

# Synchronization as a mechanism for attentional gain modulation

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## Abstract

The attentional modulation of the response of a V4 neuron to a stimulus in its receptive field was recently investigated using Macaque monkeys. When the animal focused attention into the receptive field, two distinct changes were observed: either the neuron's firing rate increased, or the coherence of the spikes with the local field potential (LFP) was increased without any significant changes in the firing rate. We investigated using model simulations whether attention-induced increases in the synchrony of local inhibitory networks could account for both of these changes. When inhibitory synchrony was increased, the coherence of model neurons with LFP, as measured by the spike field coherence, increased. The firing rate versus current ( $f - I$ ) response curves could saturate for large  $I$ , in which case attention yielded a shift of sensitivity; or the  $f - I$  curves could be non saturating, in which case attention induced approximately multiplicative gain modulation.

*Key words:* synchronization, gamma oscillations, selective attention

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## 1 Introduction

Visual scenes with enormous spatial and temporal information richness are transduced into spike trains in the sensory pathway. Human psychophysics indicates that only a small part of that information is consciously accessible. For instance, differences between two images shown in rapid succession are only visible when the subject is told to pay attention to the particular spatial location of the change (9). The mechanism for this process, selective attention, remains unclear. The neural correlate of selective attention has recently been studied in Macaque monkeys (6; 7; 3). A key finding is that attention modulates both the mean firing rate of a neuron in response to a stimulus (6; 7) as well as the coherence with other neurons responsive to the stimulus (3).

Cortical interneurons are part of dedicated networks connected by electric gapjunctions and chemical inhibitory synapses (4; 5). Interneuron networks synchronize when activated by excitatory neurotransmitters or neuromodulators. They project synchronous inhibition to output neurons of cortex thereby modulating their firing rate. Here we explore using model simulations and in vitro experiment, the hypothesis that selective attention is mediated by changes in synchrony of local interneuron networks.

When the effect of attention is modeled as an increase in synchrony of interneuron networks, we find that: attention increases the coherence of spike trains with local field potential; the firing rate can increase with attention or remain the same depending on stimulus strength; attention results either in a multiplicative gain change of firing rate response curves or a shift in the sensitivity, depending on the extent of interneuron network activation. Thus, changes in interneuron synchrony could potentially underlie a variety of seemingly unrelated observations.

## 2 Methods

*Modeling synchronous inhibitory inputs.* The model network produced an oscillatory activity that consisted of a sequence of synchronized spike volleys (2). Each spike volley is characterized by the mean number of spikes in a volley  $a_{IV}$ , their spike-time dispersion  $\sigma_{IV}$ , and oscillation frequency  $f_{osc}$  (equal to the number of volleys per second).

The method for obtaining synchronous volleys is given in Ref. (11). Each spike in the volley produced an exponentially decaying conductance pulse,  $\Delta g_{inh} \exp(-t/\tau_{inh})$  in the postsynaptic cell (*inh* stands for inhibitory), yielding a current  $I_{syn} = \Delta g_{inh} \exp(-t/\tau_{inh})(V - E_{GABA})$ . In this expression  $t$  is the time since the input pulse arrival,  $\tau_{inh} = 10$  ms is a decay constant,  $\Delta g_{inh}$  is the unitary synaptic conductance,  $V$  is the postsynaptic membrane potential, and  $E_{GABA} = -75$  mV, is the reversal potential. The resulting train of conductance pulses drove a single compartment neuron with Hodgkin-Huxley voltage-gated sodium and potassium channels, a passive leak current,

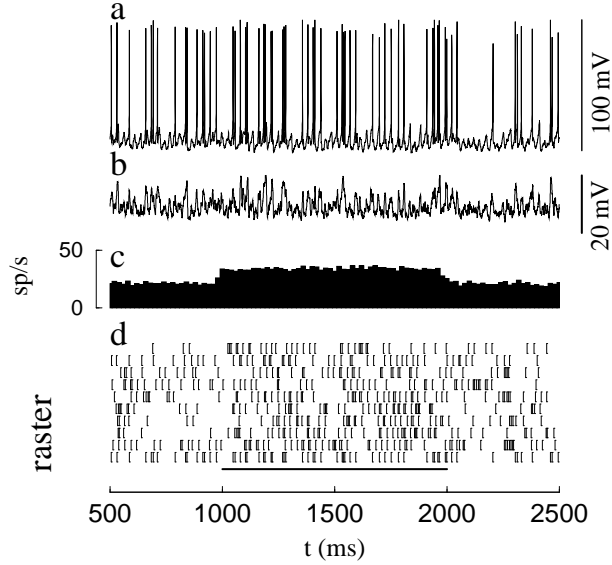


Fig. 1. Increasing inhibitory input synchrony led to an increased firing rate. We show (a) the membrane potential, (b) the local field potential (LFP), (c) the firing rate as a function of time, and the rastergram of the first ten trials. During the time interval between  $t = 1000$  and  $2000$  ms (indicated by the bar in (d)),  $\sigma_{IV}$  was reduced from 4 ms to 2 ms.

the synaptic currents described above, and a white noise current with mean  $I$  and variance  $2D$  (11).

*Stimulus and attention.* The model was run under four different conditions, attention was either directed away or toward the receptive field of the neuron, in combination with either a stimulus present in the receptive field or without a stimulus. The effects of attention were modeled by changing the parameters of the synchronous inhibitory drive. Typically the value of  $\sigma_{IV}$  was reduced in the attended state, leading to an increase in input synchrony. The stimulus-induced synaptic inputs were not temporally patterned. Neurons either received temporally homogeneous excitatory and inhibitory Poisson processes with rates  $\lambda_{exc}$  and  $\lambda_{inh}$ , respectively, or they were driven by a random white noise current with mean  $I$  and variance  $2D$ .

*Experiment.* All experiments were carried out in accordance with animal protocols approved by the N.I.H.. Coronal slices of rat pre-limbic and infra limbic areas of prefrontal cortex as well as transversal slices of hippocampus, were obtained from 2 to 4 weeks old Sprague-Dawley rats. We recorded from regularly spiking layer 5 pyramidal cells, that were identified morphologically. Current was injected into the neuron using dynamic clamp (10) to mimic the effect of a oscillatory inhibitory synaptic drive. Full experimental details are in Ref. (1).

### 3 Results

*The model can account for results obtained in in vivo experiments.* Results on attentional modulation of the firing rate and coherence of V4 neurons in macaque cortical area V4 were recently reported in three key papers (6; 7; 3). We reproduced the results by McAdams & Maunsell and those of Fries and coworkers under the assumption that attention modulates the synchrony of local interneuron networks (results not shown).

*Gain modulation on neurons with highly variable spike trains.* Cortical neurons can fire at high rates with a coefficient of variation (CV) between 0.5 and 1. A potential consequence of driving neurons with a synchronous oscillatory inhibitory drive is a decrease in variability (11). Therefore, we investigated whether attentional modulation by inhibitory synchrony could operate on neurons with high CV values (Figure 1). The model neuron was driven by a noisy synchronous inhibitory drive, a temporally homogeneous excitatory Poisson process and a white noise current. The effects of attentional modulation were simulated by decreasing  $\sigma_{IV}$  from 4 ms to 2 ms during the time interval between  $t = 1000$  and 2000 ms. During the non-attended state ( $t < 1000$  ms), the firing rate was 22.3 Hz and the CV was unity. During the attended state the firing rate increased to 34.6 Hz, with  $CV = 0.78$ . The spike field coherence (see Ref.(3)) in the gamma-frequency band (34 – 44 Hz) increased by 59%.

*Attentional modulation of  $f - I$  curves.* Ascending sensory inputs can often be represented as a depolarizing current  $I$  to neurons in the receiving cortical layers. The resulting firing rate that such an input elicits is determined by the  $f - I$  curve. The shape of the  $f - I$  curve depends on the modulating inputs to the receiving neuron. These inputs may represent the value of an additional variable, such as, for example, attentional state. There are important computational consequences when modulating inputs change the gain of the  $f - I$  multiplicatively (8). We investigated how the value of inhibitory synchrony altered the  $f - I$  curves.

In Figure 2A we compare the  $f - I$  curves obtained in experiment for  $\sigma_{IV} = 1$  ms to those for  $\sigma_{IV} = 4$  ms for two different neurons. The response could either saturate as a function  $I$ , in which case reducing  $\sigma_{IV}$  led to a shift of the  $f - I$  curve to the left. Or the response could be nonsaturating, in which case multiplicative gain changes are in principle possible. We studied using numerical simulations the changes in  $f - I$  over a wide range of parameters (Figure 2B). For  $a_{IV} = 10$ , the  $f - I$  curves were nonsaturating (Figure 2Ba). The degree of multiplicative gain modulation was investigated by rescaling all curves,  $f \rightarrow f/\lambda_f$  and  $I \rightarrow I - \Delta_I$ , to fit to the curve for  $\sigma_{IV} = 1$  ms. We found shifts  $|\Delta_I|$  up to  $0.6 \mu A/cm^2$  and  $\lambda_f$  as low as 0.5. This indicates that the main effect of inhibition for this parameter range is gain modulation. For  $a_{IV} = 50$ , the  $f - I$  curves saturated at a rate equal to the inhibitory oscillation frequency,  $f_{osc}$  (Figure 2Bb). The  $f - I$  curves were well fitted by a sigmoid function,  $f = A/2(1 + \tanh(\lambda_I(I - \Delta_I)))$ . Increasing  $\sigma_{IV}$  led to a shift to the right ( $\Delta_I > 0$ ) and stretched the sigmoid ( $\lambda_I$  increased).

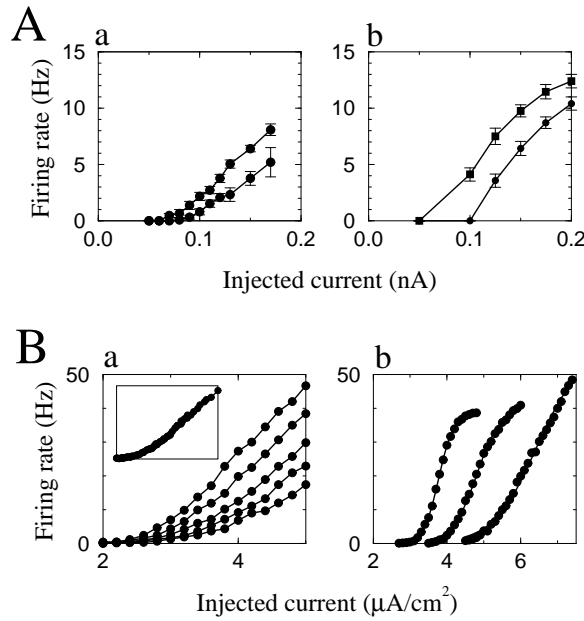


Fig. 2. Subtractive and divisive scaling of  $f - I$  curves with inhibitory synchrony. (A)  $f - I$  curves for two different neurons in rat prefrontal cortex. The firing rate did not saturate in (a), whereas it did saturate in (b). Each panel: (top)  $\sigma_{IV} = 1$  ms and (bottom)  $\sigma_{IV} = 4$  ms. (B) Model results. (a) Multiplicative gain modulation with inhibitory synchrony,  $a_{IV} = 10$ , from top to bottom  $\sigma_{IV} = 1, 2, 3, 4$  and  $5$  ms. Inset: all curves could be collapsed by a shift in the current and a rescaling of the firing rate axis. (b) Shift in neural sensitivity with inhibitory synchrony,  $a_{IV} = 50$ , from left to right,  $\sigma_{IV} = 1, 3$ , and  $5$  ms. The solid lines are fits to a sigmoid function, filled circles are simulation results.

Hence, for this set of parameters there was no multiplicative gain change.

The input activity  $a_{IV}$  is proportional to the size of the network times the mean number of neurons that are active on each cycle. The latter is determined by the extent of gap-junctional and chemical coupling, the former is determined by the extent of interneuron network activation by the stimulus. Hence, for small networks together with relatively focal activation of interneuron networks, attention leads to multiplicative gain change, whereas for large networks and stimuli that cause large activation of interneuron network, attention leads to shift in sensitivity.

## 4 Discussion

Physiological correlates of attention have been studied by recording the response of cortical neurons in Macaque monkey to either orientated gratings (area V4) or random dot patterns moving in different directions (area MT) (6; 12). The firing rate in these cases was tuned for orientation or direction. When attention was directed into the receptive field of the recorded neuron the following changes were observed (compared with attention directed out-

side the receptive field). Attention could increase the gain of the firing rate response while the neuron remained tuned for orientation/direction (6; 12). This effect was approximately multiplicative. Attention could also increase the coherence of the neuron's discharge with the local field potential (3). When the contrast of the stimulus was varied there could be saturation effects: at high contrasts attention did not increase the firing rate anymore (7). Here we presented a simple model that could reconcile these three observations. Sensory input was represented as a constant depolarizing current that was tuned for orientation and increased with contrast. Attention acted by changing the synchrony of local interneuron networks. First, increases in inhibitory synchrony led to increased coherence of output spike trains with the local field potential (Figure 1). Second, in slice experiments we observed  $f - I$  curves that either saturated or did not saturate (Figure 2). For the curves that did not saturate, the firing rate always increased with inhibitory synchrony. In that case, inhibitory synchrony could lead to multiplicative gain changes. For the curves that did saturate, the firing rate did not increase further with stimulus strength at high contrast. The firing rate at the saturation point was given by the inhibitory oscillation frequency. However, we found that the neuron could also saturate at rates corresponding to aperiodic excitatory activity, yielding a larger range of saturation points. We are presently investigating constraints on possible saturation points.

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