Signal Propagation in Networks of Integrate-and-Fire Neurons

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Introduction

Synfire vs Firing rate propagation

In literature, two different models of signal propagation have been proposed:

- **Synfire propagation**: signal is carried by waves of synchronous neuronal activity within a subset of the network neurons.
- **Firing rate propagation**: information is transmitted by an asynchronous elevation in the firing rate of the neurons carrying the signal.

The aim is hence to study if firing-rate and synfire coded signals can propagate through spontaneously active networks, without any assumption on their topology.

The model

Network architecture and neuronal model

The network is composed by 10000 leaky integrate-and-fire neurons, with 4 : 1 excitatory-inhibitory ratio, connected randomly with probability 0.02.

COBA vs CUBA

Two models are employed for the analysis, differing in the responses to presynaptic inputs.
The equation for the membrane potential of the CUBA model is:

$$\tau \frac{dV}{dt} = (V_{rest} - V) + g_{ex}(E_{ex} - V_{rest}) + g_{inh}(E_{inh} - V_{rest})$$

While for the COBA:

$$\tau \frac{dV}{dt} = (V_{rest} - V) + g_{ex}(E_{ex} - V) + g_{inh}(E_{inh} - V)$$

The model

Synapses dynamics and model parameters

In the previous equations, $\tau = 20$ ms, $V_{rest} = -60$ mV, $V_{thr} = -50$ mV, $E_{ex} = 0$ mV, $E_{inh} = -80$ mV and $\tau_r = 5$ ms.

When a presynaptic neuoron spikes, $g_{exc} \to g_{exc} + \Delta g_{exc}$ for the conductance of the corresponding postsynaptic target if the presynapaptic neuron is excitatory, $g_{inh} \to g_{inh} + \Delta g_{inh}$ if it is inhibitory. Otherwise:

$$\tau_{ex} \frac{dg_{ex}}{dt} = -g_{ex}$$

$$\tau_{inh} \frac{dg_{inh}}{dt} = -g_{inh}$$

with $\tau_{ex} = 5$ ms and $\tau_{inh} = 10$ ms.

Network dynamics
Measures

To characterise sustained asynchronous activity, the following quantities are measured:

- Membrane potentials, averaged and individual.
- Population firing rate, computed with the averages on all the firing rates across the network.
- Interspike intervals distribution ISI for each neuron.
- The coefficient of variation (CV) of the ISI distributions.

In particular, three conditions should be met and looked for, in order to support signal propagation in self-sustained irregular and asynchronous regime:

- Sustained activity.
- Low firing rates.
- CVs of the ISI distributions near to 1.

Network dynamics

Parameter Search

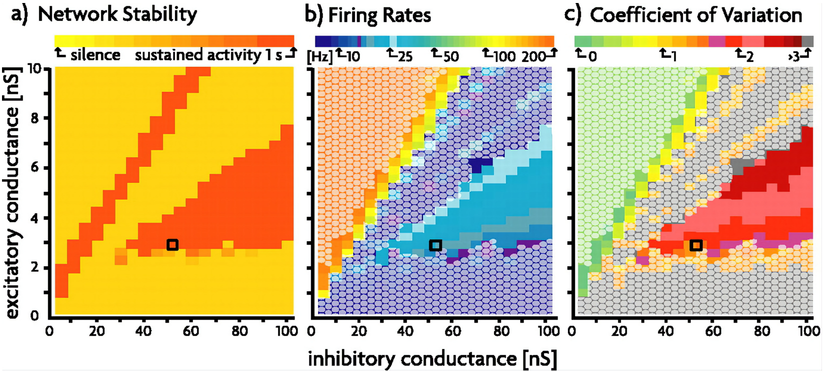

Figure: Network activity duration (**a**), average firing rate (**b**) and average CV of ISI distributions (**c**) varying the synapses conductances. Black squares indicate the parameter chosen for the next simulation.

Network dynamics

Simulation example

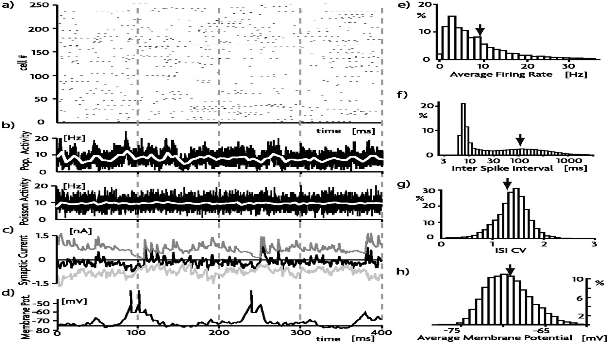

Figure: Raster plot (**a**) and comparison of population activity with Poissonian one for 250 sample neurons (**b**); synaptic currents (**c**)) and membrane potential for a sample neuron (**d**). Distribution of average individual single firing rates (**e**), ISI distributions (**f**), distribution of CV of ISIs (**i**) and of the average membrane potentials (**h**).

Network dynamics
Comments on the simulation

- Raster plot, average activity and autocorrelation do not reveal any evident temporal structure.
- Comparison with a Poisson process with analogous mean activity shows that the latter is more regular, though the fluctuations sizes are comparable.
- Inhibitory and excitatory currents are balanced, keeping the average potential at -70 mV.
- A random selected neuron shows bursting activity and irregular firing.
- ISI distributions highlight a bursting behaviour of the population, with two different time scales represented by two separated peaks.

Differences between CUBA and COBA models

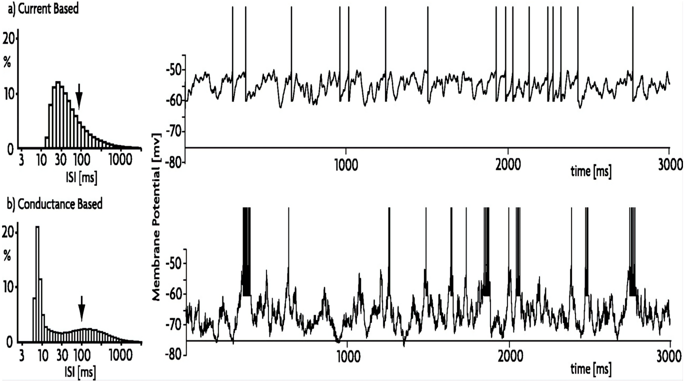

Figure: ISI distributions and membrane potentials of a sample neuron for CUBA model (**a**) and for COBA model (**b**).

Differences between CUBA and COBA models

Comments

- Synaptic strength of CUBA model must be modified to obtain the same firing rate of COBA.
- ISI distribution and sample trace of CUBA model shows absence of bursting behaviour, similarly to Poissonian spiking.
- A constant depolarising current must be injected to all CUBA neurons in order to have sustained activity.

Cause of differences

The different behaviours arise from the voltage dependence of EPSPs and IPSPs amplitudes in the COBA model, caused by the driving-force, which shrinks EPSPs and increases IPSPs with increasing depolarisation, and does the opposite during hyperpolarisation. This creates a stabilisation mechanism essential for sustained activity, keeping the membrane potential steadier than for CUBA.

Signal propagation

Method

To test how signal propagates through the network, existing pathways are searched in the following way:

1. The input to the network is received from a layer 0 of neurons, not belonging to the actual network and whose Poissononian activity is artificially modulated modifying their mean rate $r_0(t)$.
2. A layer 1 of 33 neurons is selected randomly in the network, receiving input from layer 0.
3. Layers i=2,3,4,5,6 of 33 neurons are selected among the ones receiving more than 3 synapses from the previous layer, with the constraint of not receiving inputs from the other previous layers.
4. Signal propagation is controlled by modifying the properties of the pathway neurons and synapses.

Signal propagation

Modification of the signalling pathways

Three strategies are used to modify the pathway properties:

1. Depolarisation of the pathway neurons: this increases the firing rates, but no propagation is observed beyond layer 1.
2. The gain of pathway neurons is increased, modifying the strength of all their synapses: this sensitises the pathway neurons to all inputs and the balance of currents prevents the increase of firing rates. No propagation is observed.
3. Increasing only the pathway synaptic weights: this achieves propagation when the weights are increased by a $\simeq 10$ factor.

Synapses factor is defined as the ratio of the strength of excitatory pathway synapses to other synapses, minus 1.

Signal propagation

Modification of the signalling pathways

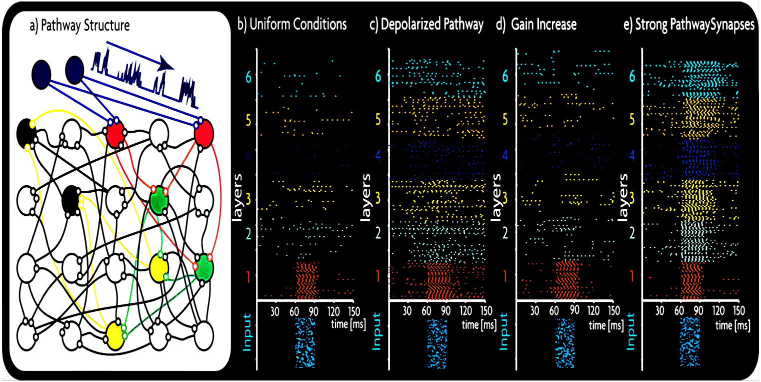

Figure: Illustration of pathways in the network (**a**); raster plots under original condition (**b**) and for the three different strategies.

Optimal synaptic enhancement
Methods

With a constant input by layer 0, it is possible to find the optimal synapse factor by looking at the average firing rate of each layer: the value for which the firing is the same in all layers is chosen to be the optimal one.

Optimal factors are computed for different input rates: COBA model presents a larger plateau than CUBA one, allowing variety of inputs to be transmitted with a fixed synapse factor.

An alternative measure is provided by the average probability of spiking for a pathway neuron within 5 ms from a presynaptic spike in the previous layer: increasing the synaptic factor, this increases from near 0 to 0.4.
The same probability is increased by almost a factor 3 with synchronous triplets of presynaptic spikes.

Optimal synaptic enhancement

Results

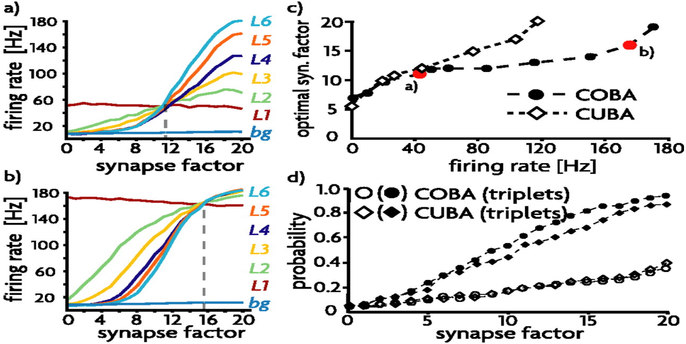

Figure: Firing rates of layers in response to constant input at 50 spike/s (**a**) and 170 spike/s (**b**) varying the synapse factor, optimal synapse factor varying the rate of the input (**c**) and probability of postsynaptic spike following a presynaptic spike in the previous layer for CUBA and COBA model (**d**).

Synfire propagation
Methods

- Synfire propagation is tested evoking synchronous spikes in layer 0.
- Propagation occurs only increasing the synapses by a factor 12: however, the tight synfire packet loses its coherence propagating across the layers, causing long-lasting activity.
- This happens due the fact that, while probability of spikes increases linearly with the number of presynaptic spikes, the total number of evoked spikes grows faster because of multiple spikings of single neurons: multiplication of spikes in successive layer occurs, lengthening the duration of the propagation.
- Weakening all synapses onto pathway neurons (by a factor 10) and increasing just the pathway ones (x30), synfire propagation is correctly achieved.
- Rise times are larger if the signal is turned off than if it is turned on, and increase across the layers.

Synfire propagation

Results

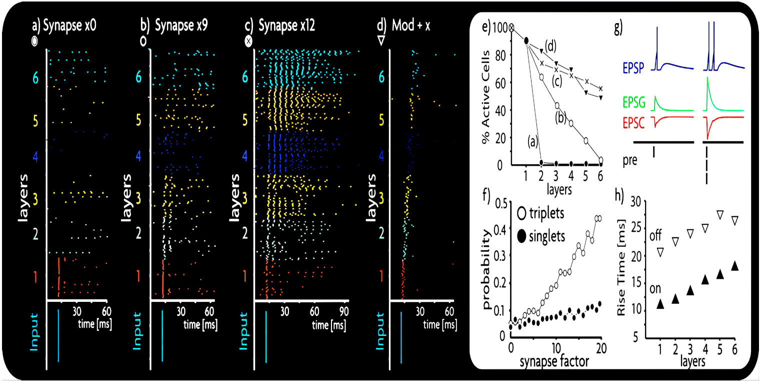

Figure: Synfire propagation for different synapse factors (**a**, **b**, **c**), and with gain modulation (**d**). Number of active cells in the wave front of a synfire event (**e**). Probability of spiking following presynaptic singlets or triplets (**f**). Multiple spiking (**g**). Rise time delays for square pulse input at 100 spike/s (**h**).

Different inputs
Similarity measure

Signal propagation is further tested with a white noise low-pass filtered at 50 ms (half-wave rectified) as firing rate of layer 0, showing again similarities among the layers rates.

Similarity and propagation delay

A more quantitative similarity measures among the layer and layer 0 is defined as:

$$C_i(\tau) = \frac{\langle (r_0(t) - \bar{r}_0)(r_i(t+\tau) - \bar{r}_i) \rangle_t}{\sqrt{\langle (r_0(t) - \bar{r}_0)^2 \rangle_t \langle (r_i(t+\tau) - \bar{r}_i)^2 \rangle_t}}$$

Similarity is defined as the maximum of $C_i(\tau)$, while the **propagation delay** is defined as the value of τ at which the maximum occurs.

The delays varies from 0 to 20 ms (for layer 6), while similarities values are larger for COBA model than for CUBA.

Again, similarities values critically depend on the synapse factor.

Different inputs

Frequency dependence and Multiple pathways

Finally, the input signal is sinusoidally modulated, to test the frequency response:

- Transmission is most accurate for $f \simeq 5$ Hz, and drops in accuracy at $f \simeq 20$ Hz
- Looking at the propagation delays, we see that the maximum rate of change in frequency is $\simeq 6$ Hz/ms: faster changes are not elaborated by the network, and signals working at this rate get lost because of the lengthening phenomenon.

Multiple pathways

It is possible to feed simultaneously more than one signal to the different pathways of the network: transmission quality drops because of interference, but transmission above noise level is still possible.

Different inputs

Similarity, frequency dependence and multiple pathways

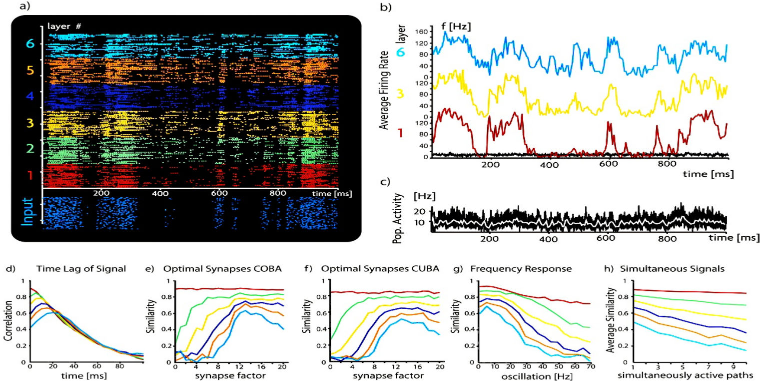

Figure: Raster plots, firing rates of each layer and population activity varying the input (**a**, **b**, **c**). Correlation among the layers in function of time delay (**d**), similarities in function of the synapse factor (**e**, **f**). Similarities for sinusoidal input (**g**) and for multiple signals in 10 different pathways (**h**).

Logical gates

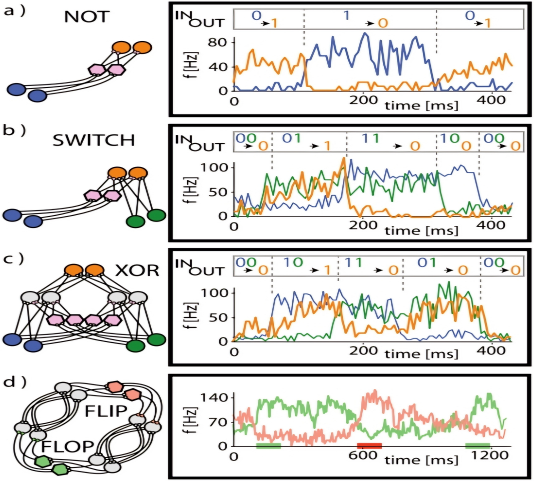

Figure: Logical circuits (left) and firing rates of their inputs and outputs (right). Hexagons represent inhibitory neurons.

Bibliography

[1] Tim P. Vogels and L. F. Abbott. "Signal Propagation and Logic Gating in Networks of Integrate-and-Fire Neurons". In: *Journal of Neuroscience* 25.46 (2005), pp. 10786–10795. ISSN: 0270-6474. DOI: 10.1523/JNEUROSCI.3508-05.2005. eprint: https://www.jneurosci.org/content/25/46/10786.full.pdf. URL: https://www.jneurosci.org/content/25/46/10786.