Dynamics and storage capacity of cortical networks with small-world topology

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We study the storage of phase-coded patterns as stable dynamical attractors in recurrent neural networks with small-world topology. The synaptic strength of existent connections is determined by a learning rule based on spike-time-dependent plasticity, with an asymmetric time window depending on the relative timing between pre- and postsynaptic activity. We store multiple patterns and study the network capacity for fully-connected and sparse networks with different topologies. We study networks where each neuron is connected only to a small number $z \ll N$ of other neurons, Connections can be short range, between neighboring neurons placed on a regular lattice, or long range, between randomly chosen pairs of neurons. We find that a small fraction of long range connections is able to amplify the capacity of the network. This imply that a small-world-network topology is optimal, as a compromise between the cost of long range connections and the capacity increase.

Recent advances in brain research have generated renewed awareness and appreciation that the brain operates as a complex nonlinear dynamic system, and synchronous and phase-locked oscillations may play a crucial role in information processing, such as feature grouping, saliency enhancing [1–3] and phase-dependent coding of objects in short term memory [4]. Many results led to the conjecture that synchronized and phase locked oscillatory neural activity play a fundamental role in perception, memory, and sensory computation [5, 6].

There is increasing evidence that information encoding may depend on the temporal dynamics between neurons, namely, the specific phase alignment of spikes relative to rhythmic activity across the neuronal population (as reflected in the local field potential, or LFP) [4, 7–11]. Indeed phase-dependent coding, that exploits the precise temporal relations between the discharges of neurons, may be an effective strategy to encode information [1, 4, 11, 18, 21, 53]. Data from rodents [7] indicate that spatial information may be encoded at specific phases of ongoing population theta oscillations in the hippocampus, while data from monkeys [11, 53] show that phase coding may be a more general coding scheme. The existence of a periodic spatio-temporal pattern of precisely timed spikes, as attractor of neural dynamics, has been investigated in different recurrent neural models [33–35, 54, 59].

We propose a model in which information about an item is encoded in the specific phases of firing, and each item correspond to a different pattern of phases among units. Multiple items can be memorized in the synaptic connections, and the intrinsic network dynamics recall the specific phases of firing when a partial cue is presented.

Each item with specific phases of firing corresponds to specific relative timings between neurons. Therefore it seems that phase coding may be well suited to facilitate long-term storage of items by means of spike-timing dependent plasticity (STDP) [13–15].

Indeed experimental findings on STDP further underlined the importance of precise temporal relationship of the dynamics, by showing that long term changes in synaptic strengths depend on the precise relative timing of pre- and post-synaptic spikes [12–17].

The computational role and functional implications of STDP have been explored from many points of view (see for example [26–32, 54, 57] and papers of this special issue). STDP has also been hypotized to play a role in the hippocampus theta phase precession phenomenon [10, 52, 55], even thou other explanations has also been proposed for this phenomena (see [51] and references therein). Here we analyze the role of a learning rule based on STDP in storing multiple phase-coded memories as attractor states of the neural dynamics, and the ability of the network to selectively retrieve a stored memory, when a partial cue is presented. The framework of storing and retrieval of memories as attractors of the dynamics is widely accepted, and recently received strong experimental support, such as in the work of Wills et al. [56], which gives strong experimental evidence for the expression of attractor states in the hippocampus.

Another characteristic of the neural network, crucial to its functioning, is its topology, that is the average number of neurons connected to a neuron, the average length of the shortest path connecting two neurons, etc. In the last decade, there has been a growing interest in the study of the topological structure of the brain network [39, 42, 43]. This interest has been stimulated by the simultaneous development of the science of complex networks, that studies
how the behavior of complex systems, like societies or computer networks or brains, is shaped by the way their constituent elements are connected.

Some networks, as for example Internet or the world wide web, have the properties that the degree distribution, that is the probability that a node chosen randomly is connected to \( k \) other nodes, has a slow power law decay. Networks having this property are called “scale-free”. Barabási and Albert [45] demonstrated that this property can originate from a process in which each node is added preferentially to nodes that already have high degree. Scale-free networks however are unlikely if the attachment of connections is subject to physical constraints, or associated with a cost [46].

Another important class of complex networks is the so called “small world” networks [47]. They combine two important properties. The first is an high level of clustering, that is the probability that, if two nodes are both connected to a third node, then they are directly connected as well. This property is characteristic of networks where the nodes are connected preferentially to the nearest nodes, in a physical (for example three-dimensional) space. The second property is the shortness of paths connecting any two nodes, characteristic of random networks. Therefore, a measure of the small-worldness of a network is given by a high ratio of the clustering coefficient to the path length.

There is increasing evidence that the connections of neurons in many areas of the nervous system have a small world structure [39–44]. Up to now, the only nervous system to have been comprehensively mapped at a cellular level is the one of Caenorhabditis elegans [48, 49], and it has been found that is has indeed a small world structure. The same property was found for the correlation network of neurons in the visual cortex of the cat [40].

In this paper we focus on the ability of STDP to memorize multiple phase-coded items, in fully connected and in sparse networks, with varying degree of small-worldness, in such a way that each phase-coded item is an attractor of the network.

Partial presentation of the pattern, i.e. short externally induced spike sequences, with phases similar to the ones of the stored phase pattern, induces the network to retrieve selectively the stored item, as far as the number of stored items is not larger then the network capacity. If the network retrieves one of the stored items, the neural population spontaneously fires with the specific phase alignments of that pattern, until external input doesn’t change the state of the network.

We find that the proposed learning rule is really able to store multiple phase-coded patterns, and we study the network capacity, i.e. how many phase-coded items can be stored and retrieved in the network as a function of the parameters of the network and the learning rule.

In Section I we describe the model used. In Section II we study the case of a fully connected network, that is a network in which each neuron is connected to any other neuron. In Section III we study instead the case of a sparse network, where each neuron is connected to a finite number of other neurons, with a varying degree of small-worldness. In Section ?? we shows numerical simulations of selective retrieval of the stored phase-coded patterns in a fully-connected spiking IF model, and finally the summary and discussion is in Section IV.

I. THE MODEL

The model has been introduced in [18], we briefly review its main ingredients here. We consider a network of \( N \) neurons, with \( N(N−1) \) possible connections \( J_{ij} \). The synaptic connections \( J_{ij} \), during the learning mode when patterns to be stored are presented, are subject to plasticity and change their efficacy according to a learning rule inspired to the STDP. In STDP [12–17] synaptic strength increases or decreases whether the presynaptic spike precedes or follows the postsynaptic one by few milliseconds, with a degree of change that depends from the delay between pre and post-synaptic spikes, via a learning window that is temporally asymmetric. We indicate with \( x_{i}(t) \) the activity, that is the firing rate, of \( i \)-th neuron at time \( t \). It means that the probability that unit \( i \) has a spike in the interval \( (t, t+\Delta t) \) is proportional to \( x_{i}(t)\Delta t \) in the limit \( \Delta t \rightarrow 0 \). According to the learning rule that we study here, introduced in [18, 21, 22], the change in the connection \( J_{ij} \) that occurs in the time interval \([-T, 0] \) can be formulated as follows:

\[
\delta J_{ij} \propto \int_{0}^{T} dt \int_{-T}^{0} dt' x_{i}(t)A(t-t')x_{j}(t')
\]  

(1)

where \( x_{i}(t) \) is the activity of the pre-synaptic neuron, and \( x_{j}(t) \) the activity of the post-synaptic one. The learning window \( A(\tau) \) is the measure of the strength of synaptic change when there is a time delay \( \tau \) between pre and post-synaptic activity.

To model the experimental results of STDP, the learning window \( A(\tau) \) should be an asymmetric function of \( \tau \), mainly positive (LTP) for \( \tau > 0 \) and mainly negative (LTD) for \( \tau < 0 \). The shape of \( A(\tau) \) strongly affect \( J_{ij} \) and the dynamics of the networks, as discussed in the following. An example of the learning window used here is shown in Fig. 1.
Writing Eq. (1), implicitly we have assumed that the effects of separate spike pairs due to STDP sum linearly. However note that nonlinear effects have been observed when both pre- and post-synaptic neurons fire simultaneously at more than 40 Hz [67, 68], therefore our model holds only in the case of lower firing rates, and in those case where linear summation is a good approximation.

\[ A(\tau) = a_p e^{-\tau/T_p} - a_D e^{-\eta \tau/T_D} \] if \( \tau > 0 \)
\[ A(\tau) = a_p e^{\eta \tau/T_D} - a_D e^{\tau/T_D} \] if \( \tau < 0 \),

with the same parameters used in [32] to fit the experimental data of [14],
\[ a_p = \gamma \left[ 1/T_p + \eta/T_D \right]^{-1}, \quad a_D = \gamma \left[ \eta/T_p + 1/T_D \right]^{-1}, \]
\[ T_p = 10.2 \text{ ms}, \quad T_D = 28.6 \text{ ms}, \quad \eta = 4, \quad \gamma = 42. \]

Notably, this function satisfies the condition \( \int_{-\infty}^{\infty} A(\tau) d\tau = 0 \), i.e. \( \tilde{A}(0) = 0 \).

The patterns of activity that we consider are periodic patterns, in which information is encoded in the relative phases, that is in the relative timing of the maximum rate of firing of the neuron. Therefore, we define the pattern to be stored by

\[ x_\mu^i(t) = \frac{1}{2} \left[ 1 + \cos(\omega_\mu t - \phi_\mu^i) \right], \quad (2) \]

where phases \( \phi_\mu^j \) are chosen randomly from a uniform distribution in \([0, 2\pi)\), and \( \omega_\mu/2\pi \) is the frequency of the oscillation of the neurons (see Fig. 2a). Each pattern \( \mu \) is defined therefore by its frequency \( \omega_\mu/2\pi \), and by the specific phases \( \phi_\mu^j \) of the neurons \( j = 1, \ldots, N \).

In the limit of large \( T \), when the network is forced in the state given by Eq. (2), using Eq. (1), the change in the synaptic strength will be given by

\[ \delta J_{ij} = \eta |\tilde{A}(\omega_\mu)| \cos \left[ \phi_\mu^i - \phi_\mu^j + \varphi(\omega_\mu) \right] + 2\eta \tilde{A}(0) \] (3)

where \( \tilde{A}(\omega) \) is the Fourier transform of the kernel, defined by

\[ \tilde{A}(\omega) = \int_{-\infty}^{\infty} A(\tau) e^{-i\omega \tau} d\tau, \]

and \( \varphi(\omega) = \arg \left[ \tilde{A}(\omega) \right] \) is the phase of the Fourier transform. The factor \( \eta \) depends on the learning rate and on the total learning time \( T \) [19, 21].

When we store multiple patterns \( \mu = 1, 2, \ldots, P \), the learned weights are the sum of the contributions from individual patterns. After learning \( P \) patterns, each with frequency \( \omega_\mu/2\pi \) and phase-shift \( \phi_\mu^i \), we get the connections

\[ J_{ij} = \eta \sum_{\mu=1}^{P} |\tilde{A}(\omega_\mu)| \cos \left[ \phi_\mu^i - \phi_\mu^j + \varphi(\omega_\mu) \right] + 2\eta P \tilde{A}(0). \] (4)

Notably, \( \tilde{A}(0) = 0 \) when we use the learning window in Fig. 1. In the present study, we choose to store patterns all with the same \( \omega_\mu \), and to ease the notation we define \( \varphi^* = \varphi(\omega_\mu) \).

In the retrieval mode, the connections are fixed to the values given in Eq. (4), and dynamic equations of unit \( x_i \) is

\[ \tau_m \dot{x}_i = -x_i + F[h_i(t)] \] (5)
where the transfer function $F(h)$ denotes the input-output relationship of neurons, $h_i(t) = \sum_j J_{ij} x_j(t)$ is the local field acting on neuron $i$, $\tau_m$ is the time constant of neuron $i$ (for simplicity, assume the same for all neurons), and $J_{ij}$ is the connection after the learning procedure given in Eq. (4). Spontaneous activity dynamics of the coupled nonlinear system is therefore determined by the function $F(h)$ and by the coupling matrix $J_{ij}$. We take the function $F(h)$ to be equal to the Heaviside function $\Theta(h)$. Note that in this case the learning factor $\eta$ is immaterial. During the retrieval mode, the network selectively replay one of the stored phase-coded patterns, depending on the initial conditions (or because a partial and corrupted version of the stored phases are given as external input for a short interval of time). Network dynamics given by Eq. (5), in absence of any external input, shows spontaneous reactivation of one of the stored phase-coded patterns when the network is initialized with $x_i(0)$ equal to the value of the pattern at time zero or a corrupted version of it. It means that we force for $t < 0$ the network with an input which resemble one of the phase-coded patterns, then when we switch off the input at time $t = 0$, the network spontaneously gives sustained activity retrieving the stored pattern. When one of the stored attractors is retrieved, the spontaneous activity of the network is an oscillating pattern of activity, with phases of firing equal to the stored phases, but frequency of oscillation that can be different (see Fig. 2). Analytical calculations [18, 19] show that the output frequency of oscillation is given by

$$\bar{\omega}/2\pi = -\tan(\varphi^*)/2\pi \tau_m,$$

and this is confirmed by numerical simulations of Eq. (5) with connections of Eq. (4).

![Fig. 2](image-url)

FIG. 2: The activity of 10 randomly chosen neurons in a network of $N = 3000$ fully connected neurons, with $P = 30$ stored patterns. The learning rule is given by Eq. (4) with $\varphi = -0.24\pi$. Neurons are sorted by increasing phase $\phi_i^0$ of the first pattern, and shifted correspondingly on the vertical axis. a) The first stored pattern, that is the activity of the network given by Eq. (2) used to encode the pattern in the learning mode, with frequency $\omega/2\pi = 20$ Hz. b) The self-sustained dynamics of the network, when the initial condition is given by the first pattern $x_i^0(0)$. The retrieved the pattern has the same phase relationships of the encoded one. In this case the overlap is $|m^1| \simeq 0.22$, and the output frequency is in agreement with the analytical value $-\tan(\varphi^*)/2\pi \tau_m = 15$ Hz.

As an example, the learning window in Fig. 1, when the frequency of the stored pattern is $\omega/2\pi = 20$ Hz, gives $\varphi^* = -0.24\pi$, and an output frequency of oscillation $\bar{\omega}/2\pi = 15$ Hz (with $\tau_m = 10$ ms). Numerical simulations of the network with $\varphi^* = -0.24\pi$, $N = 3000$ fully connected neurons and $P = 30$ stored patterns, are shown in Fig. 2a and 2b.

In the following sections, we analyze the behavior when multiple patterns are stored and we study the network capacity as a function of learning window parameters and as a function of connectivity topology.

II. CAPACITY OF THE FULLY CONNECTED NETWORK

Here we study the network capacity, in the case of fully connected network in Eq. (5), where all the $N(N-1)$ connections are subject to the learning process and therefore are given by Eq. (4).

During the retrieval mode, the spontaneous dynamics of the network selectively replay one of the stored phase-coded patterns, depending on initial condition, so that, when retrieval is successful, the spontaneous activity of the network is a oscillating pattern of activity with phase of firing equal to the stored phases $\phi_i^0$ (while frequency of oscillation is governed by the time scale of single neuron and by the parameter $\varphi^*$ of learning window). Similarity
between the network activity during retrieval mode and the stored phase-coded pattern is measured by the overlap $|m^\mu|$, introduced in [21] and studied in [18],

$$|m^\mu(t)| = \left| \frac{1}{N} \sum_{j=1,...,N} x_j(t) e^{i\phi_j} \right|$$

(6)

The overlap is equal to $\cos(\varphi^*)/\pi$ in the case of perfect retrieval, while it is $\sim 1/\sqrt{N}$ when the phases of firing have nothing to do with the stored phases. Numerically we study the capacity of the network, $\alpha_c = P_{\text{max}}/N$, where $N$ is the number of neurons and $P_{\text{max}}$ is the maximum number of items that can be stored and retrieved successfully.

We extract $P$ different random patterns, choosing phases $\phi^*_j$ randomly from a uniform distribution in $[0, 2\pi)$. Then we define the connections $J_{ij}$ with the rule Eq. (4). The values of the firing rates are initialized at time $t = 0$ at the value given by Eq. (2) with $t = 0$ and $\mu = 1$ of the first pattern, the dynamics in Eq. (5) is simulated, and the overlap Eq. (6) with $\mu = 1$ is evaluated. If the absolute value $|m^\mu(t)|$ tends to a constant greater than 0.1 at long times, then we consider that the pattern has been encoded and replayed well by the network. The maximum value of $P$ at which the network is able to replay the pattern is the capacity of the network. We have verified that a small noise in the initialization do not change the results. A systematic study of the robustness of the dynamical basins of attraction from the noise in the initialization has not been carried out yet.

![FIG. 3: Maximum capacity $\alpha_c = P_{\text{max}}/N$ of a network of $N = 3000$ fully connected neurons, as a function of the learning window asymmetry $\varphi^*$. The limit $\varphi^* = 0$ corresponds to a symmetric learning window ($J_{ij} = J_{ji}$) that is to output frequency $\omega/2\pi$ that tends to zero. The limit $\varphi^* = -\pi/2$ corresponds instead to a perfectly anti-symmetric learning window, and output frequency $\omega/2\pi = \infty$. The intermediate value $\varphi^* \simeq -0.25\pi$ gives the best performance of the network.](image)

Here we study the dependence of network capacity on the learning rule parameter $\varphi^*$. The parameter $\varphi^*$ depends on the learning window shape, and on the frequency of oscillation $\omega/2\pi$ of the pattern presented during the learning process.

In Fig. 3 we plot the capacity as a function of $0 < -\varphi^* < \pi/2$ for a fully-connected network with $N = 3000$, considering $P_{\text{max}}$ the maximum number of patterns such that the retrieved patterns have overlaps $|m^\mu| > 0.1$. We see that capacity strongly depends from the shape of learning window through parameter $\varphi^*$. The limit of $\varphi^*$ equal to zero corresponds to output frequency $\omega/2\pi$ equal to zero, and therefore to the limit of static output. We see that the capacity of the oscillating network is larger than the static limit for a large range of frequencies. When $\varphi^*$ approaches $-\pi/2$, then output frequency $\omega/2\pi = -\tan(\varphi^*)/2\pi\tau_n$ tends to $\infty$, and capacity decreases. The best performance is given at intermediate values of $\varphi^*$. Therefore, since $\varphi^*$ depends from the degree of time asymmetry of the learning window, we see that there is a range of time-asymmetry of the learning windows that gives a good capacity, while both the case of perfectly symmetric learning window $\varphi^* = 0$, and the case of perfectly anti-symmetric learning window $\varphi^* = -\pi/2$, give worse performances. Interestingly, the learning window in Fig. 1 gives intermediate values of $\varphi^*$ for a large interval of frequencies $\omega_{\mu}$.

Note that the decrease in the capacity of the network when the phase $\varphi^*$ approaches $-\pi/2$ is due essentially to the fact that the oscillations of the firing rates with respect to the mean value $1/2$ become small in this regime. When firing rates tend to a constant, the overlap defined by Eq. (6) goes to zero.
III. CAPACITY OF THE SPARSE NETWORK

Here we study the capacity of the network in Eq. (5) in the case of sparse connectivity, where only a fraction of the connections are subject to the learning rule given by Eq. (4), and all the others are zero, and we investigate the role of connectivity’s topology. We start from a network in which neurons are put on the vertices of a three dimensional lattice, and each neuron is connected only to neurons that are nearer than a distance \( R \) in unit of lattice spacing. Each neuron is connected therefore to \( z \approx 4\pi R^3/3 \) other neurons. For each neuron, we then “rewire” a finite fraction \( \gamma \) of its connections, deleting the existing short range connection and creating instead a long range connection to a randomly chosen node.

![FIG. 4: a) Maximum capacity \( \alpha_c = P_{\text{max}}/N \) of a network of \( N = 24^3 \) neurons, with \( z \) connections per neuron, with \( \varphi^* \) fixed to its optimal value \( -0.24\pi \). The red line corresponds to \( \gamma = 0 \), that is to a network with only short range connections. The green one to \( \gamma = 0.3 \), and the blue one to \( \gamma = 1 \), that is to a random network where the three-dimensional topology is completely lost. b) Maximum capacity \( \alpha_c = P_{\text{max}}/N \), for the same values of \( N \) and \( \varphi^* \) and for connectivity \( z/N = 0.11 \), as a function of \( \gamma \).](image)

We consider a network of \( N = 24^3 \) neurons. In Fig. 4(a) we plot the maximum capacity \( P_{\text{max}}/N \) as a function of the connectivity \( z/N \) for three different values of \( \gamma \). The value \( \gamma = 0 \) (red curve) corresponds to the pure short range network, in which all connections are between neurons nearer than \( R \) on the three-dimensional lattice, \( \gamma = 1 \) (blue curve) corresponds to the random network, where the three-dimensional topology is completely lost, and \( \gamma = 0.3 \) to an intermediate case, where 30% of the connections are long range, and the others are short range.

Considering that the capacity of the fully connected network \((z/N = 1)\) is \( \alpha_c \approx 0.02 \), we see that the random network with \( z/N \approx 0.1 \) already has about half that of the fully connected network. Looking then at the dependence of the capacity from the fraction of short range and long range connections, we see that the random network has a capacity that is up to two times greater than the short range network, for a connectivity \( z/N \approx 0.1 \). At the same connectivity, the network with \( \gamma = 0.3 \) has a capacity equal to 85% of that of the random network. Therefore, the presence of a small number of long range connections is able to amplify the capacity of the network. This is shown in Fig. 4(b), where the capacity as a function of \( \gamma \) for \( z/N = 0.11 \) is plotted.

This effect is not so marked in smaller networks, for example with \( N = 18^3 \) neurons, where the capacity of the \( \gamma = 0.3 \) network is nearer to that of the \( \gamma = 0 \) network. Therefore it seems plausible that for very large networks the amplifying effect of a small fraction of long range connections will be even stronger. This implies that a small-world kind of network is optimal as a compromise between the higher cost of long range connections and the capacity increase, in agreement with the observation that many areas of the brain, from C. elegans [48, 49] to the visual cortex of the cat [40], have this kind of topology.

IV. SUMMARY AND DISCUSSION

In this paper we studied the storage and recall of patterns in which information is encoded in the phase-based timing of firing relative to the cycle. We analyze the ability of the learning rule given by Eq. (4) to memorize multiple phase-coded patterns, such that the spontaneous dynamics of the network, defined by Eq. (5), selectively gives sustained activity which match one of the stored phase-coded patterns, depending on the initialization of the network. It means that if one of the stored item is presented as input to the network at time \( t < 0 \), and it’s switched off at time \( t \geq 0 \), the
spontaneous activity of the network at $t > 0$ gives sustained activity whose phases alignments match those presented before.

We compute the storage capacity of phase coded patterns in the analog model, finding a linear scaling of number of patterns with network size, with maximal capacity $\alpha_c \simeq 0.02$ for the fully connected network.

We also study the storage capacity for different degrees of sparseness and small-worldness of the connections. We put neurons on the vertices of a three dimensional lattice of size $L$, and connect each neuron to neurons that are nearer than a distance $R$ in unit of lattice spacing, with $R < L/2$, so that there will be $z \simeq (4\pi/3)R^3$ connections per neuron. Then a fraction $\gamma$ of these connections are rewired, deleting the short range connection and creating a long range connection to a random neuron. The existing connections are then defined by the learning rule Eq. (4), while other connections are zero.

Changing the proportion $\gamma$ between short-range and long-range connections, we go from a three-dimensional network with only nearest-neighbors connections ($\gamma = 0$) to a random network ($\gamma = 1$). Small but finite values of $\gamma$ give a “small world” topology, similar to that found in many areas of nervous system. We see that capacity of a random sparse network with only 10% connectivity ($\gamma = 1$, $z/N = 0.1$) already has half the capacity of the fully-connected network. Considering that creating a long-range connections has a higher cost for the neuron than a short-range connection, we have then studied also the effect of create a short-range connection instead of long-range one. We see that the random network with $\gamma = 1$ has a capacity about two times that of the short range network $\gamma = 0$ for system size $N = 24^3$. This factor is likely to increase for larger system sizes, because the larger the system, the more different are long range connections with respect to short range ones. Moreover, we find that a small-world topology, with a small fraction of long range connections ($\gamma \simeq 0.3$) already has a capacity close to that of the random network, with the same connectivity. More precisely, at $N = 24^3$ and connectivity $z/N = 0.11$, the network with 30% of long-range connections has a capacity equal to 85% of that of the random network. This is interesting considering that a long-range connection clearly has a higher cost then a short-range one. This imply that a small-world network topology is optimal, as a compromise between the cost of long range connections and the capacity increase.

The task of storing and recalling phase-coded memories has been also investigated in [54] in the framework of probabilistic inference. While we study the effects of couplings given by Eq. (4) in the network model Eq. (5), the paper [54] studies this problem from a normative theory of autoassociative memory, in which variable $x_i$ of neuron $i$ represents the neuron $i$ spike timing with respect to a reference point of an ongoing field potential, and the interaction $H(x_i, x_j)$ among units is mediated by the derivative of the synaptic plasticity rule used to store memories. In [54], the case of limited connectivity is studied, showing how recall performance depends to the degree of connectivity when connections are cut randomly. Here we show that performance also depends from the topology of the connectivity, and capacity depends not only from the number of connections but also from the fraction of long range versus short range connections.

The role of STDP in learning and detecting spatio-temporal patterns has been studied recently in [57]. They show that a repeating spatiotemporal spike pattern, hidden in equally dense distracter spike trains, can be robustly detected by a set of “listening” neurons equipped with spike timing-dependent plasticity (STDP). When a spatio-temporal pattern repeats periodically, it can be considered a periodic phase-coded pattern. While in [57] the detection of the pattern is investigated when it is the input of the “listening” neurons, in our paper we investigate the associative memory property, which makes the pattern imprinted in the connectivity of the population an attractor of the dynamics. When a partial cue of the pattern $\mu$ is presented (or in the analog case the network is initialized with $x^\mu_i(0)$), then the original stored pattern is replayed. Differently from [57], here the pattern $\mu$ is imprinted in the neural population, in such a way that exactly the same encoded phase-coded pattern is replayed during persistent spontaneous activity. This associative memory behavior, that replay the stored sequence, can be a method for recognize an item, by activating the same memorized pattern in response of a similar input, or may be also a way to transfer the memorized item to another area of the brain.

- This paper is dedicated to the memory of Prof. Maria Marinaro, who strongly contributed to this line of research and to the initial stages of this work.

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