

Large-scale modelling of neuronal systems

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Summary. — The brain is, without any doubt, the most complex system of the human body. Its complexity is also due to the extremely high number of neurons, as well as the huge number of synapses connecting them. Each neuron is capable to perform complex tasks, like learning and memorizing a large class of patterns. The simulation of large neuronal systems is challenging for both technological and computational reasons, and can open new perspectives for the comprehension of brain functioning. A well-known and widely accepted model of bidirectional synaptic plasticity, the BCM model, is stated by a differential equation approach based on bistability and selectivity properties. We have modified the BCM model extending it from a single-neuron to a whole-network model. This new model is capable to generate interesting network topologies starting from a small number of local parameters, describing the interaction between incoming and outgoing links from each neuron. We have characterized this model in terms of complex network theory, showing how this learning rule can be a support for network generation.

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1. – Description

We start from the Bienenstock, Cooper and Munro (BCM) nonlinear model for the synaptic plasticity of single neuron synapses (fig. 1), which represents each incoming synapse with a $[0; 1]$ real number, and expresses the time evolution of each incoming synapse as a function of the neuron output, the values of the synapses and previous

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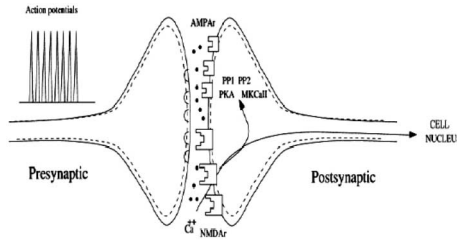


Fig. 1. – Scheme of a synaptic junction. Left side (pre-synaptic) is the axon end, right side (post-synaptic) is the dendrite.

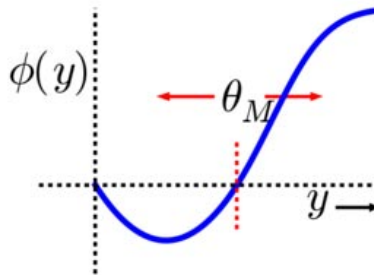


Fig. 2. – The moving threshold, as stated by the BCM theory.

neuron firing history. This formulation determines a high level of selectivity of the neuron, which at the end of the training becomes responsive to only one of the incoming stimuli. We were searching for a simple model describing a neural network evolution based on the BCM model, which obtained great experimental confirmation for the primary visual cortex development. We simplified BCM equations (generalizing them in some way) and added to the model few parameters modulating the competition between each group of links (*e.g.* incoming and outgoing). These groups emerge intuitively in the transition between the single neuron and the network model. The classical network evolution models [1], Barabasi-Alberts preferential attachment rule [2], and the Watts-Strogatz rewiring model [3], were discarded because we were looking for a continuous model which could determine the dynamics of each link with only local information available.

Bienenstock, Cooper and Munro proposed [4] for the first time a model for synaptic plasticity which could generate long-term depotentiation (LTD) without external impositions. This model was developed as a heuristic model for explaining the experimental data of the sensorial-cortex neurons selectivity to the inputs. It is based on the Hebbian model, replacing the Φ constant with a $\Phi(y, \theta_M)$, nonlinear function of y and θ_M , a parameter that regulates the plasticity direction: LTD if $y < \theta_M$ and long-term potentiation LTP if $y > \theta_M$.

The $\Phi(y, \theta_M)$ function shape is displayed in fig. 2. The competition is incorporated in the equation defining θ_M as a function of the squared mean of the output [4]. This forces the selection threshold to adapt to the output levels as time goes by. The synapses with an activation level below the neuron activation will be depotentiated, while the synapses with a stronger activation value will be potentiated, leaving only the latter in the end.

The system is described by the equations below:

$$(1) \quad \begin{cases} y &= \sigma \left(\sum_i \omega_i x_i \right), \\ \frac{dw_i}{dt} &= y (y - \theta_M) x_i \sigma'(y), \\ \theta_M &= E[y^2], \end{cases}$$

in which $E[]$ represents a time average and, for large averaging periods, corresponds to an average over the input distribution. From a statistical point of view, these equations perform a minimization of the following objective function [5]:

$$R = \frac{1}{4} E [y^2]^2 - \frac{1}{3} E [y^3],$$

which quantifies the difference from a Gaussian (symmetric) distribution. The BCM selection rule is therefore equivalent to the input combination which maximizes the non-Gaussian form of the output.

This discriminating behavior for input signals has some interesting properties, first of all the linearity of the objective function gradient with respect to the dimensionality of the problem, keeping it tractable even in high-dimensional spaces. The selectivity also allows a research of the projections of the synaptic weight vector orthogonal to the whole input vectors except one, creating a state completely described by K optimal projections, instead of $\frac{1}{2}K(K-1)$ planes which describe the boundaries between clusters. This property is cardinal when the problem dimensionality is high, because it avoids the *curse of dimensionality*, which requires an exponentially growing amount of data with the dimension increase for sufficient statistics [6].

We worked on a set of equations similar to the original BCM model [7], expanding it into a multi-neuronal system under the hypothesis of a slow variation of the synaptic weight, so to substitute the time-average with the instantaneous value of each link. Calling x_{ij} the weight of the synapses starting from neuron i to neuron j , we considered the following general equation:

$$(2) \quad \dot{x}_{ij} = x_{ij} \left(x_{ij} - x_{ij}^2 - a_{ijkl} \sum_{i \neq k, j \neq l} x_{kl}^2 \right),$$

in which a_{ijkl} is a fourth-order tensor which describes the interaction of each pair of synapses. A positive value of a_{ijkl} corresponds to a competition between link x_{ij} and x_{kl} , a negative value to a cooperation. The simplest case is the so-called homogeneous competition, with a constant tensor $a_{ijkl} = a \forall i, j, k, l$. This case is useful for mathematical analysis but is too simplistic, so we considered local interaction between links subdividing them into equivalence classes of competition. Imposing a local interaction (only synapses belonging to the same neurons could interact) we subdivided the tensor into four main classes of interaction: ingoing links, outgoing links, hierarchical links and reciprocal. The ingoing links are those links that enter into the same neuron, and were the only ones considered in the BCM model. The outgoing links are those that exit from the same neuron, and the competition among them is due to the energy cost of the maintenance of a lot of synapses. The hierarchical competition is a different selection rule

that forces the neuron to sacrifice the incoming or the outgoing connection, specializing into an input or output neuron. The last one, the reciprocal competition, controls the reciprocal connections between neurons.

$$(3) \quad \frac{dx_{ij}}{dt} = x_{ij}^2 - x_{ij} \left[x_{ij}^2 + A_r x_{ji}^2 + A_i \sum_{l \neq j} x_{il}^2 + A_o \sum_{k \neq i} x_{kj}^2 + A_g \left(\sum_{k \neq j} x_{ki}^2 + \sum_{l \neq i} x_{jl}^2 \right) \right].$$

2. – Analysis

Generic model analysis. – First we started with the analysis of the model of N nodes with symmetrical and homogeneous competition. The evolution equation can be treated analytically when there are only two nodes: when the modulating parameter A goes below a critical value, the competition is weak enough to allow both links to survive, and we observe a phase transition even in this simple bidimensional system. Then we extended these results to the n -dimensional system, showing that the system always has a Lyapunov function if the interaction between nodes is symmetrical, and the system shows an exponential convergence to a stable state with at maximum $A - 1$ alive links, distributed approximately with a Poisson function. This interaction topology can be interpreted as a mean-field interaction.

Network topological proximity. – We restricted the concept of mean field from the whole network to a subset of links, chosen from the topological proximity of each link with respect to their starting and ending nodes. We define a competition group consisting of all links incoming to the same node, one for all outgoing links and another, called hierarchical competition, comprising the incoming and outgoing links of the same node. So we have now three different parameters independent from the system dimensionality. These values are positive when two links are in reciprocal competition, and negative when they are collaborating. This model analysis is far over the pen and paper system possibility, so we worked on a wide number of simulations. When the system is composed of N nodes and $N(N - 1)$ links, the ideal algorithmic convergence of this model is $O(N^2)$, but with some simple numerical approximation we can work at $O(N^B)$ with B a real number in the interval $[1; 2]$ with strong parameter and initial condition dependencies.

Bow-tie structure. – A strong hierarchical competition forces a node to choose between incoming and outgoing links. Loosening this condition we can allow the node to stabilize in an intermediate status, with few incoming and outgoing links. The global structure is similar to the hypothesized properties of a human-made network, the World Wide Web [8], which is divided into three groups: the exit pages, with only outgoing links, the entering pages, with only incoming links, and an intermediate, strongly interconnected group with both incoming and outgoing links (see fig. 3).

Metabolic pathways structure. – This network represents the interaction of various proteins involved in metabolic functions of the cell. Each protein has a really specific interaction target, so we can impose that only one, two only in few cases, outgoing links are allowed for each protein (typical outgoing competition parameter of 0.3). We can see in fig. 4 that the resulting network has the same features as a metabolic network. A better approximation is possible by introducing a small collaboration between incoming links (co-regulation is a very common feature, so we can hypothesize to be present in this case).

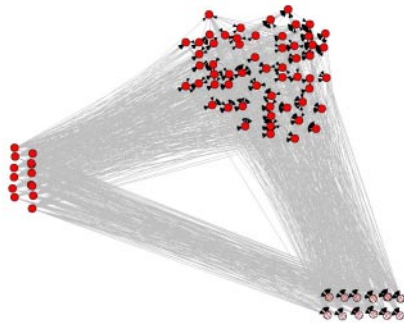


Fig. 3. – Network with a bow-tie structure, resembling the World Wide Web topology.

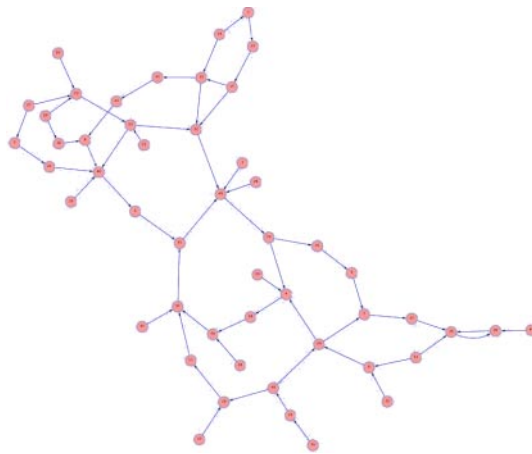


Fig. 4. – Network structure resembling a metabolic pathway.

3. – Conclusions

Network generation and evolution is still an unsolved problem, and there is not evidence that a final word would be ever possible about. The model here proposed shows how a dynamic approach to the problem is possible and, from few reasonable hypotheses (the concept of local competition and collaboration) it is possible to describe a lot of different phenomenological structures (network topologies). The concept of competition is widespread in a lot of different models, from biology to economy, due to the intrinsic minimization of a cost functional, and such behavior is surely common to any system with limited resources.

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