Information capacity of a network of spiking neurons.

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We study a model of spiking neurons, with recurrent connections that result from learning a set of spatio-temporal patterns with a spike-timing dependent plasticity rule and a global inhibition. We investigate the ability of the network to store and selectively replay multiple patterns of spikes, with a combination of spatial population and phase-of-spike code. Each neuron in a pattern is characterized by a binary variable determining if the neuron is active in the pattern, and a phase-lag variable representing the spike-timing order among the active units. After the learning stage, we study the dynamics of the network induced by a brief cue stimulation, and verify that the network is able to selectively replay the pattern correctly and persistently. We calculate the information capacity of the network, defined as the maximum number of patterns that can be encoded in the network times the number of bits carried by each pattern, normalized by the number of synapses, and find that it can reach a value $\alpha_{\max} \simeq 0.27$, similar to the one of sequence processing neural networks, and almost double of the capacity of the static Hopfield model. We study the dependence of the capacity on the global inhibition, connection strength (or neuron threshold) and fraction of neurons participating to the patterns. The results show that a dual population and temporal coding can be optimal for the capacity of an associative memory.

I. INTRODUCTION

Precise spatio-temporal patterns of spikes, where information is coded both in the population (spatial) distribution and in the precise timing of the spikes, has been hypothesized to play a fundamental role in information coding, processing and memory in the brain [1–4].

Notably, precise spatio-temporal memory traces, stored during experience, are replayed during post-experience sleep, with a different time scale but with the same phase-relationship [5–7], It has been conjectured that spontaneous replay of stored patterns during sleep is relevant for memory consolidation.

Indeed, an important feature of cortical activity, reported in a variety of in vivo studies, is the similarity of spontaneous and sensory-evoked activity patterns [8–10] Recently the spontaneous and evoked activity similarity has been reliably observed also in dissociated cortical networks [11], reinforcing the idea that the emergence of cortical recurring patterns, both during spontaneous and evoked activity, is the result of the cortical connectivity (with its micro-circuits and dynamical attractors) [11].

Several neural codes (firing rate, population code, temporal code, phase of spike code, and combinations of these) have been proposed in order to explain how neurons encode sensory information. For long time the rate code hypothesis has been considered adequate, but there is increasing evidence that the timing of spikes relative to others emitted by the same or other neurons may be highly relevant in many situations [3, 4, 12–14].

Recently [3], the performance of different neural codes in encoding natural sounds in the auditory cortex of alert primates has been compared. It has been demonstrated that both temporal spike patterns and spatial population codes provide more information than firing rates alone,

and that they provide complementary informations. Results in primary visual and auditory cortices show that period of slow oscillatory network activity can be used as internal reference frame to effectively partition spike trains and extract phase information [15]. Combining both spatial population activity with temporal coding mechanisms into a dual code provides significant gains of information [3, 13, 14]. A dual code consisting of adding a phase label to population code was found to be not only more informative, but also more robust to sensory noise [3].

Following these experimental results, in this paper we study storage and retrieval of spatio-temporal patterns of activity, where each pattern is formed by a subset of the neurons, firing in a precise temporal order. Therefore, in each pattern the information is coded both in the binary spatial part, indicating which units are active (as in the Hopfield model), and in the temporal part, indicating the spiking order and the precise phase relationships of the units that are active in that pattern.

A fundamental ingredient of the model is the spike-timing dependent plasticity (STDP) rule that shapes the connections between neurons. In the first learning stage, the network is forced to replay the patterns to be encoded, and the STDP learning rule is applied to determine the connections. While within the class of usual autoassociative Hebbian rules (as in the Hopfield model) the connections are symmetric, and therefore the dynamics of the network relaxes towards static patterns, in our case the plasticity crucially depends on the temporal order of the spikings, and results in asymmetric connections between neurons, so that the attractors of the dynamics are spatio-temporal patterns with a defined order of spiking of the neurons. We add, to the connection determined by the STDP rule, a term representing a global

inhibition, that reduces the probability that a neuron not participating to the pattern fires incorrectly.

The model is different from other models of memory storage of dynamical patterns, as sequence processing neural networks [16, 17] and synfire chains [18–21], because in such models patterns are characterized by pools of neurons that fire synchronously, each pool can belong only to one chain, and each neuron can belong to more than one pool, thus firing at different times within the pattern. In our case, a pattern is characterized by a pool of neurons that are inactive during all pattern evolution, while other neurons fire sequentially, so that no synchrony between neurons is required, and each active neuron is characterized by a precise time of firing with respect to other active neurons within the pattern.

Therefore our model is more similar to the Polychronization model introduced by Izhichevich [22] where precise reproducible time-locking patterns emerges in network dynamics. Differently from our model, in the model of Izhichevich polychronous groups are not stable attractors from dynamical system point of view, they emerge with a stereotypical but transient activity that typically lasts less then 100 ms [22].

II. THE MODEL

We simulate a network of N leaky integrate-and-fire neurons, where a number P of spatio-temporal pattern are encoded in the connections. The activity of the neuron $j = 1, \ldots, N$ in pattern $\mu = 1, \ldots, P$ is given by the periodic spike train

$$x_j^\mu(t) = \xi_j^\mu \sum_{n=-\infty}^{\infty} \delta \left[t - \left(\frac{\phi_j^\mu}{2\pi} + n \right) T^\mu \right],$$

where $\xi_j^\mu = 0, 1$ are randomly and independently drawn binary variables indicating if neuron j participates or not to the pattern, $0 \leq \phi_j^\mu < 2\pi$ are randomly and independently drawn variables indicating the phases of firing, T^μ is the period of the pattern, and the integer number n spans all the spikes emitted by the neuron. We extract randomly P patterns, where $0 < M \leq N$ of the neurons are active, that is have $\xi_j^\mu = 1$, while the remaining $N - M$ have $\xi_j^\mu = 0$, and we extract randomly the phases ϕ_j^μ for the M active neurons.

Then, in the first learning stage, we set the connection between pre-synaptic neuron i and post-synaptic neuron j using the learning rule

$$J_{ij} = -I_0 + E_0 \sum_{\mu=1}^{P} \frac{T^\mu}{\hat{T}} \int_0^{\hat{T}} dt \int_0^{\hat{T}} dt' \, x_i^\mu(t') A(t-t') x_j^\mu(t), \quad (1)$$

where $\hat{T} \gg T^\mu$ is the learning time, I_0 is an overall inhibition, E_0 is a parameter determining the strength of the connections for co-active neurons, and $A(\tau)$ is a spike-timing dependent plasticity (STDP) kernel, that makes the connection dependent on the precise relative timing of the pre-synaptic and post-synaptic activity, as observed in neocortical and hippocampal pyramidal cells [23–25]. As shown in Fig. 1, the kernel is such that the connection between i (pre) and j (post) is potentiated if neuron j fires few milliseconds after neuron i, and depressed if the order is reversed. Note that the normalization $T^\mu/\hat{T}$ ensures that the connections do not depend on the learning time $\hat{T}$, if it is large enough that border effect can be neglected. This rule extends the rule used in [26, 27], with the addition of the global inhibition term I_0, that inhibits the activity of neurons not participating to the pattern.
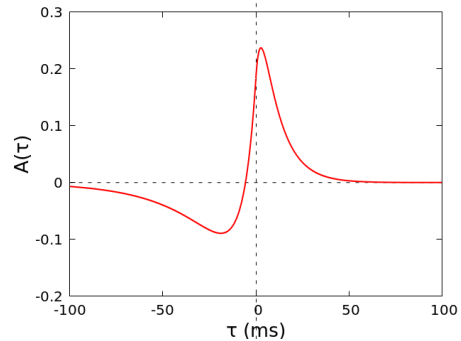

FIG. 1. The learning kernel $A(\tau) = a_p e^{-\tau/t_p} - a_d e^{-\eta\tau/t_p}$ if $\tau > 0$, and $A(\tau) = a_p e^{\eta\tau/t_d} - a_d e^{\tau/t_d}$ if $\tau < 0$, with $a_p = (1 + \eta t_p/t_d)^{-1}$, $a_d = (\eta + t_p/t_d)^{-1}$, $\eta = 4$, $t_p = 10.2$ ms, $t_d = 28.6$ ms. The parameters are the same used in [28] to fit the experimental data of [24].

After learning a number P of patterns with the learning rule (1), we simulate the dynamics of the network by considering a leaky integrate-and-fire model of neurons, where the membrane potential obeys the equation

$$\frac{dV_j}{dt} = -V_j(t)/\tau_m + I_j(t)$$

(membrane capacity is set to one), with

$$I_j(t) = \sum_{\hat{t}_i > \hat{t}_j} J_{ij} e^{-(t-\hat{t}_i)/\tau_s},$$

where $\hat{t}_i > \hat{t}_j$ are all the spikes in input to the neuron j after the last spike of neuron j, membrane time constant $\tau_m = 10$ ms and synapse time constant $\tau_s = 5$ ms. When the potential reaches the threshold Θ (conventionally set to $\Theta = 1$), the neuron fires and the potential is reset to the resting value $V = 0$. Note that, among the parameters I_0, E_0 and Θ, only two are independent. We have chosen to set $\Theta = 1$, but one could as well set for example $E_0 = 1$, and study the dependence of the model with respect to I_0 and Θ.

The dynamics of the network is started by a short cue, i.e. a short train of $H \ll M$ spikes forced in a subset of neurons with the order given by one of the stored

patterns. The times of this train of spikes are given by $t_{i,\mathrm{cue}} = (i/N)T_{\mathrm{cue}}$, with $i = 1 \ldots H$, where T_{cue} can be different from the period T^μ of the pattern. In the following the number of neurons is $N = 6000$, if not otherwise stated, the period of the patterns is $T^\mu = 125$ ms, $H = M/10$, and $T_{\mathrm{cue}} = 83$ ms.
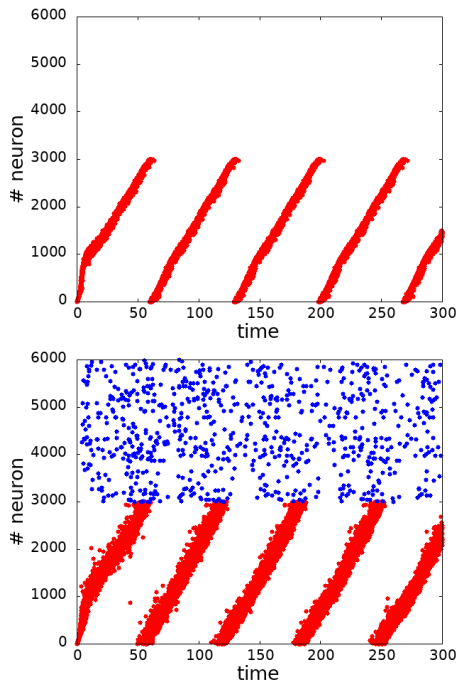
III. RESULTS

FIG. 2. Two examples of successful replay, initiated by a stimulus cue, for the network with $N = 6000$ and $M = 3000$. Each dot represents a spike of the neuron indicated by the y-axis at the time indicated by the x-axis. On the y-axis the first 3000 neurons are the ones participating to the pattern being replayed, with increasing phase of firing, and the following 3000 are the neurons not participating to the pattern. In both cases A and B, the parameters used are $I_0 = 0.0133$ and $E_0 = 0.2856$, the length of the cue is $H = 300$ and its period $T_{\mathrm{cue}} = 83$ ms. A) In this case the number of patterns is $P = 30$, and the order parameter is $m = 0.995$. None of the neurons not participating to the pattern fires during the dynamics. B) The number of patterns is $P = 180$, and the order parameter is $m = 0.938$. In this case there are several spikes also from the neurons that do not participate to the pattern, as an effect of the worse quality of the replay.

After inducing the short cue in the network, we observe the subsequent spontaneous dynamics, to see if the network is able to reproduce completely and persistently the pattern being stimulated by the cue. In Fig. 2, we show two examples of successful replay with $M = 3000$, that is half of the neurons are active in each pattern. In the case of Fig. 2A, the number of stored patterns is

$P = 30$. On the y-axis the first 3000 neurons are the ones participating to the pattern, with increasing phase of firing, and the following 3000 are the ones not participating. The raster plot shows that, after the cue that lasts ~ 4 ms, the neurons continue to fire approximately in the order corresponding to the pattern that has been stimulated, that therefore has been retrieved with high fidelity. On the other hand, in Fig. 2B the number of stored patterns is $P = 180$, and the quality of the replay is worse. The order of firing of the neurons is less precise, as shown by the thickening of the plot, and several neurons fire although they do not belong to the pattern being retrieved. With these parameters, when the number of stored patterns becomes larger than $P_{\max} \simeq 200$, the network is not able to retrieve any of the patterns, and the dynamics following the cue becomes completely chaotic.

In order to quantify the quality of the selective cue-induced replay of the pattern, we define the overlap q^μ as

$$q^\mu([t_0, t_1]) = \max_{T^w} \left| \frac{1}{N_s} \sum_{j=1}^{M} \sum_{t_0 \leq t_j^* \leq t_1} e^{2\pi i t_j^*/T^w} e^{-2\pi i t_j^\mu/T^\mu} \right|,$$
(2)

where the sum is done over the spikes t_j^* emitted in a given interval of time $[t_0, t_1]$ by the neurons belonging to the pattern μ, N_s is the total number of spikes (included those emitted by neurons not belonging to the pattern) and we take the maximum over the time window T^w. The overlap tends to the value $q^\mu = 1$ if the neurons belonging to the pattern fire with the same order of the pattern, with a period of replay T^w in general different from the period T^μ characterizing the pattern in the learning stage, and those not belonging to the pattern do not fire. When the quality of the replay is worse, because some of the neurons not belonging to the pattern fire, or if the order of replay is not exact, the value of the overlap q^μ is lower than one. Note that the order parameter does not make any assumption on the time scale of the replay, in agreement with experimental results showing that the reactivation of memory traces from past experience happens on a compressed timescale during sleep and awake state [2, 5–7].

We compute the overlap in the interval $[t_0, t_1] = [100\,\mathrm{ms}, 300\,\mathrm{ms}]$. In the case of Fig. 2, the value of the overlap is $q^\mu = 0.995$ in Fig. 2A and $q^\mu = 0.938$ in Fig. 2B.

In Fig. 3 we show the value of the overlap as a function of the number of stored patterns. The overlap abruptly goes from a value close to one, when the replay is successful, to a value close to zero when replay fails. Failure may happen both because there is not sustained activity at all, or because the sustained activity is chaotic and not similar to the pattern to be retrieved. We can measure the storage capacity of the network as the maximum number $P_{\max}$ of patterns that can be stored and retrieved with an overlap greater or equal to 0.5. The storage capacity for the parameters of Fig. 3 therefore is
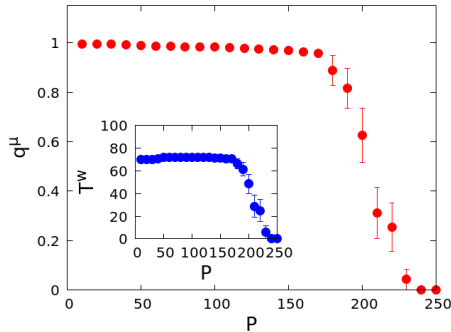
FIG. 3. Plot of the overlap q^μ as a function of the number P of patterns encoded in the network, for $N = 6000$, $M = 3000$, $I_0 = 0.0133$, $E_0 = 0.2856$, $H = 300$, $T_{\text{cue}} = 83$ ms. Inset: period of the replay T^w.

$P_{\max} = 200$. In the Inset, we show the period of replay T^w, that is approximately constant for almost all values of the number P of patterns encoded, and decreases to zero when P gets near to its maximum value.

We have then studied the capacity of the network as a function of the network parameters I_0 and E_0, for different number M of active neurons. To compare the capacity for different values of M (and with the case of static patterns, for example with the Hopfield model), it is convenient to consider the information content of each pattern encoded, that is the number of bits carried by each pattern. This is given by the base two logarithm of the number of different patterns that can be encoded. For the Hopfield model we have 2^N possible patterns, so that the number of bits of each pattern is $B = \log_2 2^N = N$.

In the case of dynamical patterns considered here, where M of the N neurons are active, we have $\binom{N}{M}$ possible choices of the active neurons, and $M!$ possible sequences of the active neurons, so that the number of bits carried by a single pattern is given by

$$B = \log_2\left[\binom{N}{M}M!\right] \simeq M\log_2 N.$$

We therefore define the information load per synapse of the network as $\alpha = PB/N^2$, where P is the number of patterns encoded and B the number of bits of each patterns. Note that in the case of the Hopfield model this gives the usual definition $\alpha = P/N$. The information capacity is defined as the maximum value of the load, $\alpha_{\max} = P_{\max}B/N^2$, such that the patterns can be effectively retrieved.

In Fig. 4, we show the information capacity $\alpha_{\max} = P_{\max}B/N^2$ of a network with $N = 6000$ neurons, as a function of the overall inhibition I_0, and connection strength E_0, for A) $M = 6000$, B) $M = 2000$ and C) $M = 1000$, with a cue of length $H = M/10$ spikes. In the case $M = 6000$, when all the neurons participate to the pattern, the maximum capacity is $\alpha_{\max} = 0.167$, that is obtained for a value $I_0 \simeq 0$ of the global inhibition, and $E_0 \simeq 0.1$.

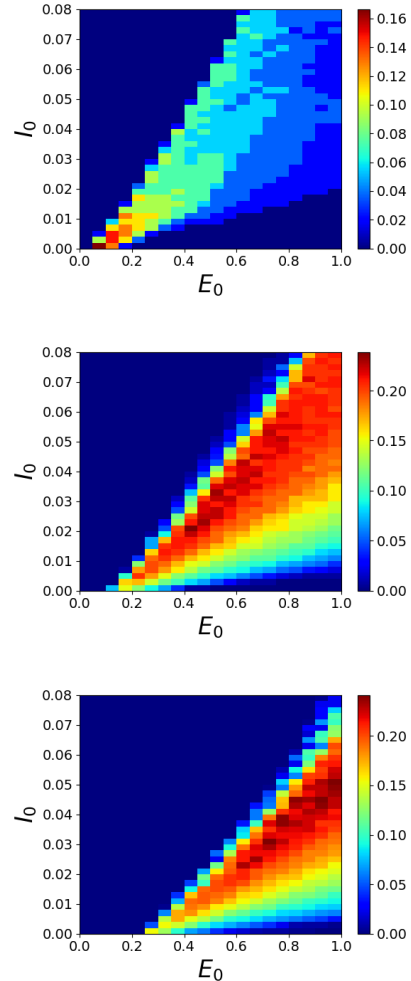FIG. 4. Plot of the information capacity $\alpha_{\max} = P_{\max}B/N^2$ of a network of $N = 6000$ neurons, as a function of the overall inhibition I_0 and connection strength E_0, for A) $M = 6000$, B) $M = 2000$ and C) $M = 1000$.

When the number M of neurons in the pattern becomes lower than N, the maximum of the capacity is obtained for increasing values of both I_0 and E_0. For $M = 2000$ we find a maximum $\alpha_{\max} = 0.239$ at $I_0 \simeq 0.022$ and $E_0 \simeq 0.45$, while for $M = 1000$ the maximum is $\alpha_{\max} = 0.248$ at $I_0 \simeq 0.054$ and $E_0 \simeq 0.95$. The main reason for which higher values of E_0 are needed for lower M, is to compensate the lower number of terms of the sum in Eq. (1), at fixed neuron threshold. On the other hand, the global inhibition serves to avoid the firing of neurons that do not participate to the pattern being replayed, and therefore increases with he ratio $(N-M)/M$ between the neurons participating or not.

In Fig. 5, we show the maximum value of the capacity as a function of the fraction M/N. The overall maximum capacities are obtained for values of the fraction of neurons participating to the patterns around $M/N \simeq 0.2$.
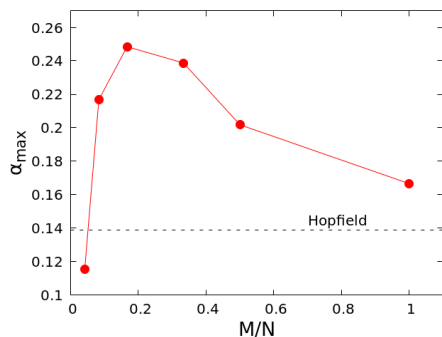
FIG. 5. Maximum value of the information capacity as a function of the ratio M/N, where $N = 6000$ is the total number of neurons of the network, and M the number of neurons participating to the patterns.

This means that storage of dual population and phase coding patterns is more efficient than phase coding alone ($M/N = 1$, where the pattern is defined only by the phases ϕ_j^μ [29–31]). Notably the information capacity of such dual coding is enhanced also with respect to the binary population coding alone of the Hopfield model (where the pattern is defined only by the activities ξ_j^μ).
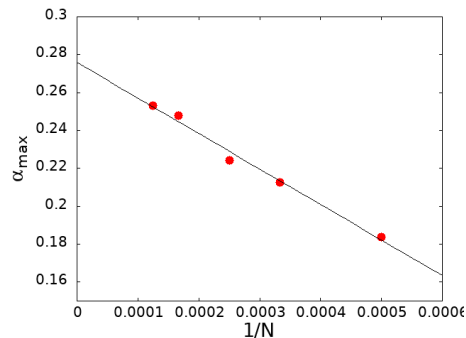

FIG. 6. Dependence of the maximum value of the information capacity from the size of the network, for a fraction $M/N = 0.2$ of active neurons. The best fit is given by $\alpha_{\max} = 0.276 - 187/N$.

In Fig. 6, we show the maximum capacity as a function of the network size N, for a fixed value $M/N = 0.2$ of the fraction of neurons participating to the pattern. The capacity grows with the size of the network, and tends to a value $\alpha_{\max} = 0.276$ for very large sizes. Notably the capacity is almost the double of that of the Hopfield model ($\alpha_{\max} = 0.139$), and practically equivalent (slightly larger) than that of the binary sequence processing Hopfield-like model ($\alpha_{\max} = 0.269$) [16].

IV. DISCUSSION

In this paper we have studied the information capacity of a spiking network, able to store and selectively retrieve patterns defined by a binary spatial population coding, as in the Hopfield model, nested with a phase-of-firing coding. The spatial population binary variable ξ_j^μ determine the M active neurons in pattern μ, while the phase-of-firing variable ϕ_j^μ define the precise relative timing of firing of those active neurons. The success of retrieval is measured by the order parameter q^μ, introduced in eq. (2), that extends the order parameter of Hopfield model, since it requires both that (1) the $N - M$ neurons silent in the pattern are silent in the retrieval, and (2) the M neurons active in the pattern emits a spike with the right phase relationship ϕ_j^μ (with possibly a different period of oscillation). The order parameter is insensitive to the time scale of the replay, in agreement with experimental results showing that the reactivation of memory traces from past experience happens on a compressed timescale during sleep and awake state[2, 5–7].

To study the memory capacity, we measure the maximum number $P_{\max}$ of stored patterns that can be successfully and selectively retrieved, when a cue is presented, and in order to compare capacity of networks with different value of M, also the maximum information capacity $\alpha_{\max}$, i.e. the amount of information (measured as the maximum number of patterns times the number of bits of each pattern) per synapse.

The ability to work as an associative memory for such spatio-temporal patterns is crucially dependent from the learning rule introduced in Eq. (1) where, in addition to an overall inhibition, the connections between neurons co-active in a pattern are determined by a kernel depending on the precise timing of the spikes between the pre-synaptic and post-synaptic neurons. Note that this rule follows more closely the idea of Hebb, with respect to the Hopfield case, since connections between neurons that are not active in the same pattern have a negative weight contribution $-I_0$, while neurons which are both active in the same pattern have a contribution that is positive if the pre-synaptic neuron fires few milliseconds before the post-synaptic one, or negative if the reverse is true. The rule in Eq. (1) extends the rule [26, 27, 29–33] used for storing phase-coding-only patterns (i.e. $M/N = 1$), and include a crucial global inhibition term, allowing the storage of patterns with dual coding $M/N < 1$.

Notably here we found that a fraction $M/N \simeq 0.2$ gives the highest information capacity, meaning that the storage of dual coding patterns, where information is stored both in the population (spatial) distribution of active neurons and in the timing of the spikes, is more efficient then phase coding alone ($M/N = 1$). At $M/N \simeq 0.2$ not only the capacity is higher, but the region of the parameters E_0 and I_0 where capacity is near-maximal is larger, so that a fine-tuning of the parameters is less important.

We also found that a crucial role is played by the value of the global inhibition I_0. When the fraction of neurons

participating to the pattern is smaller, higher values of I_0 are needed in order to reduce the occurrence of "false positives", that is neurons not participating to the pattern that fire incorrectly.

We find that the maximum capacity at $M/N = 0.2$ grows with N, and tends to $\alpha_{max} = 0.276$ for very large size, a value close (slightly higher) than the maximum capacity found for sequence processing networks, where discrete time dynamics, binary patterns sequence, with a Hopfield-like asymmetric learning rule was studied. It's interesting that there seems to be a unique maximum information capacity for storing dynamical patterns, in which time has been introduced in different ways, the sequence of binary patterns with Hopfield-like chain learning rule $\xi^\mu \xi^{\mu+1}$ [16], and the dual coding patterns of spike defined here, with a biologically inspired STDP-based learning rule.

These findings may help to elucidate experimental observations where both spatial and temporal coding schemes are found to be present, representing different independent variables which are simulataneously encoded and binded together in the memorized patterns, such as for example the location of the event and its behavioural and sensory content [13, 14].

V. ACKNOWLEDGEMENTS

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