli are presented simultaneously, the attentional input directed to the location of one stimulus enhances the activity around this location. The enhancement of inhibition around this location, and the existence of lateral inhibitory connections, induces a decrease of activity in the vicinity, leading to biased competition (see Fig. 5). When the attentional input oscillates in the gamma frequency range, it induces locally a gamma oscillation in the network.

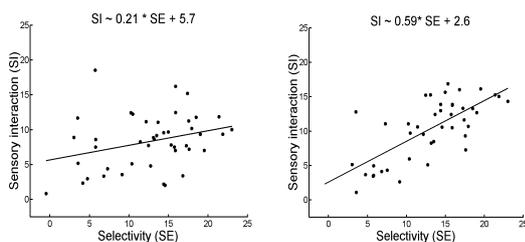


Fig. 5: Sensory interaction as a function of selectivity for all responding PNs. The best line-fit equation is given above the graph. Left: PNs for which the weaker stimulus is attended. Right: PNs for which the stronger stimulus is attended.

Finally, the CRF modulations induced by these different attentional inputs are found to depend on the input type and also on the neuronal type (see Fig. 6).

Note that any combination of the two types of inputs we have considered, even if we did not thoroughly tested them, may lead to the same conclusions. Therefore, different forms of attentional inputs can lead to the observed attentional modulations.

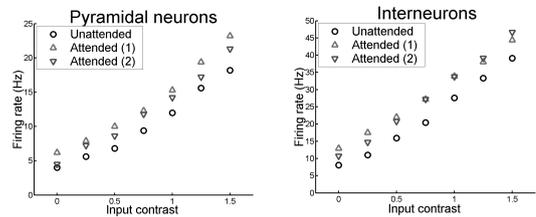


Fig. 6: Attentional modulation of the CRF for PNs (left) and INs (right). The attentional input either oscillates in the gamma frequency range (1, up triangles) or its mean increases (2, down triangles).

### 4. Conclusion

The biophysical model we have proposed reproduces in a unified and quantitative way the experimentally observed neural activity in V4, and the diversity of its modulations induced by attention. We have not only proposed candidates for the attentional input to V4 but have given an explanation of the network mechanisms leading to the observed attentional modulations.

We will now use this model to investigate the role of these modulations at a cognitive level. In this way, we will be able to give a quantitative answer to the long standing questions regarding the roles of the firing rate modulations and of the gamma band network oscillation on the processing of information in downstream layers. The possibility that recurrent networks of excitatory and inhibitory neurons are in a dynamical regime where neuronal inputs are balanced has been mainly studied theoretically. More recently, *in vitro* [14] and *in vivo* [15] experiments have found that cortical networks are actually in this regime. These results are in favor of the mechanism we propose here to explain the high firing variability.

The finding of multiple forms of attentional inputs is biologically relevant. Actually, the attentional signal could originate from different brain areas [12], depending on the task the animal is engaged in, and these areas may not have the same kind of neural activity, and consequently not provide a unique form of attentional input to V4. Related to this, it has been reported recently that attentional modulations can depend on the degree of task difficulty [16]. Finally, the existence of multiple attentional inputs may explain the diversity of CRF modulations that has been reported [2,3], and we predict that they may depend on the neuronal type.

Our model has important advantages compared to related models. A general architecture for attention has been proposed, consisting of a sensory area connected bi-directionally to a prefrontal area [17]. The persistent neuronal activity generated by this prefrontal area has been hypothesized to be the source of the attentional

input. On the contrary, and suggested by experiments, the attentional input in our model can have different origins and different forms. Secondly, our simple excitatory and inhibitory network is able to reproduce the experimental results, without the need to invoke several types of interneurons [18].

In a future study, we will address in more detail the modulations of the network oscillatory behavior that occur with stimulus presentation and attention in multiple frequency bands [5,19].

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