1 Classifying synaptic dynamics using multiple time scale expansion

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Abstract

We seek to classify synaptic dynamics in a unitary, closed form formalism, and take a probabilistic approach wherein the neurons are characterized only by their ensemble average firing rate. We use the multiple time expansion technique, and assume that the long time history dependence comes only from the synaptic dynamics, while the short time history dependence is characterized using firing rate derivatives. The result of this approach is that basic types of synaptic dynamics can be associated with orthogonal polynomials in the firing rate and its derivatives. No neuronal model was needed to build this formalism. The lowest order symmetric term corresponds to Hebbian learning. Using a model for neuronal noise it is possible to make a transformation from the instantaneous representation of the synaptic dynamics (in terms of derivatives of the firing rate) to the time dependence representation (synaptic modification in terms of the time interval between the firing of pre- and post- synaptic neurons). The lowest order antisymmetric polynomial accurately fits the experimental results of Bi and Poo in rat hippocampal neurons (J. Neurosci. 1998). Qualitatively and quantitatively new learning rules are characterized.

Introduction There is a considerable literature on experimental results on synaptic plasticity, some of which cannot be explained using a standard Hebb-like model for the plasticity dynamics (Bi, Poo; J. Neurosci. 1998). We seek a theoretical model capable of classifying the possible learning types, starting from the assumption that all the information a neuron sends is contained in its ensemble average firing rate f (i.e. the probability that given the same inputs the neuron will fire at time t). This is a reasonable assumption since it is a way to filter out the noise, and does not depend on a fixed externally chosen parameter (like the length of the averaging window in the time average method). Being a differentiable function (as opposed to the instantaneous firing rate, which is a sum of δ functions) calculus methods can be applied.

Methods We can describe the evolution of a network using a system of history dependent equations for the ensemble average firing rate. The evolution of the synaptic weights can be described by an operator W.

$w'_{ij}(t) = W_{ij}(f_k(v), w_{lm}(v))$ where $v \in (t-\tau, t)$, τ sets a bound to the extent of history dependence and i, j, k, l, m index the neurons

The long term history dependence can be included into new variables x. The short term history dependence can be expressed in terms of derivatives of the firing rate, obtaining thus a system of ordinary differential equations

$w'_{ij}(t) = F_{ij}(f_k^{(n)}(t), w_{lm}(t), x_a(t))$ where a indexes the long term history dependence in the system except of the synaptic weights.

We are going to constrain the function F_{ij} for the specific requirements of synaptic plasticity.

Results

Instantaneous representation Since in the evolution equation for the synaptic weight the values of all variables at a given time appear, we call this the instantaneous representation . We search for all the possible dynamics given the following biologically realistic constraints:

1. All the long term history dependence comes only from synaptic plasticity (ignoring thus all the contributions from neuromodulators etc.).

$w'_{ij}(t) = F_{ij}(f_k^{(n)}(t), w_{lm}(t))$ where $n \in \mathbf{N}$

2. The learning is local: modification in the synaptic weight depends only on the pre- and postsynaptic neurons

$w'_{ij}(t) = F_{ij}(f_i^{(n)}(t), f_j^{(n)}(t), w_{ij}(t))$

3. The learning is binary: each term in the synaptic weight modification equation depends on both pre- and postsynaptic neurons activity

$w'_{ij}(t) = F_{ij}(f_i^{(n)}(t) \cdot f_j^{(n)}(t), w_{ij}(t))$

4. The dependence of the dynamics of a synapse on its own value is mainly to set a bound. Far from the bound its dynamics is approximately independent of its value

$w'_{ij}(t) = F_{ij}(f_i^{(n)}(t) \cdot f_j^{(n)}(t))$

5. Since, compared to the synaptic strength, the rest of the processes take place at significantly shorter time scales, only the first few terms in the expansion in f_i and its derivatives are significant (however, we can get to arbitrarily good precision by including higher order derivatives)

$w'_{ij}(t) = F_{ij}(f_i(t) f_j(t), f'_i(t) f_j(t), f_i(t) f'_j(t), f'_i(t) f'_j(t), ...)$

6. Since the range of variation of the firing rate is small (e.g. 3 orders of magnitude: 0.1-100 Hz) any function of f can be well approximated by a polynomial so (we can again get to arbitrarily good precision by including higher powers).

The first order learning type which satisfies the previous constraints is (with the implied notation that all the functions are taken as the value at time t):

$$\begin{aligned}\frac{dw_{ij}}{dt} &= a_{11} f_i f_j + \\ &+ a_{12}(f'_i f_j - f_i f'_j) + b_{12}(f'_i f_j + f_i f'_j) + \\ &+ a_{13} f'_i f'_j + b_{13}(f''_i f_j - f_i f''_j) + c_{13}(f''_i f_j + f_i f''_j) + ...\end{aligned}$$

Thus the basic learning rules should contain only some of these terms. The instantaneous representation Slightly different learning rules can be obtained by adding small contribution from the higher order terms to the basic learning rules.

Hebbian learning We express some already known rules in this formalism (k is a multiplicative constant):

Hebb$\frac{1}{t}\left(w_{ij}(t) - w^0_{ij}\right) = k \cdot [\frac{1}{t}\int_0^t f_i f_j dt' - \frac{1}{t^2}\int_0^t f_i dt' \int_0^t f_j dt'']$

$w_{ij}(t) = w^0_{ij} + k \cdot [\int_0^t f_i f_j dt' - \frac{1}{t}\int_0^t f_i dt' \int_0^t f_j dt'']$

taking the derivative with respect to t and doing a Taylor expansion of the integral for small t we obtain:

$\frac{dw_{ij}}{dt} = k\frac{t^2}{12} f'_i f'_j$

which corresponds exactly to one of the terms previously predicted.

Generalizing the Hebb rule to:

$w_{ij}(t) = w^0_{ij} + k \cdot [\int_0^t f_i f_j dt' - \frac{1+\alpha}{t}\int_0^t f_i dt' \int_0^t f_j dt'']$

with $\alpha \lll 1$, we obtain:

$\frac{dw_{ij}}{dt} = k \cdot [\frac{t^2}{12} f'_i f'_j + -\alpha f_i f_j]$

Thus, the Hebb rule covers the zero and second order symmetric terms.

Time dependence representation In order to make a connection to dual patch experiments we should be able to calculate what the modification in the synaptic weight would be, when we force the pre- and postsynaptic neurons to fire at a given time, from the instantaneous representation. Having a model for the noise and assuming that the cell is characterized only by its ensemble average firing rate, there is a canonical way to make the transformation.

The noise model we use predicts that if in one trial the neuron fires at time t_0, receiving the same inputs the probability that it will fire at time t is:

$f\left(t\right)=\alpha\exp\left(-\beta\frac{\left|t-t_0\right|}{RC}\right)+n$
where RC is the time constant of the cell
$\beta\cong\frac{\Delta v}{\sigma_v}$
Δv is the typical current over the threshold when the cell fires
σ_v is the variance in the random current
α being a normalization constant
n is the background firing rate

The variation in the synaptic weight after one firing from both pre and postsynaptic neurons is for the Hebb rule (obtained by taking $t_0=0$ in f_i and $t_0=\tau$ in f_j):

$\Delta w_{ij}\left(\tau\right)=\int_{-\infty}^{\infty}f_i'f_j'dt=k\cdot\left(1-\beta\frac{|\tau|}{RC}\right)e^{-\beta\frac{|\tau|}{RC}}$

which corresponds to the second graph in the figure (using the values $RC=20mw$, $\beta=3$).

By doing the same calculation for the first order antisymmetric term we obtain:

$\Delta w_{ij}\left(\tau\right)=\int_{-\infty}^{\infty}(f_if_j'-f_i'f_j)dt=k\cdot\beta\frac{\tau}{RC}e^{-\beta\frac{|\tau|}{RC}}$

which corresponds to the first graph in the figure. This graph replicates experimental results from hippocampal cell culture (Bi, Poo; J. Neurosci. 1998). This result appear very naturally as one term in the instantaneous representation, and it is a continous function, in contrast with previous models (Song et all; Nat. Neurosci. 2000).

New learning types So far we have demonstrated what type of terms may exist in a learning rule. For a way to group them an additional property has to be added:

7. For uncorrelated firing of the pre- and postsynaptic neurons small synaptic depression occurs (as a first approximation it is unmodified).

We formulate this constrain in the time dependence representation as:

$\int_{-\infty}^{\infty}\Delta w_{ij}\left(\tau\right)d\tau=0$

Both the antisymmetric learning rule and Hebb learning rule follow this constraint.

The noise model we used make $\Delta w_{ij}\left(\tau\right)$ to be exponentially decaying at $\pm\infty$ while the constraint 7 makes the total area under the curve 0; thus we can characterize the qualilatively new learning rules by the number of times the graph crosses the zero line (i.e. number of solution for $\Delta w_{ij}\left(\tau\right)=0$).

Conclusions We have built a formalism capable of describing synaptic plasticity in a time independent way (instantaneous representation). No neuronal model was needed to build this formalism. We have seen that each learning rule can be associated with a polynomial in the pre- and postsynaptic firing rate. The 2nd order symmetric term corresponds to Hebb learning rule. By using a probabilistic neuronal model we can calculate for any learning rule the modification in the synaptic weight when the pre- and postsynaptic neurons are forced to fire at a given time (time dependence representation). The first order

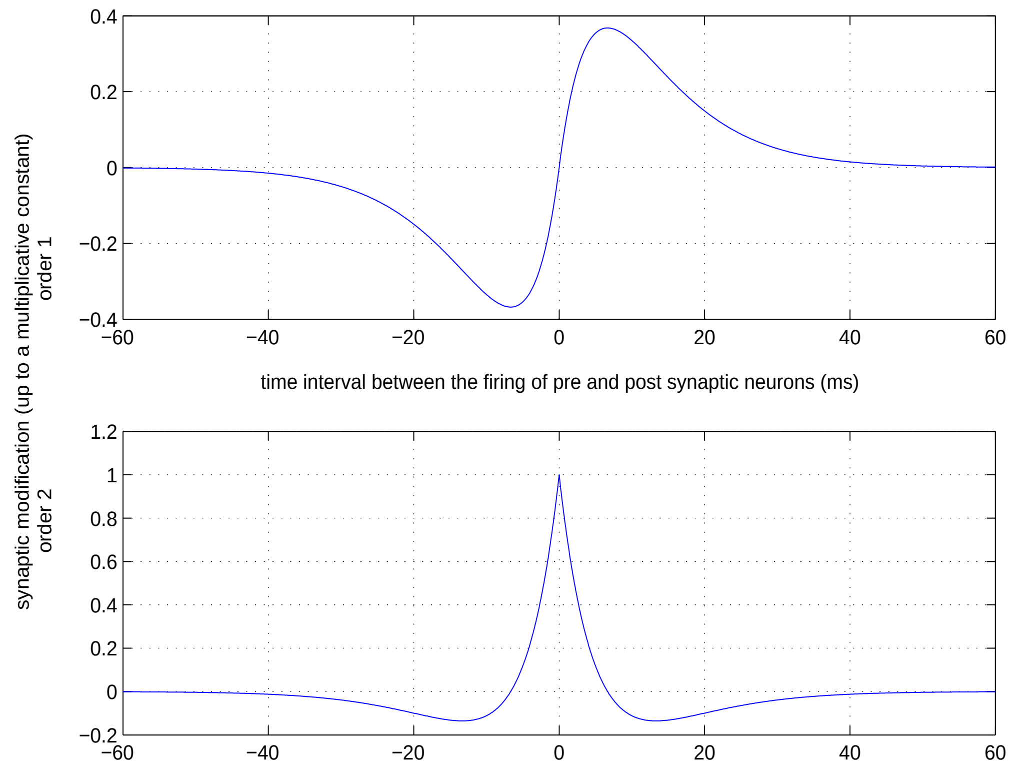

Figure 1: Synaptic weight modification as a function of the firing time interval. The figure shows a graphical representation of the synaptic plasticity time dependence obtained from the first two orders in the instantaneous representation. The first order antisymmetric polynomial is presented in the first graph, while the second order symmetric term (Hebb) is presented in the second graph.

antisymmetric polynomial fits the dual patch experiments from rat hippocampal cell culture quite accurately. We can characterize any learning rule by a polynomial, but qualitatively different ones are expected to be characterized by only one parameter (number of different time intervals between the firing of the pre- and postsynaptic neurons for which the synapse is left unmodified, which is 1 for the first order antisymmetric learning rule (Bi and Poo), 2 for the second order symmetric one (Hebb)).

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