Conditions for a large out-degree in the graph of synaptic connections in case of unsupervised synaptic plasticity

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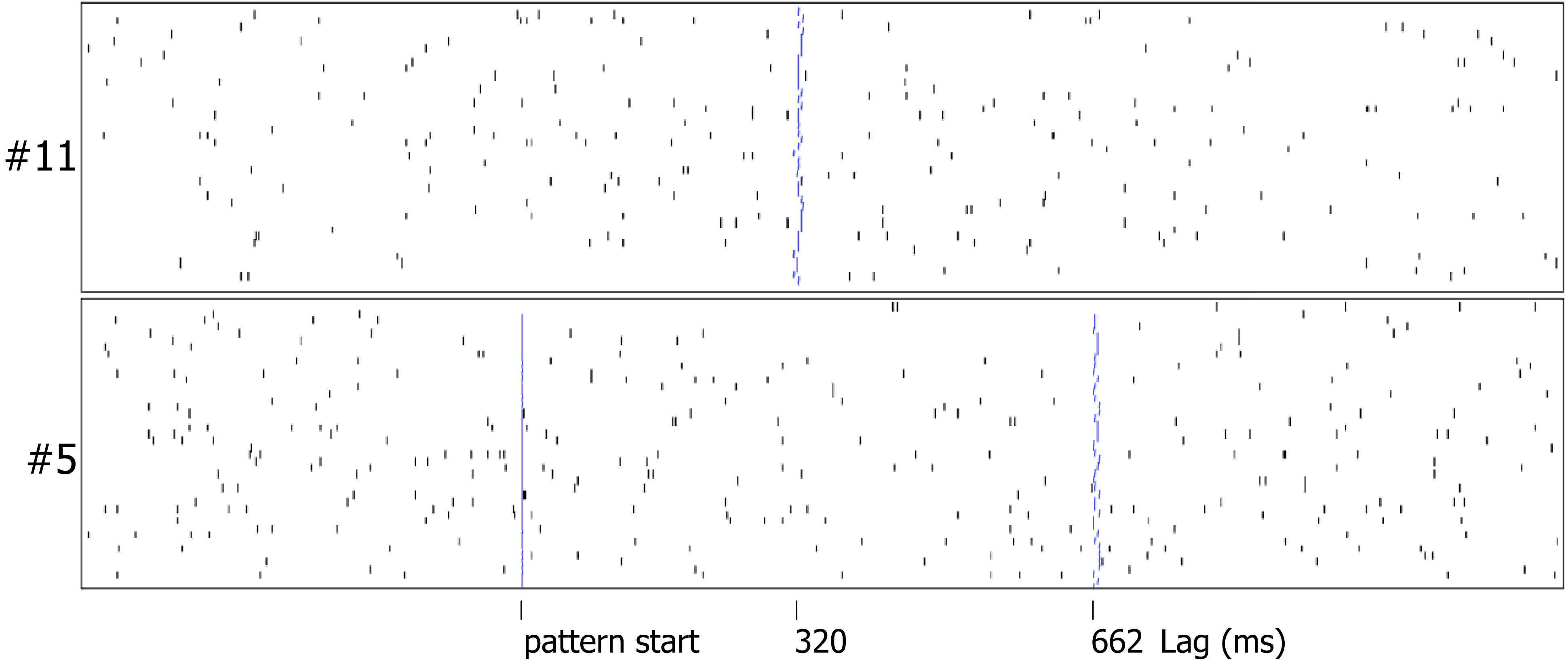
Motivation

Experimental evidence show the occurrence, above chance levels, of recurrent spatiotemporal patterns of firing with jitters as low as few ms over intervals of hundreds of ms. These patterns of activity were observed in association to specific behavioral tasks in rodents and primates.



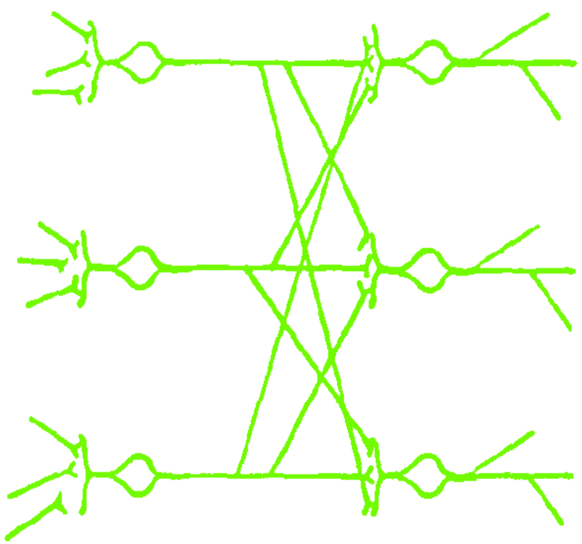
Villa A.E.P., Tetko I.V, Hyland B., Najem A. (1999) Spatiotemporal activity patterns of rat cortical neurons predict responses in a conditioned task , Proc. Natl. Acad. Sci. USA 96: 1006-1011.

Motivation

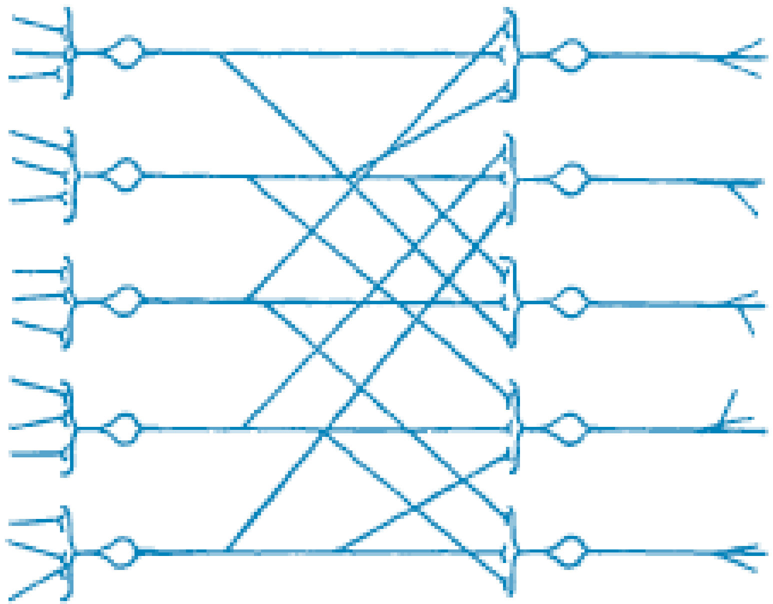
Such an impressive time accuracy has raised several questions about the possible underlying networks able to sustain it.

The model of synfire chains was proposed by Abeles (1982, 1991).

complete diverging/converging chain

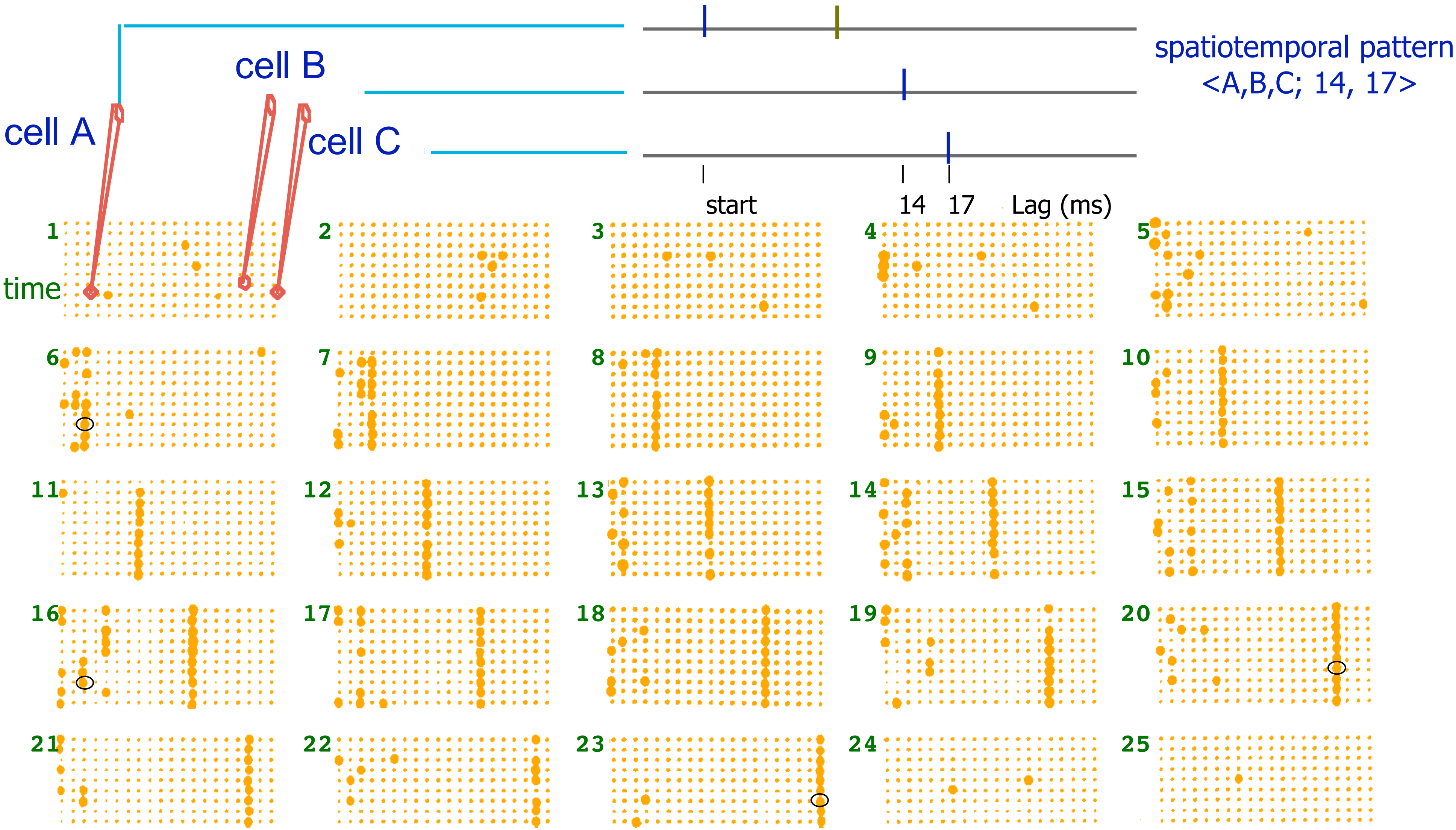


partial diverging/converging chain



Abeles M. (1982) Local cortical circuits, Springer Verlag / Berlin-Heidelberg-New York.

Motivation



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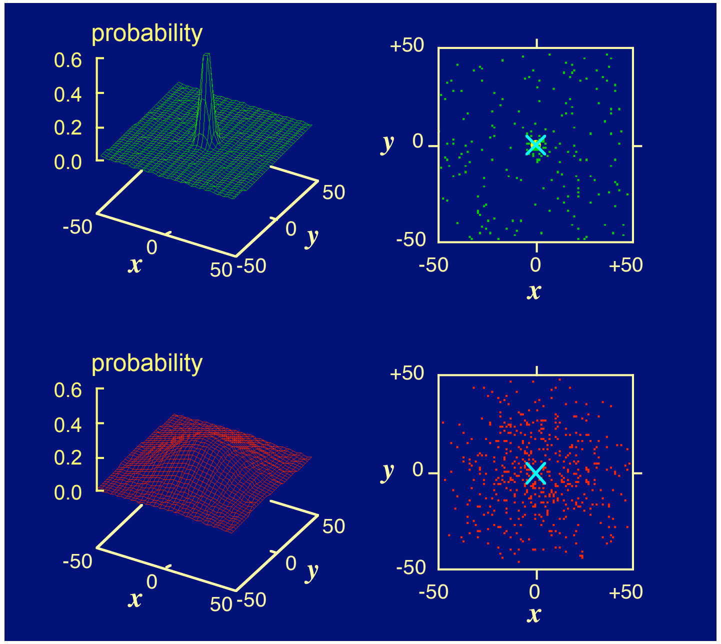
Model

- **Connectivity**

We consider a graph Λ that contains 2 types of neurons



- Excitatory neurons at every vertex $\Lambda^+ = [-N,N]^2$
- Inhibitory neurons at every vertex

$$\Lambda^- = (1/2;1/2) + 2\Lambda^+$$
$$= \{(1/2\,;\,1/2) + (x,y) : x=2k \text{ and } y=2n\}$$

such that $\Lambda = \Lambda^+ \cup \Lambda^-$

- **Potential**

$X_v(t)$ denotes the membrane potential of a neuron at point $v \in \Lambda$ at discrete time t.

$X_v(t)$ is a random process, $X_v(t) \in [0,1]$.

If $X_v(t) = 1$ we say that the neuron v fires at time t.

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Network

We consider the Markov process $(X_v(t), G(t), W(t)),\ t \in \{0,1,\ldots\}$, where

$X_v(t) = (\ X_v(t),\ v \in \Lambda\ )$;

$G(t)$ is a (random) graph with a set of vertices Λ and a set of directed edges $L(t)$, which represent synaptic connections such that if $(u,v) \in L(t)$ then there is a synaptic connection from neuron u to neuron v at time t.

$W(t) = \{w_t(u,v),\ (u,v) \in L(t)\ \}$ is a set of synaptic weights.

- if a neuron u is excitatory ($u \in \Lambda^+$) then
  $w_t(u,v) \in \{0,\ \alpha_0, \alpha_1, \alpha_2\}$, where $0 < \alpha_0 < \alpha_1 < \alpha_2 \le 1$.

- if a neuron u is inhibitory ($u \in \Lambda^-$) then
  $w_t(u,v) \in \{0,\ -\gamma\}$, where $0 < \gamma \le 1$.

Also define $w_t(u,v) \equiv 0$ if $(u,v) \notin L(t)$.

Initial state

Let us define the initial state $(X_v(0), G(0), W(0))$

$X_v(0) = X_v$ for all v , where X_v are independent random variables uniformly distributed on $[0,1]$.

$G(0)$ is a random graph on Λ such that any edge (u,v) is presented with a probability

$$p_0(u,v) = \begin{cases} q\,, & \text{if } |u-v| \le d\,, \\ p\,, & \text{otherwise,} \end{cases}$$

independent of other edges, such that $p << q$ where

$p = p(N)$ is the probability to establish a long-range connection,

$q \sim const$ is the probability to establish a short-range connection.

Then $L(0)$, the set of edges of $G(0)$, is a random set of edges chosen with the above probabilities.

$W(0) = \{ w_0(u,v) : (u,v) \in L(0) \}$ is in *medium* strength: $w_0(u,v) = \begin{cases} \alpha_1, & \text{if } u \in \Lambda^+ \\ -\gamma\,, & \text{if } u \in \Lambda^-. \end{cases}$

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Network activation

Let us assume that at time $t = kT \in \{0, 1, 2, \ldots\},\ k \geq 0$ the neurons with indices in set $A_k \subset \Lambda$ are activated by an external stimulus, such that

$$X_v(kT) = 1 \text{ , if } v \in A_k \ .$$

We call
$$A(t) = \begin{cases} A_k, & \text{if } t = kT, \\ 0, & \text{otherwise.} \end{cases}$$

Any firing neuron sends an impulse to its target neurons in the network along the edges of graph $G(t) = (\Lambda,(L(t)))$.

We define a refractory period $\boldsymbol{\tau}$, $T >> \boldsymbol{\tau}$, such that if a neuron v fires at time t, then

$$X_v(t + i) = 0 \text{ , } 1 \leq i \leq \boldsymbol{\tau} \ .$$

At time $t + \boldsymbol{\tau} + 1$ the state of neuron v is reset to a random variable which is an independent copy of X_v :

$$X_v(t + \boldsymbol{\tau} + 1) =_d X_v \ .$$

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Propagation of stimulation

The spread of activation through the network is defined by the following algorithm:

1. Assume the external stimulation occurs at time $t = kT$, for some $k \geq 0$.
2. Define $E(t+1) = \left\{ v \in \Lambda \setminus A_k \ : \ X_v(t) + \sum_{u \in A_k} w_t(u,v) \geq 1 \right\}$.
3. If $E(t+1) = \varnothing$ then stop the algorithm .
4. Else, assume the sets $E(t) := A_k$, $E(t+1), \ldots, E(t+n)$ are defined.
5. Find $E(t+n+1) = \left\{ v \in \Lambda \setminus \cup_{i=0}^{n} E(t+i) \ : \ X_v(t) + \sum_{v' \in E(t+n+1) \cup E(t+n)} w_t(v',v) \geq 1 \right\}$.
6. If $E(t+n+1) = 0$ then stop the algorithm and define $A(t)$ to be the activation due to the stimulation at time t such that: $A(t) = \cup_{i=0}^{n} E(t+i)$.
7. If $t+n+1 = (k+1)T$ then stop the algorithm and define :

   $$E(t+n+1) = \left\{ v \in \Lambda \setminus \cup_{i=0}^{n} E(t+i) \ : \ X_v(t) + \sum_{v' \in E(t+n+1) \cup E(t+n)} w_t(v',v) \geq 1 \right\} \cup A_{k+1} .$$
8. Increment n .
9. Go to 5.

Spike Timing Dependent Plasticity

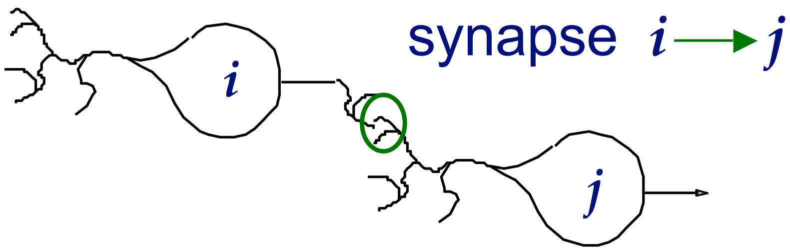
After we defined the activated set $E(t)$ the synaptic weights are updated for all $v \in \Lambda$

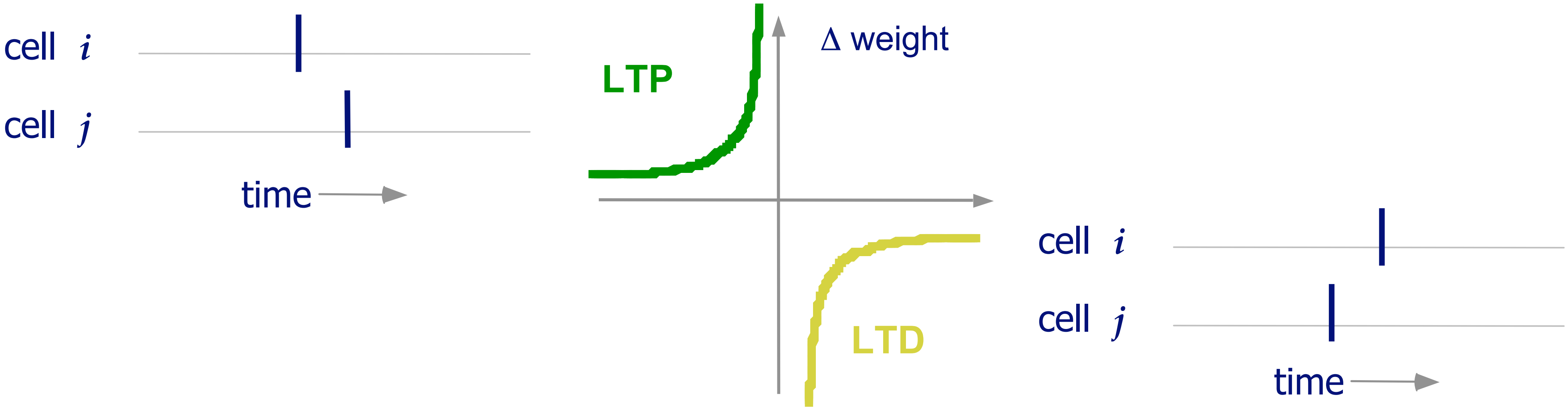
$$w_t(v',v) = \begin{cases} \alpha_2, & \text{if } v \in E(t),\ v' \in E(t-1) \cap E(t-2), \text{ and } w_{t\text{-}1}(v',v) > 0\ , \\ \alpha_0, & \text{if } v \notin E(t),\ v' \in E(t-1) \cap E(t-2), \text{ and } w_{t\text{-}1}(v',v) > 0\ , \\ w_{t\text{-}1}(v',v), & \text{otherwise}\ . \end{cases}$$

This means that the excitatory connection is strengthened if the postsynaptic neuron fires within two time steps after the firing of the presynaptic neuron.
The connection is weakened in the reverse temporal order of firing.

Notice that the inhibitory connections are not modified at this stage.

Spike Timing Dependent Plasticity





Notice that an excitatory synaptic connection is called *effective* whenever the postsynaptic neuron fires shortly after the presynaptic neuron.

Evolution of the in- and out-degrees

We consider some marginal cases, namely the evolution of the *long*-range connections after the first simulation occurred at time $t = 0$.

The probability that $u \in E(1)$, when $|A_0| = \varepsilon N$ and $p(N) = c/N$, is approximately $\alpha_1 c\varepsilon$.

Hence, even when $|A_0|$ is a positive but small fraction of N , the expected value is $\mathrm{E}|E(1)| \approx \alpha_1 c\varepsilon\,(1-\varepsilon)N = \alpha_1 c\,(1-\varepsilon)|A_0|$.

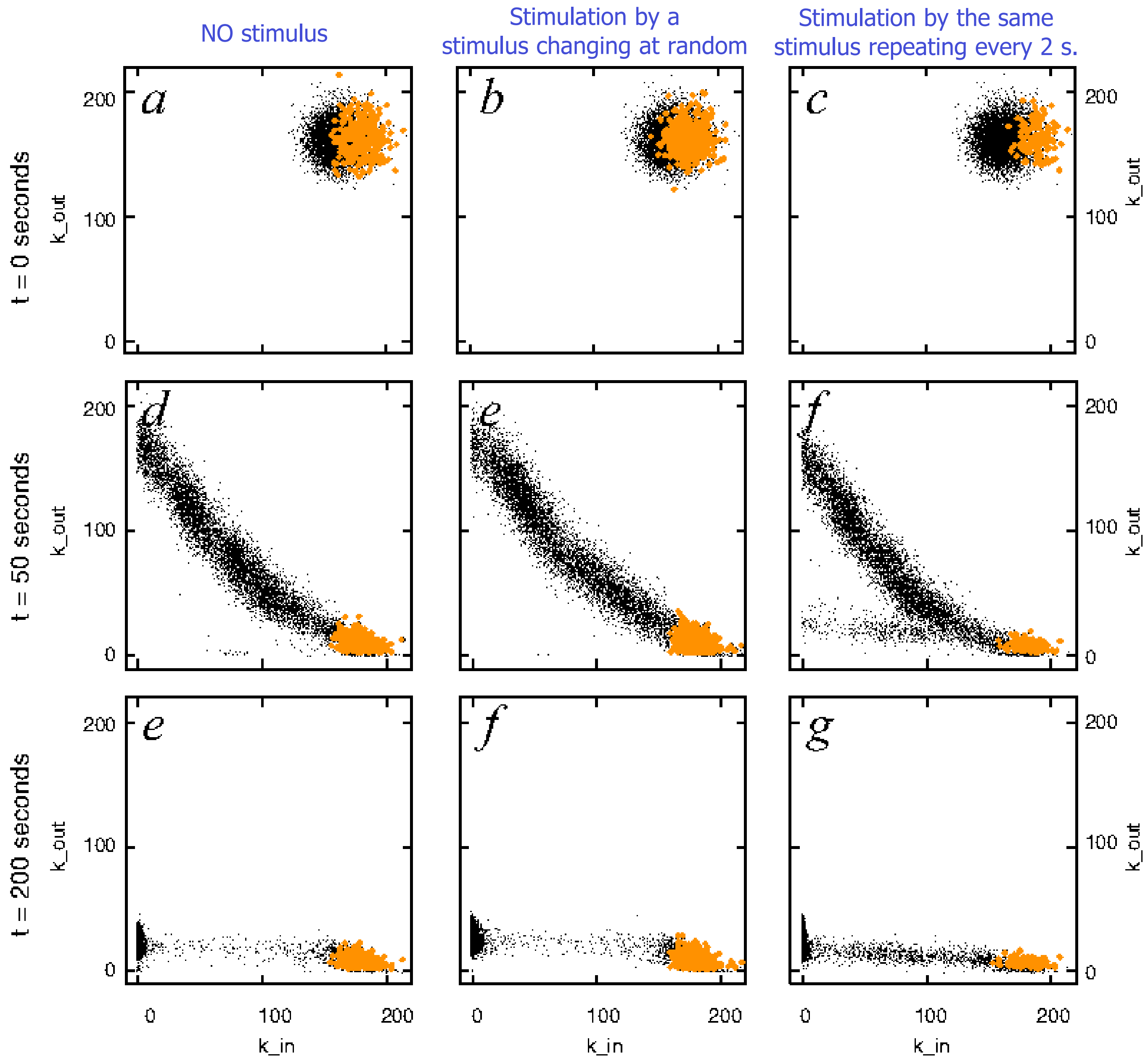
Let denote v_{in} the average in-degree for the neurons in $E(1)$, and v_{out} the average out-degree for the neurons in A_0 .

Then we have $v_{out}|A_0| = v_{in}\mathrm{E}|E(1)|$ and hence:

$$\frac{v_{in}}{v_{out}} = \frac{|A_0|}{\mathrm{E}|E(1)|} \approx \frac{1}{\alpha_1 c\,(1-\varepsilon)}$$

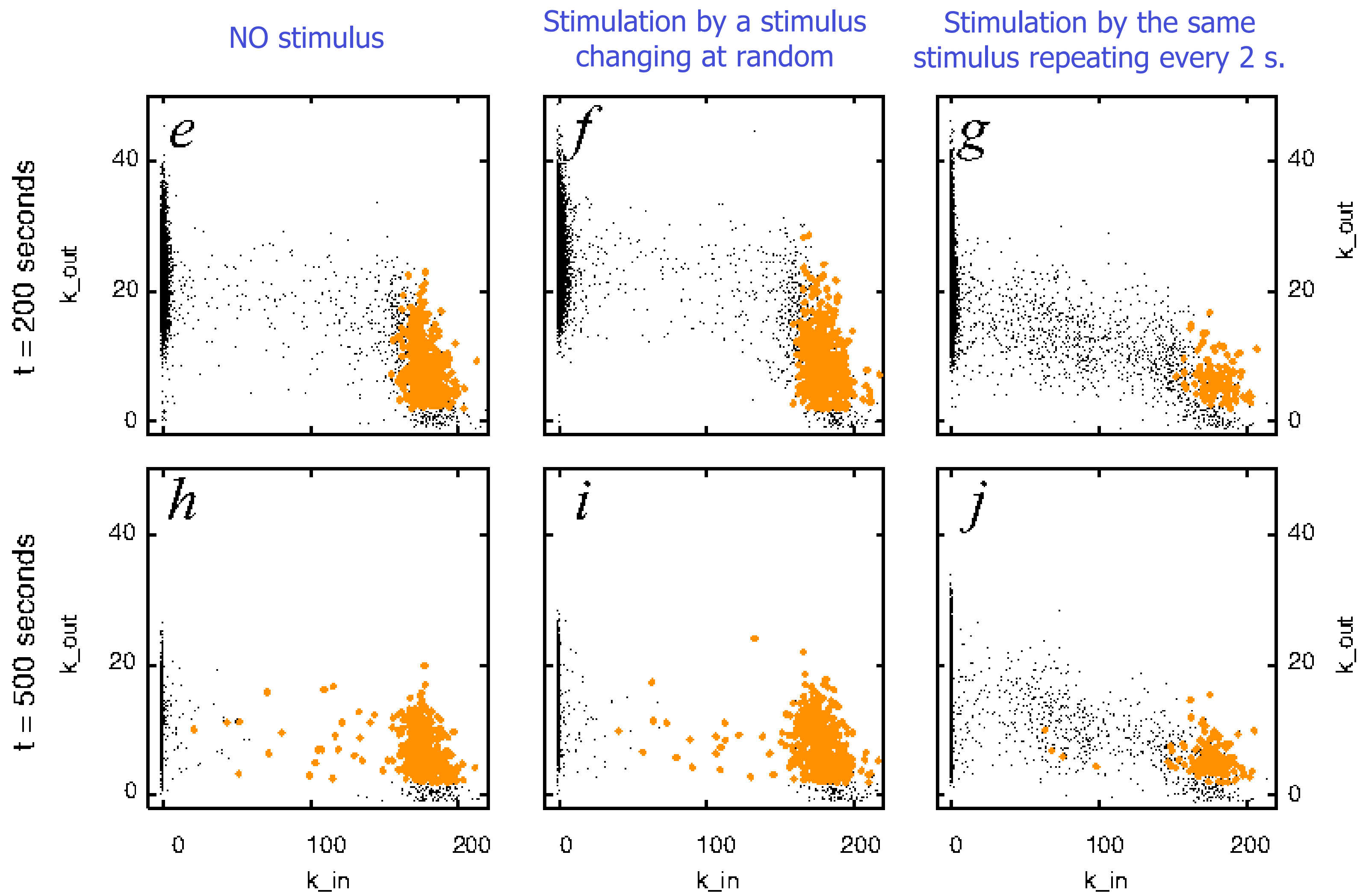
This explains why during synaptic pruning the plasticity of the synaptic connections tends to favor convergence, i.e. an in-degree larger than the out-degree.

Evolution of the in- and out-degrees



• **SIU**
Strongly-**I**nterconnected-**U**nit:= unit not directly stimulated and projecting to at least 3 other **SIUs**

Evolution of the in- and out-degrees



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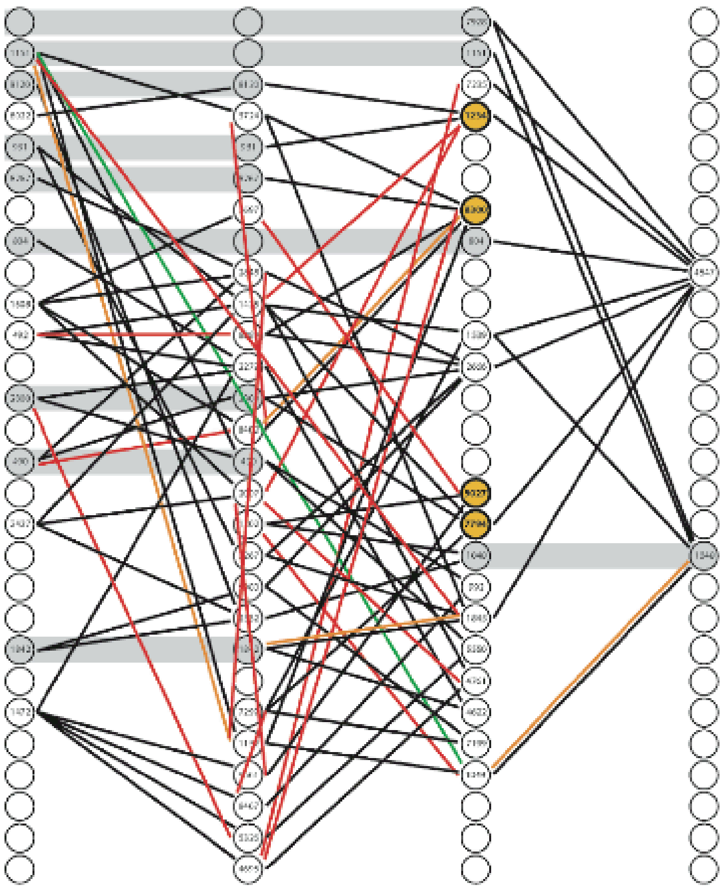
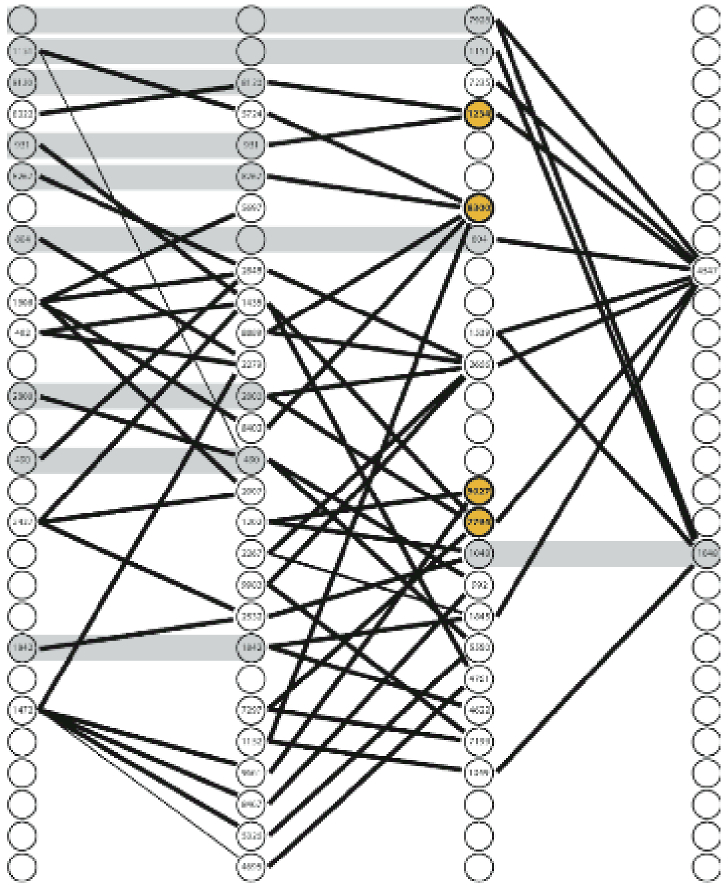
Evolution of the in- and out-degrees

In fact, a "convergent" pattern of connectivity remains dominant through the entire network, even when the network reaches a steady state, as observed by Iglesias and Villa (2005) and independently confirmed by Turova and Villa (2007).





Conditions for obtaining a larger out-degree with STDP

The *necessary* conditions are:

- a neuron should be activated several times between two consecutive stimulations;
- on each successive firing the target neurons that become activated should be independent.

Some *sufficient* conditions are:

- a neuron is firing and its effective synaptic projections are strong (i.e., synaptic weight α_2, either due to a direct stimulation or to the stimulus-induced propagation of activity in the network)
- then there is a *high probability* that those synaptic links will transmit again an impulse at the next firing, while other independent links become stronger.

Hence a neuron will increase the number of effective synaptic connections at each new firing within a certain interval. If the interval between the consecutive firing is large, then the previously established effective links may become weaker or even disappear.

Propagation of activity by excitatory neurons

We shall roughly estimate the size of $A(t)$, the activation due to a single stimulation.

- **Subgraph of the *long*-range connections only**

After a discharge of neuron v , $X_v(t)=1$, the probability that a neuron u , with membrane potential X_u uniformly distributed on $[0,1]$, fires at time $t+1$ is at least $\alpha_1 p(N)$, where $p(N)$ is the probability to establish a *long*-range connection.

It is known from the theory of random graphs that if a probability of an edge is $p=\frac{c_0}{N}$ where $c_0>1$, then with a *high probability* a graph will have a connected component spanning through a positive part of the graph.

This implies that if $p(N)=\frac{c}{N}$ and $\alpha_1 c>1$, then there is *positive probability* that the excitation of even a single neuron will generate an excitation of a positive part of the network.

Propagation of activity by excitatory neurons

- **Subgraph of the *short*-range connections only**

After a discharge of neuron v , $X_v(t) = 1$, the probability that a neuron u , with $|u - v| \leq d$ and membrane potential X_u uniformly distributed on $[0,1]$, fires at time $t + 1$ is at least $\alpha_1 q$, where q is the probability to establish a *short*-range connection.

It is known from percolation theory that in the case of closest neighbours, i.e. when $d = 1$, there exists $0 < p_{critical} < 1$ such that if $\alpha_1 q < p_{critical}$, then with probability 1 the excitation from a single neuron will activate only a finite number of neurons.

In the case of dimension 2, then $p_{critical} = 1/2$.

Propagation of activity by excitatory neurons

- **Model with *long*- and *short*-range connections but only formed by excitatory neurons**

It was shown recently (Turova and Vallier, 2006) that the activity of a network with both local and global connections is characterized by a non-trivial phase transition.

Namely, even when $\alpha_1 q < p_{critical}$ and $\alpha_1 c < 1$, there is *positive probability* that the excitation of a single neuron may spread to a positive part of the network.

Discussion

Questions to address in the future:

- Is it possible to establish a relation between the structure of the network and the operations that it can perform ?
- What is the firing pattern of those neurons appearing at several layers, thus forming loops of feedback activity ?
- What kind of stimulus variability and frequency of occurrence is necessary for obtaining a large out-degree ?

References

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Turova T.S. and Vallier T., (2006) *Merging percolation on* Z^d *and classical random graphs: Phase transition*. (arXiv:math.PR/0612644, submitted).

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