

Modulation of synchrony without changes in firing rates: Supplementary Material.

Quadratic Integrate and Fire neurons

Linear integrate and fire neurons as used in the model of two cortical columns have been shown to well reproduce the firing rate of cortical neurons under a noisy injected current (Rauch et al., 2003). However, their response with respect to oscillating input is different of that of cortical neurons of type I (see e.g. Fourcaud-Trocmé et al, 2003). To test whether this difference influences the results obtained in the paper, the model was run with quadratic integrate and fire neurons (QIF) which represent the normal form of type I neurons (Ermentrout, 1996). The network was left exactly the same as for the LIF, but the membrane dynamics was switched to

$$\tau_m \frac{dV_m}{dt} = \alpha (V_m - V_T)^2 - I_T + G_E (V_E - V_m) + G_I (V_I - V_m).$$

When the membrane voltage reached a threshold voltage $V_t = 100$ mV, a spike was triggered and the membrane potential was reset to $V_r = -63$ mV. Without any refractory time, the membrane dynamics started from the new value. The parameters were chosen to approximately match the input output curves of the QIF neurons with the ones of the LIF (see Figure S1) and are given in Table S1. Additional parameters that were introduced are the strength of the nonlinearity α and the threshold current I_T . The external input, the weights between cells and all other parameters were left the same.

Table S1: Parameters of the QIF neuron model

	V_t [mV]	V_r [mV]	τ_m [ms]	V_T [mV]	α []	I_T [mV]	V_E [mV]	V_I [mV]
E	100	-63	20	-56	2.5	22	0	-80
I	100	-63	10	-56	2.5	20	0	-80

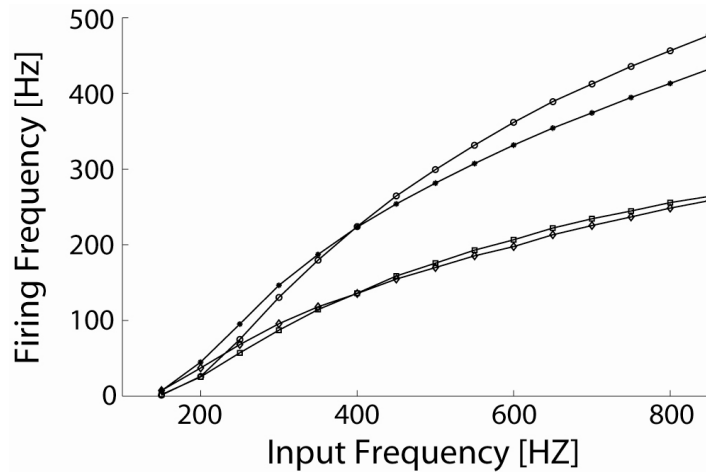


Figure S1: Firing rates of excitatory (squares) and inhibitory (circles) Linear IF neurons compared to excitatory (diamonds) and inhibitory (stars) Quadratic IF neurons in response to a poisson spiking input from 10 input neurons. Input Frequency: Average rate of input neurons.

The network with the QIF neurons was simulated for the same parameters as the LIF network. Some quantitative differences were observed, however the overall results stayed the same. Figure S2 shows the results at a single input frequency, similar to Figure 3A in the paper. The firing rate is the average firing rate of all neurons within the network including both excitatory and inhibitory populations.

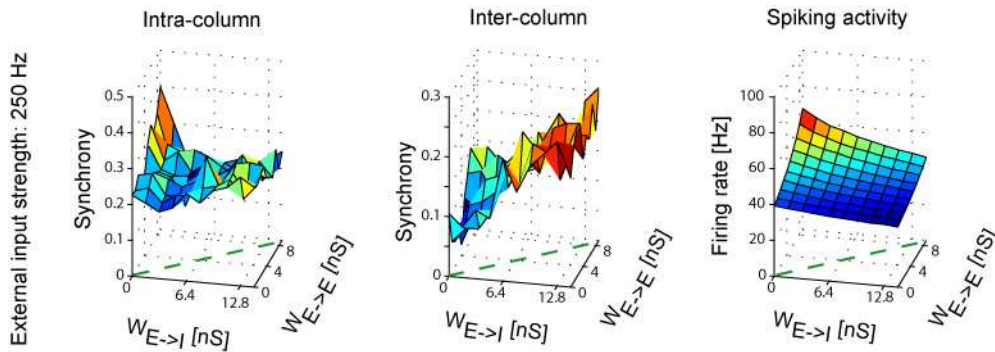


Figure S2: Intra-column, inter-column synchrony and spiking activity as a function of the strength of long range connections. Compare to Figure 3A in the main paper. The firing rate was calculated as the average rate of all neurons in the network (excitatory and inhibitory).

We also calculated the modulation ratios along the diagonal as in the case for the LIF neurons. The results are given in Table S2. They show that also in the case of the QIF neurons, changes in inter-column synchrony and oscillations were much higher than changes in firing rates.

Table S2: Ratios of modulation in population responses with QIF neurons.

	External input strength [Hz]						
	150	200	250	300	350	400	450
Firing rate E	0.057	0.038	0.025	0.020	0.019	0.012	0.016
Firing rate I	0.1620	0.1167	0.1132	0.1112	0.1092	0.1030	0.1025
Firing rate all neurons	0.097	0.078	0.082	0.083	0.080	0.071	0.072
Inter-column synchrony	1.251	0.560	0.555	0.576	0.340	0.258	0.279
Intra-column synchrony	0.322	0.258	0.098	0.163	0.246	0.365	0.328
Inter-column oscillations	0.711	0.884	0.601	0.882	0.711	0.560	0.562
Intra-column oscillations	0.144	0.466	0.160	0.370	0.349	0.206	0.228

The values correspond to the difference between the maximum and the minimum values at different synaptic weights (with $W_{E,I}/W_{E,E}$) divided by their sum.

One main difference between LIF and QIF neurons was the way the network oscillated. The increase of oscillation frequency that was observed with LIF neurons was not seen with the QIF neurons. Figure S3 shows the values of the firing rate of excitatory neurons, oscillations and synchrony in the same way as Figure 4 in the main paper. In Figure S3B it can clearly be seen that the location of the peak in the oscillation power was not depending on the input frequency as strongly as in the case of the LIF.

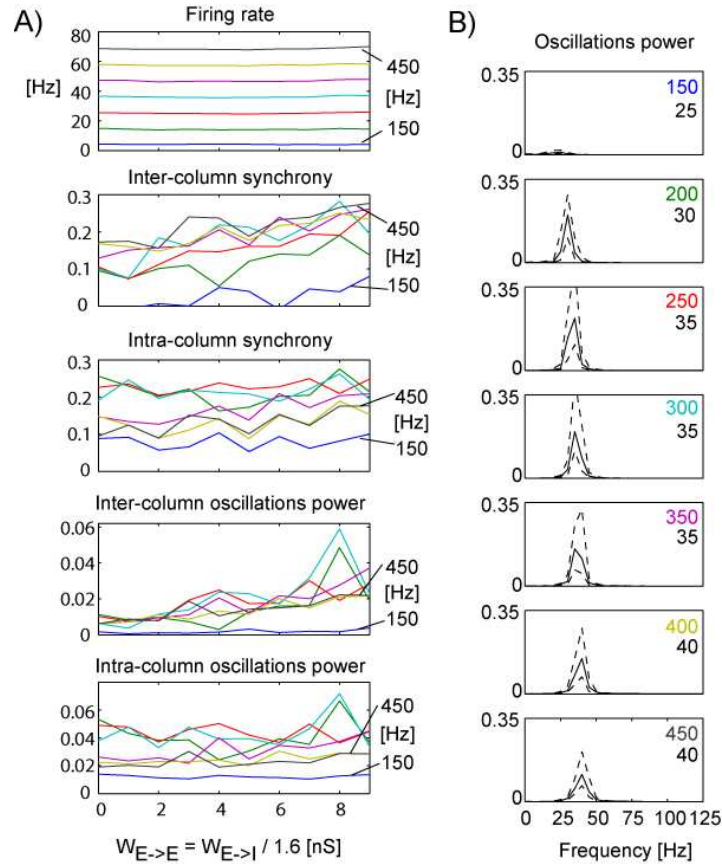


Figure S2: A) Firing rate of excitatory neurons, synchrony and oscillations power for all cases studied where $W_{E,I} = 1.6 W_{E,E}$. Different colors indicate different frequencies of the poissonian input ranging from 150 Hz to 450 Hz. The modulation ratios of all the curves are given in Table S2. B) Distribution of the power spectra for different input frequencies. The solid lines correspond to the medians and the upper and lower dashed lines are the 75th and 25th percentiles. The colored numbers refer to the different external input frequencies and the black number is the frequency with the maximum power.

Overall, the simulations with quadratic integrate and fire neurons confirmed the results obtained for the linear integrate and fire neurons.

Analytical confirmation of constant excitatory rate in a linear approximation

It is intuitively clear, that by changing the excitation as well as the inhibition between two columns in the correct way, the rate of the excitatory population of each column can be kept constant. The inhibitory neurons, of course, change their firing rate. By assuming, that the current frequency relationship of the neurons is linear, one can solve the linear rate equations for stable excitatory rate (see Dayan and Abbott, 2001). The approximation of each population by a firing rate variable is based on the assumption that the network is in a steady state, which is not fulfilled in networks with large oscillations. Therefore, the following analysis has surely its limits, but it shows, that small or no changes in firing rate are a direct consequence of the proportional change of $W_{E,E}$ and $W_{E,I}$.

The firing rates r of the two populations in column 1 can be written as

$$\begin{aligned}\dot{r}_{E,1} &= -r_{E,1} + f\left(I_{E,1} + w_{EE}r_{E,1} - w_{IE}r_{I,1} + W_{EE}r_{E,2}\right) \\ \dot{r}_{I,1} &= -r_{I,1} + f\left(I_{I,1} + w_{EI}r_{E,1} - w_{II}r_{I,1} + W_{EI}r_{E,2}\right)\end{aligned}$$

where $f(x) = x$, if $x > 0$, and $x = 0$ otherwise, is a linear threshold function. The input currents I are constant and represent the average over all poisson input spike trains. By the further assumption, that the rates are symmetric between the two columns ($r_{E,1} = r_{E,2} = r_E$ and $r_{I,1} = r_{I,2} = r_I$) and that the total input is positive, these equations simplify to

$$\begin{aligned}r_E &= I_E + w_{EE}r_E - w_{IE}r_I + W_{EE}r_E \\ r_I &= I_I + w_{EI}r_E - w_{II}r_I + W_{EI}r_E\end{aligned}$$

If now r_E is set to be constant:

$$\begin{aligned}-w_{IE}r_I + W_{EE}r_E &= c_1 \\ -r_I - w_{II}r_I + W_{EI}r_E &= c_2\end{aligned}$$

By substituting r_I in the second equation by the one obtained from the first equation one gets

$$\left[W_{EI} - \frac{(1 + w_{II})W_{EE}}{w_{IE}} \right] r_E = c_2 - \frac{(1 + w_{II})c_1}{w_{IE}}$$

Again, the term on the right hand side of the equation is constant and, therefore,

$$\left[W_{EI} - \frac{(1 + w_{II})W_{EE}}{w_{IE}} \right] = const.$$

This yields a linear dependence of W_{EI} on W_{EE} with slope $(1 + w_{II})/w_{IE}$. The linear relationship of the weights is of course a consequence of the assumption of linear IF function. However, any other monotonically increasing function f will give rise to a solution of constant rate r_E , where the

increase in input to r_E due to a change in W_{EE} can be compensated by an increase in W_{EI} and therefore in r_I . Of course, the relationship will not be linear anymore.

References:

Dayan P, and Abbott LF. *Theoretical Neuroscience*. MIT Press. Cambridge, Massachusetts, 2001.

Ermentrout B. Type I membranes, phase resetting curves, and synchrony. *Neural Computation* 8(5): 979-1001, 1996.

Fourcaud-Trocmé N, Hansel D, van Vreeswijk C and Brunel N. How Spike Generation Mechanisms Determine Neuronal Response to Fluctuating Inputs. *Journal of Neuroscience* 23(37):11628-11640, 2003.

Rauch A, La Camera G, Lüscher H-R, Senn W, Fusi S. Neocortical Pyramidal Cells Respond as Integrate-and-Fire Neurons to In Vivo-Like Input Currents. *Journal of Neurophysiology* 90(3):1598-1612, 2003