From statistical inference to a differential learning rule for stochastic neural networks

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Stochastic neural networks are a prototypical computational device able to build a probabilistic representation of an ensemble of external stimuli. Building on the relationship between inference and learning, we derive a synaptic plasticity rule that relies only on delayed activity correlations, and that shows a number of remarkable features. Our delayed-correlations matching (DCM) rule satisfies some basic requirements for biological feasibility: finite and noisy afferent signals, Dale’s principle and asymmetry of synaptic connections, locality of the weight update computations. Nevertheless, the DCM rule is capable of storing a large, extensive number of patterns as attractors in a stochastic recurrent neural network, under general scenarios without requiring any modification: it can deal with correlated patterns, a broad range of architectures (with or without hidden neuronal states), one-shot learning with the palimpsest property, all the while avoiding the proliferation of spurious attractors. When hidden units are present, our learning rule can be employed to construct Boltzmann-Machine-like generative models, exploiting the addition of hidden neurons in feature extraction and classification tasks.

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INTRODUCTION

One of the main open problems of neuroscience is understanding the learning principles which enable our brain to store and process information. Neural computation takes place in an extremely noisy environment: experiments show that various sources of variability and fluctuations make neurons, synapses, and neural systems intrinsically stochastic [1]. Such internal noise can originate at different levels, for instance from the unreliable transmission of synaptic vesicles, from the random opening and closing of ion channels or from the trial-to-trial variability in neural responses to external stimuli [2–6]. At the same time, even the typical sensory input is often blurry and ambiguous. A probabilistic inference framework is thus the natural choice for modeling all the uncertainties affecting neural learning [7].

A widespread belief is that learning occurs at the synaptic level, both in terms of creation of new connections and by synaptic strength potentiation or depression [8–10]. Synaptic plasticity can be encoded in a learning principle that relates the modulation of the efficacy of a synapse to its pre- and post-synaptic neural activity. The simplest synaptic plasticity rule, Hebb’s rule, states that positive correlation between pre- and post-synaptic spikes leads to long-term potentiation (LTP), while negative correlation induces long-term depression (LTD). One important feature of Hebbian plasticity is its capability to shape the connectivity of neural architectures in a way that captures the statistics of the stimuli. This issue has been addressed in a number of modeling studies, starting from the classical theory of development of neural selectivity [11], to more modern accounts of neural tuning that use homeostasis-stabilized Hebbian plasticity in large spiking network models [12].

On the other hand, it has long been recognized that Hebbian plasticity is capable of generating attractor dynamics in a variety of recurrent architectures: the concept of attractor neural network is one of the most important in modern neuroscience, in that it can account for a variety of neurophysiological observations of persistent activity in various brain areas. Examples include line attractor (neural integrator) models in oculomotor control [13], ring attractor models in head direction systems [14], and a plethora of models of persistent neural activity whose common feature is a local connectivity pattern which stabilizes bump attractors by means of lateral inhibition.

The main intuition that led to the introduction of the prototypical model of attractor network – the Hopfield model – was that the frustration phenomenon in disordered systems (spin glasses), namely the proliferation of metastable states due to the strongly heterogeneous nature of the couplings, could be exploited to embed uncorrelated patterns as steady states of a network dynamics. In the Hopfield model, a straightforward application of Hebb’s rule leads to a definition for the synaptic weights that allows for an extensive number of attractors to be stored, but exhibits a phenomenon known as catastrophic forgetting [15]: all memories are lost, due to the existence of an absorbing spin glass state uncorrelated with the memories, as soon as the maximum number of attractors is exceeded. Since the original introduction of the Hopfield model [16], many generalized Hebb rules have been proposed, able to deal with sparse patterns or low activity levels, see e.g. ref. [15]. Moreover, Hebbian learning has been profitably used to embed attractor states in a variety of neural network models spanning from binary units to graded neurons (rate models) [17] and spiking networks [18].

Different lines of research concerning attractor neural networks in Statistical Mechanics and Computational Neuroscience have strong ties with the study of generative energy-based models: the formalism of Boltzmann Machines allows for a generalization to neural networks with hidden neural states [19, 20]. This introduction, though, comes at the price of serious technical complications in the definition of a viable learning rule. Some of these models have become popular also in the machine-learning community, after proving themselves as useful tools in several deep-learning applications. This stimulated the development of various learning heuristics, the most renown being Contrastive Divergence (CD) [21], and inference methods [22–25].

An alternative direction of research is motivated by many inference problems in biological systems, where couplings are typically asymmetric and possibly time-varying. The study of the dynamics and learning in these purely kinetic models is complicated by the lack of analytical control over the stationary distribution [26–28]: a number of interesting mean field techniques based on generalization of TAP equations have been proposed [26–28] in this context.

In the present study, we approach many of these problems from a unified perspective: the main goal of the paper is to devise a biologically plausible learning rule which could allow a general stochastic neural network to construct an internal representation of the statistical ensemble of the stimuli it receives. In the following, we consider the case
of asymmetric synaptic couplings and derive a learning scheme in which the updates involve only purely local and possibly noise-affected information. The proposed plasticity rule does not rely on the presence of supervisory signals or strong external stimuli, and proves to be compatible with Dale’s principle, which requires the homogeneity of the neurotransmitters released by one neuron across its synaptic terminals [29, 30]. In this work, we define the learning process in an on-line context, and our analysis will be restricted to the case of discrete time dynamics.

In the Results section, for clarity of exposition we will mostly focus on the specific case of fully-visible neural networks, giving only a brief overview on the extension to networks comprising hidden neurons. This last setting is largely expanded upon in the Appendix, where we also provide further analytical insights and the implementation details of our numerical experiments.

RESULTS

We present our main results in three different subsections. In the first one (The model), we derive the new plasticity rule in a framework that encompasses a wide variety of unsupervised and semi-supervised problems, such as the construction of attractor networks and learning in generative models with more complicated structures. In the second one (Fully visible case), we specialize to the case of attractor networks containing only visible neurons. After describing a link with the maximum pseudo-likelihood method, we study the numerical performance of the new learning rule in various settings, showing how it deals with finite external fields, different coding levels and the constraint of Dale’s law. We then test the rule in the case of correlated memories, we investigate its proneness to create spurious attractors and we measure its palimpsest capacity. Finally, in the third section (Adding neuronal states) we give an introduction to the more complex case of stochastic networks with hidden neurons, and review some of the results, presented in Appendix F, that were obtained in this setting.

The model

We consider the customary simple setup of a network of \( N \) stochastic binary neurons \( s = \{s_i\}_{i=1}^N \), with each \( s_i \) either in \( \{-1, +1\} \) or \( \{0, 1\} \), connected by a set of asymmetric synaptic weights \( J_{ij} \neq J_{ji} \), which evolves with a discrete-time synchronous dynamics described by the Glauber transition probability: the next state \( s' \) of the system depends on the current state \( s \) according to the following factorized probability distribution

\[
P(s' | s; \beta) = \prod_{i=1}^N \sigma(s'_i | h'_i; \beta),
\]

with \( \sigma(\cdot) \) being a sigmoid-shaped neural activation function defined by \( \sigma(s | h; \beta) \propto e^{-\beta s h} \) (the proportionality constant being set by normalization), and \( h'_i = h'_{iext} + \sum_{j \neq i} J_{ij} s_j - \theta_i \), being the total neural current – or local field – obtained by adding up the recurrent contributions from other neurons to the external stimulus \( h'_{iext} \). The quantity \( \theta_i \) serves as a local threshold. The dynamics of the system is thus stochastic, and the parameter \( \beta \) (which has the role of an inverse temperature in analogous physical models) provides a measure of the dynamical noise in the system. When the synaptic couplings \( J \) are finite and the external fields are time independent, the dynamics is known to be ergodic and a steady state defined by a unique stationary distribution is approached [20]. However, the analytical form of this steady state distribution is not known for general asymmetric kinetic models of the type we consider here.

In the following, we formulate the problem of learning as an unsupervised task where the network has to adapt its parameters in accordance with some plasticity rule: the goal is to learn an internal representation of a target probability distribution, which is to be inferred from a set of external stimuli conveyed to a subset of the neurons. Suppose we are given a time-independent binary pattern, a vector \( \xi \) of length \( N_V \leq N \) with components \( \xi_i = \pm 1 \), to be learned by the neural network. This pattern is presented to a group \( V = \{1, \ldots, N_V\} \) of “visible” neurons in the form of an external field of variable intensity \( \lambda_{iext} \) in the direction of \( \xi \), i.e. \( h'_{iext} = \lambda_{iext} \xi_i \) for \( i \in V \), while the complementary subset \( H = \{N_V + 1, \ldots, N\} \) of “hidden” neurons receive no external input. We want to model the scenario in which the stimulus intensity is high (although not as large as to clamp the neurons) at the onset, and rapidly vanishes. The initial presence of the field biases the dynamics of the system; in the retrieval phase, if the stimulus \( \xi \) is sufficiently close to a pattern \( \xi' \) that the network has learned, the stationary probability distribution of the visible neuronal states should get focused in the direction of \( \xi' \) even after the stimulus is no longer present.

For the sake of comparison, the classical Hopfield network with Hebbian learning can be framed in the same setting, as follows: we assume that there are no hidden neurons, and the dynamics of the stimulus presentation is a simple two-step process in which the stimulus intensity \( \lambda'_{iext} \) is initially effectively infinite (such that the other components of the inputs become irrelevant and the dynamics of the neurons becomes deterministic and fixed, i.e. such as to clamp...
the network) and then drops to 0. The learning rule in that case actually only uses the information about the state of the network during the clamped phase: $\Delta J_{ij} \propto s_i s_j$ where $s = \xi$ as a consequence of the clamping. In the retrieval tests, the clamped phase is used to initialize the network, which subsequently evolves by its own internal dynamics in absence of further stimuli.

In our framework, we exploit the dynamics of the stimulus during the learning phase, extracting the correlations that the stimulus induces on the network dynamics and using them to train the network: since the final goal of the network is to learn from the driving effect of the external field, we may require the dynamical evolution in the freely evolving network to maximally resemble the stimulus-induced evolution. Intuitively, this amounts at training the network to compensate the gradual vanishing of the external field by adapting its own recurrent connections. This requirement can be framed formally as the minimization of a Kullback-Liebler (KL) divergence between two different conditional probability distributions corresponding to different levels of intensity of the external field, $P(s'|s; \lambda_1^{\text{ext}})$ and $P(s'|s; \lambda_2^{\text{ext}})$, averaged over some initial state probability distribution $P(s)$. The analytical details can be found in Appendix B. As explained in more detail below, the distribution $P(s)$ is supposed to be concentrated (for the visible part of the network) around the direction of the pattern $\xi$, such that $s'$ will also be concentrated around $\xi$ as the combined effect of the initial conditions, the external field and of the recurrent connections; when the effect of the external field decreases, the recurrent connections will tend to compensate for this. If these conditions can be met, then the procedure can be applied repeatedly.

As an initial simplified case, consider the same setting as the Hebbian learning, i.e. the limiting case of an infinite $\lambda^{\text{ext}}$, in which the visible part of the network dynamics is clamped. The stationary probability distribution can thus be factorized over the visible neuronal states $s_V$:

$$P_{\text{clamp}}(s;\xi) = \prod_{i \in V} \delta_{s_i,\xi} \, P(s_H|s_V),$$

where $\delta_{x,y}$ denotes the Kronecker delta symbol which equals 1 if $x = y$ and 0 otherwise. Here, the conditional probability of the hidden neuronal states $s_H$, given the visible, cannot be written explicitly without losing generality. In our learning scheme, we seek to minimize the difference between the initial (fully clamped) situation and the subsequent zero-field situation; this requirement produces the following simple learning rules for the synaptic couplings and the thresholds:

$$\Delta J_{ij} \propto \left( \langle s_i' s_j' \rangle_{\text{clamp, } \infty} - \langle s_i' s_j \rangle_{\text{clamp, } 0} \right)$$

$$\Delta \theta_i \propto \left( \langle s_i' \rangle_{\text{clamp, } \infty} - \langle s_i' \rangle_{\text{clamp, } 0} \right),$$

where $s$ and $s'$ denote two successive states of the network, as above, and $\langle \cdot \rangle_{\text{clamp, } \lambda^{\text{ext}}}$ is defined as an average over the possible dynamical responses starting from a state sampled from $P_{\text{clamp}}$:

$$\langle s_i' s_j' \rangle_{\text{clamp, } \lambda^{\text{ext}}} = \sum_{s',s} s_i' s_j' P(s_i' | s; \lambda^{\text{ext}}) P_{\text{clamp}}(s;\xi)$$

$$\langle s_i' \rangle_{\text{clamp, } \lambda^{\text{ext}}} = \sum_{s',s} s_i' P(s_i' | s; \lambda^{\text{ext}}) P_{\text{clamp}}(s;\xi)$$

In the limiting case we simply have $\langle s_i' s_j' \rangle_{\text{clamp, } \infty} = \xi_i \xi_j$ for the visible neurons. In general, however, efficiently obtaining an accurate estimate of this average can pose serious technical challenges.

Since the case of a clamping stimulus is biologically unrealistic, we explore a setting in which the amplitude of the external signal is comparable to the recurrent contribution exerted by the surrounding neurons: instead of trying to match the dynamical response of a clamped model with a freely-evolving one, we introduce a learning protocol based on a time dependent field intensity $\lambda^{\text{ext}}(t)$, which decreases to zero starting from a finite initial value $\lambda_{\text{max}}$. In the following we will consider a staircase signal intensity $\lambda^{\text{ext}}(t)$, lowered by a fixed amount $\Delta \lambda$ after every $2T$ steps of the time-discretized network dynamics (see fig. 1). We should remark, however, that the results presented hereafter are quite robust with respect to variations in the precise details of the dynamical protocol for the field, and that the above choice was purely made for simplicity of presentation and analysis.

The training protocol prescribes the network to try and match its dynamical behavior at a given level of the field $\lambda$ with that at a lower level $\lambda - \Delta \lambda$, where the dynamical behavior is measured in terms of the time-delayed correlations between neurons

$$\langle s_i' s_j \rangle_{\lambda} = \sum_{s',s} s_i' s_j P(s_i' | s; \lambda) P(s)$$
Figure 1. DCM Learning protocol scheme. This represents the learning process for one pattern presentation. The blue curve shows the stepwise dynamics of the external field $\lambda^{\text{ext}}$ as a function of the time $t$ of the network dynamics. The first time period ($T_{\text{init}}$ time steps, shaded) serves for initializing the network state in the proximity of the pattern. The protocol then proceeds in windows of $2T$ steps, each one divided in two phases. In the middle of each window the field intensity drops by $\Delta \lambda$. The time-delayed correlations are recorded separately for the two phases. The parameters are updated at the end of each window, in correspondence of the $\star$ symbols, according to eq. (6).

and $P(s)$ is some initial probability distribution roughly concentrated around the presented pattern $\xi$ for the visible neurons. More precisely, we suppose that the overall distribution $P(s'|s;\lambda)P(s)$ induces a dynamics which is confined around $\xi$ and ergodic within such region. When that is the case, sampling the temporal averages as the system evolves can provide an estimate of the averages involved in the above expression. It is reasonable to assume, and confirmed by our experiments, that this condition will be satisfied if the initial field $\lambda_{\text{max}}$ is sufficiently large, thus creating an effective basin of attraction, and if the system evolution manages to keep this confinement in place even when the field is decreased by adapting the recurrent connections.

Our learning protocol is thus defined as follows (see fig. 1): the network will first record for $T$ time steps its time-delayed correlations at a given value of the field $\lambda^{\text{ext}}(t) = \lambda$; then, it will do the same for another $T$ steps at a lower level, $\lambda^{\text{ext}}(t+T) = \lambda - \Delta \lambda$, after which it will adjust its parameters such as to try to match the two sets of measurements (see below). The protocol will then restart with the same field $\lambda^{\text{ext}}(t+2T) = \lambda - \Delta \lambda$ (but with updated network parameters), proceeding in this way until the field has dropped to zero. The network state is never reset during these steps; rather, it keeps following the dynamics of eq. (1). An extra initial period of $T_{\text{init}}$ steps (we generally set $T_{\text{init}} = T$ in our simulations) at $\lambda_{\text{max}}$ field is used to prepare the network and bias it in the direction of the pattern.

Therefore, in this approximation, we obtain a new plasticity rule (the notation $\langle \cdot \rangle_{t,\lambda}$ here denotes empirical averages over time in presence of a given field $\lambda$, and we switch to using $t$ and $t+1$ to denote two consecutive time steps):

$$\Delta J_{ij} \propto \langle s_{i}^{t+1}s_{j}^{t} \rangle_{t,\lambda} - \langle s_{i}^{t+1}s_{j}^{t} \rangle_{t,\lambda-\Delta \lambda},$$

$$\Delta \theta_{i} \propto \langle s_{i}^{t+1} \rangle_{t,\lambda} - \langle s_{i}^{t+1} \rangle_{t,\lambda-\Delta \lambda},$$

which simply tries to match the time-delayed correlations in the consecutive time windows, until the signal has vanished and the system evolves freely. All the needed information is thus local with respect to each synapse. In order to learn a given extensive set of $\alpha N$ patterns, the same procedure has to be repeated cyclically: a pattern is presented with decreasing intensity while the network adapts its parameters, then the network moves to the next pattern. The
network is not reset even between one pattern and the next. We call this learning rule “delayed-correlations matching”, DCM for short. The full algorithm is detailed in Appendix D together with the corresponding pseudo-code.

It is not necessary for the field dynamics to end up exactly at zero intensity: following the same idea proposed in ref. [31], the learning scheme described above can be made more robust if one requires the network to face the presence of an antagonist field, that tries to interfere with the drawing effect of the basin of attraction. By considering a negative minimal intensity \( \lambda_{\text{min}} < 0 \), one can in fact both speed up the learning process and induce larger basins of attraction. If instead the aim is to learn new basins of attraction coherently, trying not to affect the previously stored memories, it can be useful to choose a positive \( \lambda_{\text{min}} > 0 \): this ensures that the sampling process doesn’t leave the neighborhood of the presented pattern, risking to end up in a different memory and possibly delete it (we will consider this prescription in the one-shot learning scenario).

### Fully visible case

When a network with no hidden neurons is considered (\( N_V = N \)), the learning problem effectively reduces to that of constructing a stochastic attractor neural network with binary units. Kinetically persistent neuronal states can be indeed observed even with asymmetric synaptic couplings \( J \). We will require the network to embed as stable and attractive memories an extensive set of i.i.d. random binary ±1 patterns, denoted by \( \{ \xi^{\mu}_i \}_{\mu=1}^{M} \), with \( M = \alpha N \) (each \( \xi^{\mu} \) is an \( N \)-dimensional vector, and \( \mu \) represents a pattern index). The number of stored patterns per neuron \( \alpha \) is the so called storage load of the network.

Since the learning procedure is defined as a cyclical minimization of a KL-divergence evaluated at the \( M \) patterns, the limiting case with just two dynamical steps and infinite initial field considered in eq. (3) can here be reinterpreted exactly as an on-line optimization of the so called log-pseudo-likelihood:

\[
\mathcal{L} \left( \{ \xi^{\mu} \} | J_{ij}, \theta; \beta \right) = \frac{1}{M} \sum_{\mu=1}^{M} \sum_{i=1}^{N} \log P \left( s_i = \xi^{\mu}_i \big\{ s_j = \xi^{\mu}_j \big| \big\{ s_i = \xi^{\mu}_i \big| \lambda^{\text{ext}} = 0 \right),
\]

which is most frequently found in an inference framework [32, 33], where the parameters of a generative model have to be inferred from a finite set of complete observations (see Appendix B 1).

In this case, the update for the synaptic couplings can be written more explicitly and allows for a clear comparison with the standard Hebbian plasticity rule:

\[
\Delta J_{ij} \propto \left( \xi^{\mu}_i \xi^{\mu}_j - \sum_{s_i^{t+1}} P \left( s_i^{t+1} \big| \big\{ s_j = \xi^{\mu}_j \big| \lambda^{\text{ext}} = 0 \big\right) s_i^{t+1} \xi^{\mu}_j \right).
\]

The DCM rule is explicitly asymmetric, and its differential form produces a homeostatic mechanism constantly trying to reproduce externally induced correlations in the network dynamics. While in the initial stages of the learning process the synaptic weights are modified according to a typical Hebbian prescription - potentiation in case of positive correlations and depression with negative ones - the comparator effectively avoids the possibly uncontrolled positive feedback loop of the Hebbian principle: no change in synapses will occur when the correlations in the absence of the stimulus already match the ones of the learned patterns. Incidentally, we also note that in the noise-free limit \( \beta \to \infty \) the perceptron learning rule is recovered (see Appendix B 2). In the case of \( s_i \in \{-1,+1\} \) neurons, we studied numerically the trend of the maximum storage load achievable with the DCM rule as a function of the required width of the basins of attraction. We introduced an operative measure of the basin size, relating it to the level of corruption of the memories before the retrieval: a set of \( M = \alpha N \) patterns is considered to be successfully stored at a noise level \( \chi \) if, initializing the dynamics in a state where a fraction \( \chi \) of the pattern is randomly corrupted, the retrieval rate for each pattern is at least 90\% (for additional details see Appendix D 1). In fig. 2 we compare the DCM rule with the Hopfield model, which is known to achieve a maximum storage load of \( \sim 0.14N \).

If we move to the more biologically plausible scenario of finite time-dependent external fields (eq. (6)), we clearly see in fig. 3 that an infinite signal is actually redundant. If the external field intensity is high enough, the recorded time-delayed correlations carry enough information about the pattern to be learned. If instead the signal component in the local field is dominated by the recurrent contribution from other neurons the dynamics becomes completely noisy. Since the average strength of the connections between the neurons increases with the number of stored memories, the maximum storage load grows with the signal amplitude. Nevertheless, the results of pseudo-likelihood are already almost saturated at small fields intensities \( \lambda_{\text{max}} \sim 1 \), and the DCM rule generally works well even when the stimulus
intensity is relatively small compared to the total recurrent input (see inset of fig. 3). The implementation details are described in Appendix D.

We also considered an alternative model with somewhat more biologically plausible features, using \( s_i \in \{0,1\} \) neurons (see Appendix A) and sparse \( \xi' \in \{0,1\} \) patterns, and forcing the synapses to satisfy Dale's law. This means that two sub-populations of excitatory and inhibitory neurons should be defined, the sign of their outgoing synapses being fixed a priori. Note that this restriction reduces the theoretical maximum capacity of the network, although not dramatically (roughly by half [34]). For simplicity, we restricted our analysis to the case where only excitatory synapses are plastic and a separate inhibitory sub-network provides a feedback regulatory effect, whose goal is to maintain the network activity \( S^t = \sum_{i=1}^{N} s_i^t \) around a desired level \( N_f \) (the same sparsity level as the learned patterns), and preventing epileptic (all-on) or completely switched off states. We tested three different effective models that implement an inhibitory feedback mechanism: (i) a generalization of the global inhibitory mechanism described in ref. [34], tuned such as to counterbalance the oscillations of the network activity around the desired level; (ii) a soft “winner-takes-all” mechanism, effectively playing the role of a global inhibitory unit [35–45]; (iii) a model with adaptive thresholds that allow the Dale’s principle model to behave approximately like the unconstrained one. The details, including the derivation of the parameters of all these schemes, are reported in Appendix C. For all of them, the results are comparable to the ones shown in fig. 4.

Figure 2. Maximum storage load as a function of the width of the basin of attraction for a network of \( N = 400 \) visible neurons. The red and blue curves show the results for Hopfield model and the DCM rule, respectively. The noise level \( \chi \) operatively measures the width of the basins of attraction (it is the fraction of corrupted bits that the network is able to correct, see the text for a more precise definition). Each curve is an average over 10 samples (error bars are smaller than point size). The inverse temperature parameter is set to \( \beta = 2 \) in order to fall within the retrieval phase of the Hopfield model. The critical capacity at zero temperature is lower than the Gardner bound, \( \alpha_c = 2 \), because of the stochastic component of the dynamics.
Figure 3. Maximum storage load as a function of the field intensity for a network of $N = 400$ neurons. The correlations were recorded in windows of $T = 20$ time steps and the field intensity step was $\Delta \lambda = \lambda_{\text{max}}/3$. The noise level in the retrieval phase is set to $\chi = 0.3$ and the temperature to $\beta = 2$. The curve was obtained by averaging over 100 samples. The inset shows a comparison between the recurrent and external components of the inputs, for the same data points of the main panel. The mean recurrent input was computed as the square root of the mean values. This shows that the DCM rule is effective even for relatively small stimuli.

Comparison with Hebbian plasticity rule

Most real-world data is inherently sparse and redundant, so that it is crucial for a plasticity rule to be able to deal with a pattern set exhibiting internal correlations. The most trivial way of introducing a positive correlation among the patterns is to bias the probability distribution from which the patterns are extracted, i.e. using the probability distribution $P(\xi_i) = b \delta(\xi_i - 1) + (1 - b) \delta(\xi_i + 1)$ for the patterns components, with $b \in (0, 1)$ ($b = 1/2$ being the unbiased case). The Hebbian learning rule needs to be adapted for enabling learning of biased patterns [46] (see Appendix D 4), and the modification requires explicit knowledge of the statistics of the stimuli. The DCM rule is instead able to adapt to the case of unbalanced patterns without any modification, and achieves a much better performance, as can be seen in fig. 5.

A more realistic way of introducing pattern correlations can be studied in the $s_i \in \{0, 1\}$ case, where it is possible to generate a set of patterns as combinations of sparse features drawn from a finite length dictionary (i.e. we pre-generate a set of sparse patterns – the dictionary of features $\mathcal{D}$ – and then generate each stimulus by taking a small random subset of $\mathcal{D}$ and superimposing the patterns within it; see Appendix D 4). In the limit of an infinitely large dictionary one produces uncorrelated patterns, but correlations set in as the length of the dictionary is reduced. In fig. 6 we show how the DCM rule is able to take advantage of the decrease in the information content of the patterns as the total number of features is reduced.
Another drawback of the plain Hebb rule is the introduction of spurious memories while the desired patterns are embedded as attractors. These spurious states usually appear in overlapping regions of the basin of attraction of different stored memories, and are therefore referred as mixture states [15]. As can be seen in fig. 7, the problem of spurious attractors is almost completely avoided when the DCM rule is employed, since it is able to store the patterns more coherently and the basins of attraction are not likely to interfere with each other.

One-shot learning

Finally, we also tested the DCM learning rule in a one-shot on-line setting: each pattern is presented to the network until it becomes a stable attractor and then is never seen again. In this scenario the relevant measure of the performance is the so called palimpsest capacity [47]: after an initial transient, the network is expected to enter a steady-state regime in which an old memory is lost every time a new one is learned. Our numerical results, obtained in the $s_i \in \{-1, +1\}$ case (fig. 8), show that – quite remarkably – by simply adding a weight regularization the DCM rule achieves an extensive palimpsest capacity, slightly above $\sim 0.05 N$. This property was verified by a scaling analysis. Similar results can be obtained in the $s_i \in \{0, 1\}$ case only with the adaptive threshold regulatory scheme (see Appendix D3 for more details).

Another local learning rule that is known to perform well in an online setting was proposed by Storkey [48], and
Figure 5. Maximum storage load as a function of the bias in the distribution of the patterns for networks of size $N = 200$ (dashed curves) and $N = 400$ (full curves). The correlation is introduced trivially: each pattern is built by extracting spins from a biased distribution $P(\xi_i) = b\delta(\xi_i - 1) + (1 - b)\delta(\xi_i + 1)$. The blue curves show the scaling properties of the capacity of the DCM rule as a function of the bias. The drop in the performance for small biases is due to finite size effects, and the performance improves with $N$. The red and green curves show the results for the naive Hebb rule and the generalized Hebb rule adapted to the biased case, respectively (see Appendix D4). For larger $N$ the capacity for all unbalanced cases is expected to drop to 0. All the curves were obtained by averaging over 10 samples (error bars are small than the point size).

reads:

$$\Delta J_{ij} = \Delta J_{ji} \propto (\xi_i^\mu \xi_j^\mu - h_i^\mu \xi_j^\mu - h_j^\mu \xi_i^\mu)$$

(9)

where $h_i = \sum_k J_{ik} \xi_k$ are the local fields. The last two terms can penalize the weights when the memory is already stored ($h_i$ has the same sign of $\xi_i$) and the local field becomes excessively large, building a regularization mechanism directly into the learning rule. Limiting the growth of the synaptic weights is in fact necessary in order to avoid entering a spin glass phase, where all the memories are suddenly lost and learning can no longer take place [49]. However, Storkey’s rule fails when tested against our retrieval criterion in a finite temperature setting (we are setting $\beta = 2$ in the parallel Glauber dynamics). This not only shows that the DCM is able to embed attractors arbitrarily robustly (depending on the temperature considered during training), but also stresses the fact that the retrieval criterion that was employed throughout this paper is very strict compared to alternative definitions. For example, if we consider the criterion proposed in [48] the DCM rule palimpsest capacity is measured to be as high as $\sim 0.3N$. 
Figure 6. Maximum storage load as a function of the length of the dictionary of features. We study the critical capacity of the generalized Hebb rule (red curve) and the DCM rule (blue curve) when the patterns are generated as combinations of features, chosen from a dictionary of varying length $L$. In the inset, the mean Pearson correlation in a dataset of 200 patterns is shown as a function of the dictionary length. In the numerical experiments every feature had a fixed sparsity of $f = 0.1$ and each pattern was obtained as a superposition of $F = 6$ features (see Appendix D4). The curves were obtained by averaging over 10 samples (error bars are smaller than the point size).

Adding hidden neuronal states

When hidden neurons are introduced, the stochastic neural network turns into a rather general computational device, which can be framed as a parametric probabilistic model able to develop an internal representation of the statistics of external stimuli. This kind of neural network could recover a partially corrupted memory, as in an attractor neural network, but it could also be exploited as a generative model, able to produce new samples in accordance with the statistics inferred from the training data.

Even in the case with undirected symmetric synaptic couplings – the Boltzmann Machine – the inference and learning problems become NP-hard, since the time required for the dynamics to reach thermal equilibrium is bound to grow exponentially with the network size [50]. A well studied solution to these problems is to consider a simplified synaptic structure, in which the connections of the network are restricted to the ones between visible and hidden neurons, the so-called Restricted Boltzmann machine (RBM) [51]. We will focus on the same rigid architecture.

The DCM learning rule can still be understood in a KL minimization framework. As before, in the infinite signal limit we obtain a log-pseudo-likelihood optimization procedure, except that now the inference is from incomplete observations and an average over all the possible hidden neuronal states is required (see Appendix F). In this limit the synaptic couplings are updated as:
Figure 7. Number of spurious attractors for a network of \( N = 400 \) neurons. This figure shows the number of distinct spurious attractors found during 10000 independent random walks, of 200 time-steps, after a small number of patterns were learned by the network (see Appendix D2). The red curve represents the Hebb rule (the first peak is due to finite size effects). The blue curve shows the behavior of the DCM rule. The curves were obtained by averaging over 10 samples (error bars are standard errors).

\[
\Delta J_{ij} \propto P(s_j | s_V = \xi) \xi_i s_j - \sum_{s \in \mathcal{H}} \prod_{k \in \mathcal{H}} P(s_k | s_V = \xi) P(s'_i | s_H) s'_i s_j.
\]  

(10)

This equation is closely linked to the contrastive divergence method, CD-\( k \), a heuristic algorithm for approximating the maximum likelihood method for RBMs [21]. The first term in eq. (10) requires sampling from the probability distribution of the hidden neuronal state induced by a clamping stimulus on the visible neurons, as in the positive phase of CD-\( k \), while the second term can be estimated by implementing a Gibbs sampling chain starting from a visible state prepared in correspondence of the stimulus but subject to no external field, as in CD-\( k \)'s negative phase. This relationship could shed some light on the apparently surprising performance that can be obtained with CD, even when a very small number of Gibbs sampling steps \( k \) is chosen: this means that the partition function of the model is estimated very crudely, restricting sampling only to the mode induced by the seed of the Gibbs chain. This is in fact what the pseudo-likelihood method would require [24]. CD-\( k \), however, is defined in the context of models with symmetric interactions and therefore does not apply to asymmetric kinetic models of the type considered throughout this work.

In the presence of hidden neurons we can still apply the heuristic prescription described above (eq. (6)), yielding a plasticity rule that matches time-delayed correlations, recorded during the network dynamics. In order to test numerically how a biologically plausible system could perform against a state-of-the-art learning method, we also derived the Thouless-Anderson-Palmer (TAP) mean-field equations [52] for approximating the steady-state distribution.
Figure 8. Scaling properties of the palimpsest capacity. In this figure we show the results obtained when testing the DCM learning rule in the context of one-shot learning, for the case of \( s_i \in \{-1, +1\} \) neurons. The full curves show the results for \( N = 100, N = 200, N = 400 \) and \( N = 800 \), illustrating the scaling properties of the palimpsest capacity. The dashed gray curves are extrapolated as the mean of the last 3 measurements. All the points are obtained by averaging over 10 samples.

In Appendix F we consider the problem of learning the statistics of a dataset of real-world images \cite{53}. The performance of the DCM rule is assessed in the customary feature extraction, generative, and classification tasks and compared with that of the TAP approach, on same neural network architectures. While there is an obvious degradation in the learning performance, we also observe that the robustness of our learning model is still allowing the network to learn despite the presence of noise and strict detrimental biological constraints.

**DISCUSSION**

In this work we studied the problem of learning in general stochastic neural network models. Starting from a KL divergence minimization condition, we derived analytically a differential update rule closely related to the Maximum Pseudo-likelihood method, able to store an an ensemble of patterns of neuronal activity, conveyed to the network in the form of external fields. With some slight modifications, we obtained a version of the rule that allowed us to introduce a number of important requirements for biologically plausibility, concerning not only the network structure but the learning process as well. We further showed that all the needed information could be collected during the dynamics of the network by some kind of short term memory mechanism, locally keeping track of correlations, and that the updates could be implemented by a comparator simply trying to maintain externally induced correlations by
increasing the synaptic weights.

Our DCM learning rule bears great resemblance with classical Hebb plasticity, in that synaptic modifications are driven only by the information about activity correlations locally available at the synapse. However, the DCM rule can be applied in a general framework where asymmetric synapses are allowed, at odds with the previous learning paradigms. Moreover, the rule relies on finite external signals, that are not able to quench the network dynamics completely. Apart from retaining a higher biological plausibility, this is one of the reasons why this rule can embed an extensive number of patterns while minimizing the patterns cross-talk, avoiding the creation of spurious memories. The stochastic network becomes capable of learning in a purely on-line context, including in the extreme limit of one-shot learning.

The differential form of the plasticity rule also allows for a good retrieval performance when the memories are correlated, both in the case of simply biased memories and in the case of patterns obtained as combinations of features. In the sparse case, we showed the robustness of the DCM rule to the introduction of the excitatory-inhibitory differentiation constraint (Dale’s principle), and proposed various inhibitory mechanism which proved to be able to control the activity level of the network and to prevent the dynamics from reaching epileptic states.

Finally we showed how the very same learning rule allows a more general network, in which hidden neurons are added, to perform well in feature extraction, generation and classification tasks, when dealing with real-world data. By means of comparison with a state-of-the art method, we argue that, by implementing the proposed learning rule, a stochastic neural network obeying strong biological requirements could preserve great modeling potential. In particular, the similarities with Boltzmann Machine learning [20, 51] (see also below) suggest that the DCM rule may be a viable candidate for feature extraction and inference: for example, in experiments with patterns formed from combining features from a dictionary (as for those of fig. 6), we may hope to recover the individual features as internal representations in the hidden part of the network. We performed preliminary experiments in this direction and the results are indeed promising. In this paper, however, our numerical analysis was limited to the well-studied case of directed visible-to-hidden synapses and digit recognition, and the exploration of hybrid and more general architectures and tasks is left for future work.

Future possible research directions include the generalization of this learning framework to continuous time dynamics and more realistic spiking network models, and the problem of learning dynamical activation patterns instead of static ones. It must be noted that the idea of learning recurrent weight matrix in a network model by matching some measure of a driven system to that of an autonomous one is not new. The general strategy for stabilizing dynamical patterns has been rediscovered under several denominations in the broad context of reservoir computing and generally involves the matching of local currents [54–56], with notable examples both in the discrete time step deterministic setting [57] and in spiking network models [58, 59]. These models have the advantage of capturing the dynamical complexity of neural systems. We note that, on the other hand, they rely on some non-local learning strategies.

Our model also shares some similarities with the Equilibrium Propagation algorithm (EP) for energy-based models of ref. [60], but with some crucial differences. The main similarity relies in the fact that the resulting update rule for the synaptic weights uses the difference between the correlations measured with the network in a weakly-clamped state (using the EP terminology) and a free state. This is also reminiscent of the original algorithm for training Boltzmann Machines proposed in ref. [20]. The major difference in our model is the use of time-delayed correlations, which stems from the different approach used in our derivation and allows us to work in the general setting of asymmetric synaptic connections – indeed, the synaptic symmetry in the EP approach was regarded by the authors as its most unsatisfactory requirement from a biological perspective. Additional important differences arise from the overall setting and derivation: in the EP case, the context is supervised learning, the inputs are fully clamped and drive the network towards an equilibrium (in the free phase), after which the outputs are weakly clamped (the limit of vanishing clamping is considered) and the weights updated accordingly. In our case, the context is unsupervised learning, there is no preliminary equilibration step (the network is not reset between pattern presentations), and the external driving force is relatively weak but non-vanishing (it decreases to zero gradually as training progresses).

In ref. [61], in the context of diluted neural networks, the authors used as a learning criterion the matching of equal-time correlations, still comparing a system driven by a finite field with a freely-evolving one. In that case, however, the connections were assumed to be symmetric, and the correlations were estimated with the Belief Propagation algorithm. At odds with these approaches, we presented a formulation in terms of delayed activity correlations that, while requiring a time integration mechanism, is completely local, and is used to construct general excitatory-inhibitory asymmetric networks. Another attempt at devising a learning protocol with good performances and subject to basic biological constraints was presented in ref. [34], exploiting the statistics of the inputs rather then the dynamical properties of the network. The resulting “Three thresholds” learning rule (3TLR) shares with the DCM rule most desirable features for a biological system, e.g. it can achieve near-optimal capacity even with correlated patterns. A detailed comparison of the performance of the two rules is technically and computationally demanding and unfortunately out of the scope of this work, but the 3TLR seems to require stronger driving external fields; furthermore, lowering the field results in an abrupt performance drop, while the DCM rule degrades gracefully, cf. fig. 3.
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Appendix A: Types of neurons

In this work we considered two kinds of binary neurons, $s_i \in \{-1, +1\}$ and $s_i \in \{0, 1\}$. The sigmoid-shaped function $\sigma(\cdot)$ which appears in eq. (1) takes two slightly different forms depending on the model, as a consequence of the different normalization term appearing in the two cases:

$$\sigma_{\pm 1}(s|h; \beta) = \frac{e^{\beta s h}}{e^{\beta h} + e^{-\beta h}} \quad (A1)$$

$$\sigma_0(s|h; \beta) = \frac{e^{\beta s h}}{1 + e^{\beta h}} \quad (A2)$$

In the case of $s_i \in \{-1, +1\}$ neurons, we sampled each component of the patterns independently from a potentially biased probability distribution $P(\xi_i) = b \delta(\xi_i - 1) + (1 - b) \delta(\xi_i + 1)$, with a bias parameter $0 < b < 1$. In most of our tests, however, we considered the unbiased case $b = 1/2$, except for those presented in fig. 5. In this case, the local fields are naturally balanced around zero and the thresholds $\theta_i$ can be eliminated.

In the case of $s_i \in \{0, 1\}$ neurons, we sampled each component of the memories from the prior $P(\xi_i) = \lambda \delta(\xi_i - 1) + (1 - \lambda) \delta(\xi_i + 1)$, with $\lambda < 1$, averaged over an initial state $\theta_i$. Therefore, we get the final expression for the averaged KL divergence:

$$\langle \text{KL}(P(\cdot|s; \lambda_1)||P(\cdot|s; \lambda_2)) \rangle_p = \sum_s P(s) \sum_{s'} P(s'|s; \lambda_1) \log \frac{P(s'|s; \lambda_1)}{P(s'|s; \lambda_2)}, \quad (B1)$$

The conditional probability is defined as a sigmoid-shaped neural activation function (cf. eq. (1))

$$P(s'|s; \lambda) = \prod_{i=1}^N \sigma(s'_i|h_i^\lambda), \quad (B2)$$

with local fields $h_i^\lambda$ given by: $h_i^\lambda = h_i^{\text{ext,} \lambda} + \sum_{j \neq i} J_{ij}^\lambda s_j - \theta_i^\lambda$. Here we adopt the superscript $\lambda$ to distinguish between the two networks, subject to different external field intensities $\lambda$.

Plugging the expression (B2) for the conditional probability into the definition (B1) of the KL divergence, we exploit the factorization property of the single neuron conditional probabilities, in order to isolate the $i$-th contribution and trace out all the others. Therefore, we get the final expression for the averaged KL divergence:

$$\langle \text{KL}(P(\cdot|s; \lambda_1)||P(\cdot|s; \lambda_2)) \rangle_p = \sum_i \sum_{s'_i} \sum_{s'_i'} \sigma(s'_i|h_i^\lambda) \log \frac{\sigma(s'_i|h_i^{\lambda_1})}{\sigma(s'_i|h_i^{\lambda_2})} \quad (B3)$$

The next step is to minimize this quantity, by differentiating with respect to $J_i^{\lambda_2}$ and $\theta_i^{\lambda_2}$, asking the second network to compensate for the decrease in the external field through an adaptation of its parameters. For both expressions of $\sigma$ of eqs. (A1) and (A2), the following property holds:

$$\frac{1}{\beta} \frac{\partial}{\partial h} \log \sigma(s|h; \beta) = s - \langle s \rangle_h \quad (B4)$$

where here $\langle s \rangle_h = \sum_s s \sigma(s|h; \beta)$. This allows us to derive the following simple formulas for the derivatives with respect to the parameters, for both neuronal models:
\[ -\frac{1}{\beta} \frac{\partial}{\partial J_{ik}^{\lambda_2}} \left( \text{KL} \left( P \left( \cdot | s; \lambda_1 \right) \left| P \left( \cdot | s; \lambda_2 \right) \right) \right)_P = \sum_s P \left( s \right) \sum_{s_i'} \sigma \left( s_i' | h_i^{\lambda_1} \right) \left( s_i' - \langle s_i' \rangle \right) s_k \]
\[ = \langle s_i' s_k \rangle_{P, \lambda_1} - \langle s_i' s_k \rangle_{P, \lambda_2} \]  
(B5)

\[ -\frac{1}{\beta} \frac{\partial}{\partial \theta_i^{\lambda_2}} \left( \text{KL} \left( P \left( \cdot | s; \lambda_1 \right) \left| P \left( \cdot | s; \lambda_2 \right) \right) \right)_P = \sum_s P \left( s \right) \sum_{s_i'} \sigma \left( s_i' | h_i^{\lambda_1} \right) \left( s_i' - \langle s_i' \rangle \right) \]
\[ = - \left( \langle s_i' \rangle_{P, \lambda_1} - \langle s_i' \rangle_{P, \lambda_2} \right) \]  
(B6)

As mentioned above though, the second one is not actually used in the ±1 model since we did not use the thresholds \( \theta_i \) in that case.

1. Connection with maximum pseudo-likelihood method

In the fully visible case, the clamped probability distribution eq. (2) simply becomes \( P_{\text{clamp}} \left( s; \xi \right) = \prod_{i=1}^{N} \delta_{s_i, \xi_i} \), and the average KL divergence defined in eq. (B1) can be written explicitly as:

\[ \langle KL \left[ P \left( \cdot | s; \lambda^{\text{ext}} = \infty \right) \left| P \left( \cdot | s; \lambda^{\text{ext}} = 0 \right) \right] \rangle_{P_{\text{clamp}}(\xi)} = \]
\[ = - \sum_{i=1}^{N} \log P \left( s_i = \xi_i | \{ s_j = \xi_j \}_{j \neq i}; \lambda^{\text{ext}} = 0 \right). \]  
(B7)

This expression can be recognized as one of the terms appearing in the so-called log-pseudo-likelihood \( \mathcal{L} \left( \{ \xi^{\mu} \} | J_{ij}, \theta; \beta \right) = \frac{1}{M} \sum_{\mu=1}^{M} \sum_{i=1}^{N} \log P \left( s_i = \xi^{\mu}_i | \{ s_j = \xi^{\mu}_j \}_{j \neq i}; \lambda^{\text{ext}} = 0 \right). \)

The pseudo-likelihood method provides a computationally inexpensive yet statistically consistent estimator [62] when the functional form of the joint probability distribution over the configurations is unknown, and is thus approximated in the factorized form \( P \left( s = \xi^{\mu} \right) = \prod_i P \left( s_i = \xi^{\mu}_i | \{ s_j = \xi^{\mu}_j \}_{j \neq i} \right). \) In the framework of learning, the minimization of eq. (B7) can be seen instead as a stability requirement for the memory \( \xi \), as it progressively increases the probability that the stochastic dynamics remains fixed in the attractor state.

2. Connection with the perceptron rule

In the noise-free limit \( \beta \to \infty \), where the state of the neuron \( s_i^{t+1} \) is deterministically obtained by taking the sign of the local incoming current, the pseudo-likelihood synaptic weight update would read:

\[ \Delta J_{ij} = \begin{cases} 
0 & \xi_i h_i \geq 0 \\
2 \eta \xi^{\mu}_i \xi^{\mu}_j & \xi_i h_i < 0 
\end{cases} \]  
(B8)

which is the well-known perceptron rule. Indeed, since the next state of a neuron is conditionally dependent on the previous state of the other \( N - 1 \) neurons, one can reinterpret the problem of learning a certain number of attractors as \( N \) independent perceptron learning problems. In a zero temperature setting, the incoming weights of a neuron \( i \) can be simply updated whenever its predicted state is misaligned with respect to the \( i \)-th component of the memory to be learned, \( s_i^{t+1} \neq \xi_i \), by shifting its weights in the direction of the desired state and in parallel to the pattern itself. It is known that the perceptron rule saturates the theoretical Gardner bound \( \alpha_c = 2 \) for the critical memory capacity of a fully-visible neural network at zero noise [63].

Moreover, if we follow [31] and consider negative field intensities \( \lambda_{\min} < 0 \) (instead of \( \lambda_{\min} = 0 \) as in the pseudo-likelihood method), we obtain:

\[ \Delta J_{ij} = \begin{cases} 
0 & \xi_i h_i \geq |\lambda_{\min}| \\
2 \eta \xi^{\mu}_i \xi^{\mu}_j & \xi_i h_i < |\lambda_{\min}| 
\end{cases} \]  
(B9)
This is nothing but the perceptron rule with robustness parameter $|\lambda_{\text{min}}|$, that forces the network to learn the memories so that they are attractive in a full sphere of such radius. However, any $\lambda_{\text{min}} < 0$ will also cause the maximum capacity of the network to decrease [64].

Appendix C: Inhibitory Network models

We considered three different schemes that can reproduce the effect of an inhibitory network. In the first one, the inhibitory network is replaced by a global inhibitory unit connected to all the $N$ excitatory neurons [34], which elastically drives the system towards the desired activity level through a feed-back signal. An alternative scheme can be obtained by introducing a soft “winner-takes-all” mechanism, effectively playing the role of a global inhibitory unit [35–45]. This mechanism is meant to model a continuous time scale phenomenon: the neurons with higher local activities could become active before the others and start to excite the inhibitory component of the network, whose feed-back signal is triggered when the correct fraction $f_\nu$ of neurons is already active; this signal thus depresses all the local activities of the network, preventing the remaining neurons from activating. The last inhibitory scheme is based on the introduction of locally adaptive thresholds (from a biological point of view, this mechanism can be justified with the widely observed phenomenon of thresholds variability in the central nervous system [65]).

The aim of the inhibitory feedback is to maintain the excitatory network activity around a desired level, preventing epileptic (all-on) or completely switched off states in the $\{0,1\}$ model. In the following, we provide more detailed explanations and some implementation details for each scheme.

1. The global inhibitory unit scheme

We consider a generalization of the global inhibitory unit scheme proposed in [34], for a purely excitatory stochastic neural network constituted by an ensemble of $N$ neurons. Suppose that, within the entire neuronal population, we can distinguish $G$ different groups of neurons, such that $N = \sum_{a=1}^{G} N_a$, with different sparsity levels. We introduce $G$ global inhibitory units, whose task is to maintain the activity $S^\alpha = \sum_{i=1}^{N} s_i^\alpha$ of each population of neurons at the desired level $f^\alpha N_a$. According to the global inhibitory unit scheme, each excitatory neuronal ensemble $\alpha$ receives a feed-back signal $T^\alpha \left( \{ f_\beta, S_\beta \}_{\beta=1}^{G} \right)$, which can be parametrized as:

$$T^\alpha \left( \{ f_\beta, S_\beta \}_{\beta=1}^{G} \right) = H_0^\alpha + \nu^{\alpha\alpha} (S_\alpha - f^\alpha N_\alpha) + \sum_{\beta \neq \alpha} \nu^{\alpha\beta} (S_\beta - f^\beta N_\beta), \quad (C1)$$

In this section we derive analytically an expression for both the global inhibition constant $H_0^\alpha$ and the parameters $\nu^{\alpha\beta}$ that control the elastic reaction to possible oscillations around the desired activities.

Assuming that the local fields $h_i^\alpha$ in population $\alpha$ are Gaussian distributed, the inhibitory units are required to correctly set the mean of the distribution around the mean threshold $T^\alpha = \langle \theta_i^\alpha \rangle$, so that the integral of the distribution above threshold contains exactly $f^\alpha N_\alpha$ local fields:

$$\langle h_i^\alpha \rangle = T^\alpha - H^{-1}(f^\alpha) \sigma_\alpha. \quad (C2)$$

Here $H^{-1}(x) = \sqrt{2} \text{erfc}^{-1}(2x)$ represents an inverse error function, determining the proper shift to be applied, measured in units of the standard deviation of the distribution $\sigma_\alpha$. The latter can be easily computed, giving:

$$\sigma_\alpha = \sqrt{\left( \sigma_\alpha^\alpha \right)^2 (S^\alpha - f^\alpha) + \sum_{\beta \neq \alpha} \left( \sigma_j^{\alpha\beta} \right)^2 S^\beta}, \quad (C3)$$

where $\sigma_j^{\alpha\beta}$ stands for the standard deviation of the distribution of the synaptic couplings from population $\beta$ to population $\alpha$.

By summing and subtracting $\sum_{\beta} \left( \sigma_j^{\alpha\beta} \right)^2 f^\beta N_\beta$ in the square root, assuming small deviations of the activity of the
network $S^\alpha$ from the desired activity level $f^\alpha N_\alpha$, we can expand $\sigma_\alpha$ obtaining:

$$\sigma_\alpha = \sqrt{f^\alpha (N_\alpha - 1) (\sigma_j^\alpha)^2 + \sum_{\beta \neq \alpha} \left( \sigma_j^\beta \right)^2 f^\beta N_\beta} \times (C4)$$

$$\times \left( 1 + \frac{(\sigma_j^\alpha)^2 (S^\alpha - f^\alpha N_\alpha) + \sum_{\beta \neq \alpha} \left( \sigma_j^\beta \right)^2 (S^\beta - f^\beta N_\beta)}{2 \left( f^\alpha (N_\alpha - 1) (\sigma_j^\alpha)^2 + \sum_{\beta \neq \alpha} \left( \sigma_j^\beta \right)^2 f^\beta N_\beta \right)} \right).$$

In the left hand side of eq. (C2), instead, each local field $h_i^\alpha$ is given by the sum of three different contributions, namely the external field, the recurrent input and the feed-back signal from the inhibitory unit:

$$\langle h_i^\alpha \rangle = \left( h_i^{\text{ext},\alpha} + \sum_{j \neq i} J_{ij}^\alpha s_j^\alpha + \sum_{\beta \neq \alpha} \sum_j J_{ij}^\beta s_j^\beta - H_0^\alpha + \nu^\alpha (S^\alpha - f^\alpha N_\alpha) - \sum_{\beta \neq \alpha} \nu^\beta (S^\beta - f^\beta N_\beta) \right). (C5)$$

We can compute the average by summing and subtracting $\sum_{\beta} J_{\beta} S^\beta$, obtaining:

$$\langle h_i^\alpha \rangle = h_i^{\text{ext},\alpha} + T_{\alpha} (S^\alpha - f^\alpha) - \sum_{\beta \neq \alpha} J_{\beta} S^\beta - H_0^\alpha - \nu^\alpha (S^\alpha - f^\alpha N_\alpha) + \sum_{\beta \neq \alpha} \nu^\beta (S^\beta - f^\beta N_\beta). (C6)$$

We therefore get an expression for the global inhibitory constant $H_0^\alpha$ and the parameters $\nu^\alpha_\alpha$ and $\nu^\alpha_\beta$ that satisfy eq. (C2):

$$H_0^\alpha = h_i^{\text{ext},\alpha} + (N_\alpha - 1) T_{\alpha} f^\alpha + \sum_{\beta \neq \alpha} N_\beta J_{\beta} f^\beta + H^{-1} (f^\alpha) \sqrt{f^\alpha (N_\alpha - 1) (\sigma_j^\alpha)^2 + \sum_{\beta \neq \alpha} \left( \sigma_j^\beta \right)^2 f^\beta N_\beta - T^\alpha} (C7)$$

$$\nu^\alpha_\alpha = T_{\alpha} + \frac{H^{-1} (f^\alpha) (\sigma_j^\alpha)^2}{2 \sqrt{f^\alpha (N_\alpha - 1) (\sigma_j^\alpha)^2 + \sum_{\beta \neq \alpha} \left( \sigma_j^\beta \right)^2 f^\beta N_\beta}} \quad (C8)$$

$$\nu^\alpha_\beta = T_{\alpha} + \frac{H^{-1} (f^\alpha) \left( \sigma_j^\beta \right)^2}{2 \sqrt{f^\alpha (N_\alpha - 1) (\sigma_j^\beta)^2 + \sum_{\beta \neq \alpha} \left( \sigma_j^\alpha \right)^2 f^\beta N_\beta}} \quad (C9)$$

Notice that a contribution to the global inhibitory constant $H_0^\alpha$ arises from the mean external field $h_i^{\text{ext},\alpha} = \lambda^{\text{ext}} f^\alpha$, so that neurons that do not receive an excitatory external stimulus are effectively depressed. Since the adaptation of the synaptic couplings according to the plasticity rule is considered to be adiabatic, the means and the standard deviations required for setting a correct inhibition are affected only over longer time scales and need not be updated instantaneously.

The scheme described here can be easily specialized to the simple cases of fully visible or visible-to-hidden restricted connectivity, which have been analyzed in detail in this work.

2. Soft “winner takes all” mechanism

This inhibitory scheme can be easily implemented in the synchronous dynamics considered in this work: before the new neuronal state gets extracted (eq. (1)), the local activities are first sorted with respect to their magnitude, then a global inhibitory input is added, whose value is set just below the activation of the $(f N)$-th highest excited
neuron. This procedure guarantees a fine-tuned control on the sparsity level \( f \) of the network. When the network is composed of a number \( G \) of different groups of neurons, each with a different sparsity level, the sorting operation is done inside each group. Some theoretical results show that neurons with adaptive threshold perform better than those with a constant threshold in presence of highly correlated stimuli [66]; we confirm these observations, since we have seen that this scheme is the best one in the one-shot learning task.

3. The adaptive thresholds regulatory scheme

The \( s_i \in \{0, 1\} \) case can be mapped exactly on the \( s_i \in \{-1, +1\} \) case, but this operation requires the thresholds to dynamically adapt to any change in the synaptic couplings.

In order to obtain the correct mapping one can consider the conditional probabilities of the two models, and look for a transformation of the neural variables and of the parameters which allows to move between the two scenarios. After inserting the simple change of variables \( s_i \rightarrow s'_i = \frac{s_i+1}{2} \) in the expression for the local activities in the \( s_i \in \{-1, +1\} \) model (note that in this section the \( s' \) notation is not used to denote the next step of the dynamics), we get the matching equation:

\[
h'_i = 2 \left( h_i^{\text{ext}} + \sum_j J_{ij} (2s'_i - 1) \right) = h_i^{\text{ext,t}} + \sum_j J'_{ij}s'_i - \theta'_i,
\]

which is satisfied by posing \( h_i^{\text{ext,t}} = 2h_i^{\text{ext}}, \; J'_{ij} = 4J_{ij} \) and \( \theta'_i = 2\sum_j J_{ij} = \frac{1}{2}\sum_j J'_{ij} \) in the case of \( s_i \in \{0,1\} \) neurons.

By looking at the case with \( f_v = 0.5 \) sparsity, this mapping suggests that it is possible to set the thresholds in correspondence of the average value of the incoming excitatory stimuli received by each neuron:

\[
\theta_i = \left\langle \sum_{j\neq i} J_{ij}s'_j \right\rangle_t = f_v \sum_{j\neq i} J_{ij}.
\]

This definition properly matches the one obtained from the exact mapping just in the case of \( f_v = 0.5 \). However, this choice was found to allow an extensive capacity in the on-line learning regime for the \( s_i \in \{0,1\} \) neuronal state variables even with different sparsity levels. Having set the thresholds in such a way, one gets a slightly different form for the local activations \( h_i = h_i^{\text{ext}} + \sum_{j\neq i} J_{ij} (s_j^t - f_v) \) and the learning rule eq. (B5) changes to:

\[
\Delta J_{ij} \propto \left( \langle s_i^{t+1}(s_j^t - f_v) \rangle_{t,\lambda_1} - \langle s_i^t(s_j^t - f_v) \rangle_{t,\lambda_2} \right).
\]

Appendix D: Simulation: Implementation details

We provide here detailed description of the learning algorithm in its heuristic version, described at the end of ’The Model’ section, with the update rule eq. (6). The learning protocol consists of an iterative optimization procedure where the parameters \( J \) and \( \theta \) are incrementally updated. Throughout this work we initialized the weights \( J \) uniformly at random; for the \( \pm 1 \) models, they were sampled from the interval \( \left[ -\frac{1}{\sqrt{N}}, \frac{1}{\sqrt{N}} \right] \), while for the 0/1 models they were sampled from the interval \( \left[ 0, \frac{1}{\sqrt{N}} \right] \). The thresholds \( \theta \) were set to 0 in the \( \pm 1 \) model, and initialized all to the same value in the 0/1 model (the precise value is essentially irrelevant because of the effect of the inhibitory network; we used 0.35 in our simulations).

Every pattern \( \xi^\mu \) is presented in the form of an external field \( h_i^{\text{ext}} = \lambda^{\text{ext}} \xi^\mu \), where the signal intensity is initialized at a fixed value \( \lambda_{\text{max}} \) and then progressively decreased to zero in steps of \( \Delta \lambda \). Before the learning process starts, we let the network evolve towards a state correlated with the pattern by waiting for a few iterations \( T_{\text{init}} \) of the dynamics while the external field set to its maximum. Then, the learning process starts in the “positive” phase, registering the correlations in a time window of \( T \) steps at an initial value of the external field \( \lambda \), and subsequently at a value lowered by \( \Delta \lambda \) in the “negative” phase. The parameters are updated with a fixed learning rate \( \eta \), as in eq. (6).

This procedure is repeated until the external field reaches zero. The length of the time windows \( T \) has to be chosen in such a way that the state reached at the end of each averaging procedure is still in nearly the same region.
around the pattern, otherwise another initialization phase would be needed. In our experiments, we found that a good performance is achieved when $T$ ranges from $3$ to $25$, provided the learning rate is lowered when the average is taken over very few iterations. This shows that a network implementing the DCM plasticity rule is able to learn even in the presence of an extremely low signal-to-noise ratio.

The relevant computation can be parallelized, since all the quantities involved (both in the dynamics and in the learning process) are local with respect to the synapses and the neurons. A simple pseudo-code implementation scheme for the learning protocol can be found in algorithm 1.

The learning rate is constant in time and was arbitrarily set to $\eta = 0.01$ in our simulations.

Algorithm 1: Pseudo-code implementation scheme for the DCM learning protocol (fig. 1). For simplicity, we report the scheme used for $\pm 1$ network models.

We introduced an operable measure of the basin size, relating it to the level of corruption of the memories before the retrieval: a set of $M = \alpha N$ patterns is considered to be successfully stored at a noise level $\chi$ if, initializing the dynamics in a state where a fraction $\chi$ of the pattern is randomly corrupted, the retrieval rate for each pattern is at least 90% (as estimated from 100 separate trials per pattern) after at most 1000 learning cycles (250 in the simulations with finite fields). A successful retrieval is measured when, in absence of external input, the network evolves towards a neuronal state with an overlap $\geq 0.99$ with the learned pattern in at most 50 steps of the dynamics.

2. Spurious attractors

In the numerical experiments for fig. 7, the storage load $\alpha$ was chosen to be sufficiently small, such that both the DCM rule and the Hebb rule are able to learn stable attractors. The presence of spurious attractors was detected as follows: the network state was initialized at random, and was then allowed to evolve freely for 200 time steps. After this initialization period, the magnetization was recorded for a few iterations and compared with the stored attractors. If the modulus of the overlap with any one of them was $> 0.95$, the state was considered to have reached a known attractor. Otherwise, the magnetization was recorded for some more iterations, in order to check if a stable state was reached, and if this condition occurred the magnetization was clipped to $\pm 1$ and a new spurious attractor was counted. In the following random restart, this attractor was inserted in the list of known attractors. Of course, this procedure only provides an estimate of the number of distinct spurious attractors introduced by the learning rule, but sufficient to highlight a large, qualitative difference in the behavior of DCM compared to the Hebb rule.

The first peak in fig. 7, in the Hebb’s curve plot, is due to finite size effects: the number of spurious states is expected to grow at least exponentially in a sub-extensive regime $M \ll N$. In the extensive regime, mixtures of odd number of memories can still be observed, but as the storage load $\alpha$ is increased the mixture states composed of
larger number of patterns are expected to disappear, and the growth in the number of spurious attractors is no longer exponential [67].

3. One-shot tests and palimpsest regime

In the one-shot simulations every pattern is seen by the network only once, and its memory will eventually be overwritten by the new ones. The goal is to reach a steady state regime in which, at each new presentation, the last $M$ learned memories maintain the required stability. This storage load is called the palimpsest capacity.

In order to reach the maximal capacity, the parameters have to be fine tuned so that the learning process for each memory is slow and the most recently learned ones are minimally perturbed: one has to ensure that in the freely-evolving dynamics, i.e. the last time window during the external field pulse, the neuronal state does not escape the basin of attraction of the new memory and enters a previously learned one, causing the loss of existing memories. In the simulations presented in fig. 8 we addressed this problem rather drastically by simply removing this last window, which only resulted in a slight improvement in the palimpsest capacity.

We also set $\eta = 0.01$, $\lambda_{max} = 4$, $\Delta \lambda = 1$ and the length of the time windows was chosen to be slightly faster then in the other tests, $T = 10$. In this setting the number of presentations of the same pattern, i.e. the number of external field pulses, required for reaching its desired stability is around $\sim 1000$. This number would grow in time, because of the increase in the average connectivity of the network as new memories are added, a problem that can be overcome with the introduction of a synaptic weight $L2$-regularization.

In the case of $s_i \in \{0, 1\}$ neurons, we surprisingly lose the property of an extensive palimpsest capacity. The problem seems to be related to the need for a substantial shift in the threshold, that would allow a wide basin of attraction for a new pattern, as expressed by eq. (6). This modification seems to strongly affect the network dynamics also when it hovers around a different, previously learned memory, introducing a disruptive effect in the palimpsest regime. In the normal learning task, instead, the thresholds are eventually set to a level which is compatible with all the patterns, since the learning protocol can cycle through the pattern set many times. The only way we found to obtain a good performance in the one-shot learning task for $s_i \in \{0, 1\}$ neurons with our model is to introduce an adaptive threshold regulatory scheme, stemming from a direct mapping to the $s_i \in \{-1, +1\}$ case.

4. Generation of correlated patterns

In the case of $s_i \in \{-1, +1\}$ neurons, we only introduced correlations in the form of a bias in the generation of the patterns, see section ‘Types of neurons’ above. Note that, in the biased case $b \neq 1/2$, it is known that the naive Hebb rule $J_{ij} = \frac{1}{N} \sum_{\mu, \nu} \xi_{i,\mu} s_{j,\nu}$ has to be generalized to $J_{ij} = \frac{1}{N} \sum_{\mu} (\xi_{i,\mu} - 2b + 1) (\xi_{j,\nu} - 2b + 1)$.

In the $s_i \in \{0, 1\}$ case, instead, we also generated correlated patterns as combinations of sparse features $\phi^\nu$, with $P (\phi^\nu) = f \delta (\phi^\nu - 1) + (1 - f) \delta (\phi^\nu)$, chosen from a finite length dictionary $D = \{\phi^\nu\}_{\nu=1}^L$. Every pattern contains a fixed number of features, $F$, and its components can be written as: $\xi_{i,\mu} = \Theta (\sum_{\nu} c_{i,\nu}^\nu \phi^\nu)$, with $c_{i,\nu}^\nu \in \{0, 1\}$ determining whether the feature $\nu$ appears in pattern $\mu$, and $\Theta (\cdot)$ is the Heaviside theta function, $\Theta (x) = 1$ if $x > 0$ and $\Theta (x) = 0$ otherwise.

Appendix E: TAP approximation in asymmetric sparse models

In the heuristic version of DCM, the time-delayed correlations of a network subject to varying external field intensities are needed in order to update the model parameters. In our approach, we employed a Monte Carlo scheme – which relies solely on the network dynamics – for their evaluation, as a means to fulfill some basic biological constraints. A better approximation though can be achieved with the so-called TAP approach, consisting in a second order expansion around a mean field limit, which can provide an estimation for the marginal probabilities of the neuronal state variables. The related magnetizations can then be used to compute approximate values for the pairwise correlations.

In what follows, we will apply the same procedure proposed in ref. [26] for the $s_i \in \{-1, +1\}$ case and the sequential Glauber dynamics, to the $s_i \in \{0, 1\}$ and the synchronized dynamics case. Since we are dealing with an asymmetric model, where the form of the joint probability distribution $P (s | \theta, J)$ is unknown, we have to assume a weakly interacting regime, with small $O \left(1/\sqrt{N}\right)$ couplings $J$, and in addition to be close to a mean field model with
a factorized distribution:

\[ P_{\text{MF}}^\theta (s|\theta) = \prod_{a=1}^{N} \frac{\exp(\theta_a s_a)}{1 + \exp(\theta_a)}. \]  

We introduce the parametrization \( \theta_{\text{MF}} = \theta_a - d\theta_a \) where \( d\theta_a \) is small and \( \theta_{\text{MF}} \) are the parameters of the mean field model, which can be found by minimizing the KL divergence:

\[ KL[P||P_{\text{MF}}] = \sum_s P(s|\theta,J) \log \left( \frac{P(s|\theta,J)}{P_{\text{MF}}^\theta (s|\theta)} \right). \]  

The TAP approximation is obtained by performing a Taylor expansion of the magnetizations \( m_a = \sum_s P(s_a) s_a \) in the small parameters \( J_{jk} \) and \( d\theta_i \) and applying the matching condition \( m_a - m_a^{\text{MF}} = 0 \) for all \( a \in \{1,\ldots,N\} \) up to second order:

\[ 0 = m_a - m_a^{\text{MF}} \approx \sum_i \frac{\partial m_a}{\partial \theta_i} |_{\text{MF}} d\theta_i + \sum_{i,j} \frac{\partial^2 m_a}{\partial J_{ij} \partial \theta_i} |_{\text{MF}} dJ_{ij} + \sum_{i,j} \frac{\partial^2 m_a}{\partial J_{ij} \partial \theta_j} |_{\text{MF}} dJ_{ij} + \sum_{i,j,k} \frac{\partial^2 m_a}{\partial J_{ij} \partial \theta_k} |_{\text{MF}} dJ_{ij} d\theta_k + 2 \sum_{i,j,k} \frac{\partial^2 m_a}{\partial J_{ij} \partial \theta_k} |_{\text{MF}} dJ_{ij} d\theta_k \]

After some calculations, the following derivatives, evaluated in correspondence of the mean field probability distribution, are obtained:

\[ \frac{\partial m_a}{\partial \theta_i} |_{\text{MF}} = m_a (1 - m_a) \delta_{ai} \]  

\[ \frac{\partial m_a}{\partial J_{ij}} |_{\text{MF}} = m_j m_a (1 - m_a) \delta_{ai} \]  

\[ \frac{\partial^2 m_a}{\partial \theta_i \partial \theta_j} |_{\text{MF}} = \left( m_a (1 - m_a)^2 - (m_a)^2 (1 - m_a) \right) \delta_{ai} \delta_{aj} \]  

\[ \frac{\partial^2 m_a}{\partial J_{ij} \partial \theta_k} |_{\text{MF}} = m_j m_a (1 - m_j) (1 - m_a) \delta_{ai} \delta_{jk} + \]  

\[ + m_j \left[ m_a (1 - m_a)^2 - (m_a)^2 (1 - m_a) \right] \delta_{ai} \delta_{ak} \]  

\[ \frac{\partial^2 m_a}{\partial J_{ij} \partial J_{kl}} |_{\text{MF}} = m_j m_l (1 - m_l) m_a (1 - m_a) \delta_{il} \delta_{ak} + \]  

\[ + m_l m_j (1 - m_j) m_a (1 - m_a) \delta_{ik} \delta_{ai} + \]  

\[ + (s_j s_i)_{\text{MF}} \left( m_a (1 - m_a)^2 - (m_a)^2 (1 - m_a) \right) \delta_{ai} \delta_{ak}. \]

Using the identity \( \langle s_j s_i \rangle_{\text{MF}} = \delta_{ji} m_j + (1 - \delta_{ji}) m_j m_l \) and neglecting higher orders up to \( O(d\Theta^2) \), the moment matching condition reads:

\[ \theta_a^{\text{MF}} = \theta_a + \sum_j m_j J_{aj} + \frac{1}{2} (1 - 2m_a) \sum_j (m_j (1 - m_j) J_{aj}^2. \]  

This leads to the TAP equations for the single neuron marginal probabilities when the sigmoid activation function is applied. The fixed point of these equations can be found by recursion, with a crucial caveat, namely that during the
iterative procedure the time indices of the magnetization appearing in the Onsager reaction term have to be chosen carefully, according to:

\[ m_i^{t+1} = \text{sigm} \left( \theta_i + \sum_j m_j^t J_{ij} - \left( m_i^{t-1} - \frac{1}{2} \right) \sum_j \left( m_j^t (1 - m_j^t) \right) J_{ij}^t \right) \]  

(E10)

where \( \text{sigm}(x) = (1 + e^{-x})^{-1} \) is the sigmoid function. Note that in the model presented in the main text the constant field \( \theta_i \) is further decomposed into the effect of an external field and of a negative threshold \( \theta_i \to \lambda^{\text{ext}} (\xi_i - \frac{1}{2}) - \tilde{\theta}_i \).

Once the magnetizations are estimated, one can calculate the time-delayed correlations in the same TAP approximation. The dependence of these correlations on the magnetizations can be derived starting from:

\[ \langle s_i s_j \rangle = \sum_s P(s) \sum_{s_i'} P(s_i' \mid s) \langle s_i' \rangle \]  

(E11)

After expanding the sum over \( s_i' \), one simply obtains: \( \langle s_i' s_j \rangle = \langle \text{sigm}(h_i) s_j \rangle \). In order to simplify some of the following derivations, we first consider the Taylor expansion of the connected time-delayed correlations:

\[ \chi_{ij}^D = \langle s_i' s_j \rangle - m_i m_j = \langle s_i \rangle \langle \text{sigm}(h_j) - m_j \rangle \]  

(E12)

In order to find an expression up to second order in \( d\Theta \), we need the following derivatives:

\[
\begin{align*}
\frac{\partial \chi_{ba}^D}{\partial \theta_i} &\bigg|_{\text{MF}} = 0 \\
\frac{\partial \chi_{ba}^D}{\partial J_{ij}} &\bigg|_{\text{MF}} = m_b m_a (1 - m_b) (1 - m_j) \delta_{aj} \delta_{bi} \\
\frac{\partial^2 \chi_{ba}^D}{\partial \theta_i \partial \theta_j} &\bigg|_{\text{MF}} = 0 \\
\frac{\partial^2 \chi_{ba}^D}{\partial J_{ij} \partial \theta_k} &\bigg|_{\text{MF}} = m_a m_b (1 - m_a) (1 - m_b) (1 - 2m_b) \delta_{aj} \delta_{bk} \delta_{bi} \\
\frac{\partial^2 \chi_{ba}^D}{\partial J_{ij} \partial J_{kl}} &\bigg|_{\text{MF}} = m_a m_b (1 - m_b) (1 - 2m_b) \delta_{bk} \delta_{bi} \times (\delta_{aj} \delta_{al} + (1 - \delta_{aj}) \delta_{al} m_j (1 - m_a)).
\end{align*}
\]

(E13) (E14) (E15) (E16) (E17)

Using the following relation:

\[ \langle s_a s_j s_i \rangle_{\text{MF}} = \delta_{aj} (\delta_{al} m_a + (1 - \delta_{al}) m_a m_i) + (1 - \delta_{aj}) (\delta_{al} m_a m_j + (1 - \delta_{al}) m_a \langle s_j s_i \rangle_{\text{MF}}), \]  

(E19)

we obtain the expression for the Taylor expansion up to second order:

\[ \chi_{ij}^D = (m_i (1 - m_i)) (m_j (1 - m_j)) \left( J_{ij} + \frac{1}{2} (2m_i - 1) (2m_j - 1) (J_{ij})^2 \right) \]  

(E20)

and therefore the final expression for the time-delayed correlations reads:

\[ \langle s_i' s_j \rangle = (m_i (1 - m_i)) (m_j (1 - m_j)) \times \left( J_{ij} + \frac{1}{2} (2m_i - 1) (2m_j - 1) (J_{ij})^2 \right) + m_i m_j \]  

(E21)
Appendix F: Visible-to-hidden directed synapses

In the case of an architecture restricted to visible-to-hidden directed connections, the network can be seen as a bipartite graph. At any given time the state of a neuron in one of the two subsets is conditionally dependent only on the state of the complementary subset of neurons at the previous time:

\[ P(s'_i, i \in V | s) = P(s'_i, i \in V | s_H) \]  \hspace{1cm} (F1)

\[ P(s'_i, i \in H | s) = P(s'_i, i \in H | s_V). \]  \hspace{1cm} (F2)

Because of this property the joint conditional probability \( P(s_H | s_V) \) can be factorized, and the clamped probability distribution can be written explicitly:

\[ P_{\text{clamp}}(s; \xi) = \prod_{i \in V} \delta_{s_i, \xi_i} \prod_{j \in H} P(s_j | s_V = \xi). \]  \hspace{1cm} (F3)

The learning rule can be derived from the minimization of the KL divergence between the conditional probabilities obtained when the external field intensity is \( \lambda^{\text{ext}} = \infty \) and \( \lambda^{\text{ext}} = 0 \), averaged over the clamped probability distribution. By differentiating the KL with respect to a hidden to visible synaptic coupling \( J_{ij} \) with \( i \in V, j \in H \), we get the following update rule:

\[ \Delta J_{ij} \propto P(s_j | s_V = \xi) \xi_i s_j - \sum_{s \in H, k \in H} P(s_k | s_V = \xi) P(s'_l | s_H) s'_l s_j. \]  \hspace{1cm} (F4)

As in the case of fully visible networks, the same increment would be obtained if an on-line optimization of the pseudo-likelihood of the model was instead implemented, except that now its estimation implies an average over all the possible hidden neuronal states:

\[ \mathcal{L}(\{\xi^\mu\} | J_{ij}, \theta; \beta) = \frac{1}{M} \sum_{\mu=1}^{M} \sum_{i \in V} \log \left( \sum_{s_j \in H, k \in H} P(s_k | s_V = \xi) P(s'_l | s_H; \lambda^{\text{ext}} = 0) \right). \]  \hspace{1cm} (F5)

1. MNIST Simulations

Instead of trying to construct an artificial stimulus ensemble, we use the MNIST database benchmark [53], which consists of \( 7 \cdot 10^4 \times 28 \times 28 \) grayscale images representing hand-written digits in 10 classes from 0 to 9. Images are sparse, with an average luminosity of \( \mathbb{F}_s = 0.13066 \) and every component ranging in the interval \( \xi^\mu_i \in [0, 1] \). It is rather natural to consider each pattern as an array of probabilities of finding the corresponding neurons in the active state: we therefore consider a stochastic network of \( s_i \in \{0, 1\} \) neurons, whose visible component will be successively subject to an external field corresponding to each one of the images, as before multiplied by a field intensity \( \lambda^{\text{ext}} \). We hold out the last \( 10^4 \) images as a test set for the generalization performance, and employ the first \( 6 \cdot 10^4 \) images to learn the statistics of the data.

We consider an architecture with \( |V| = 784 + 10 \) visible neurons, plus \( |H| = 1000 \) hidden neurons to guarantee a high representational capacity. The additional 10 visible neurons, one for each digit, can allow the network to learn input-output correlations: these neurons received a supervised input indicating the correct label of the image during the learning phase [68], and were present in all the simulations described in the following; however, they are exploited only for the classification task, being unessential for the usual generative tasks.

In order to point out how the DCM is able to deal with all the biological constraints we are considering in this work, we offer the direct comparison between two different learning models. In the first numerical experiment, which serves as a benchmark reference, the network was trained in the infinite signal limit (\( \lambda_{\text{max}} \sim 50 \) is sufficient) corresponding to the pseudo-likelihood method, with unconstrained synapses, no inhibitory mechanism and using the time-delayed correlations obtained in the TAP approximation. In the second numerical experiment, meant to test the DCM rule...
In a more biologically plausible, we studied a purely excitatory network and implemented the soft “winner-takes-all” inhibitory scheme, fixing an average hidden activity of $f_h = 0.2$. The network was required to learn from finite external fields ($\lambda_{\text{max}} = 3$, $\Delta \lambda = 3/2$ and $\lambda_{\text{min}} = 0$) and to estimate the correlations simply through its own dynamics (specifically, we considered $T = 15$), as described in sec. 1. In both experiments the networks cycled 2 times through the $6 \cdot 10^4$ training images of the MNIST dataset.

In the second experiment setting, a very high level of noise can become extremely detrimental: with large hidden layers the network is often prone to falling into a completely symmetric state, with very poor performance. One would instead want to exploit the initial randomness in the synaptic couplings as a tool for breaking this otherwise problematic symmetry between the hidden neurons. This can be either achieved by choosing a lower temperature $\beta = 30$ (we choose this setting, to be compared with $\beta = 2$ in the first experiment) or by rescaling the initial random configuration of the synaptic couplings.

**Receptive fields**

A first comparison of the learning performance in the two cases is attained by visualizing the receptive fields of the hidden neurons, which can show how each different hidden unit specializes in the detection of a unique feature of the pattern set learned by the neural network. The receptive fields of the hidden neurons are represented by the synapses $J_{ij}$ with a fixed $i \in \mathcal{H}$ and $j$ running through the visible indices $\mathcal{V}$. These arrays can be reorganized as a $28 \times 28$ grayscale images as well, after renormalizing each component in the interval $[0,1]$: the obtained image represents, for any hidden unit, its optimal stimulus. A sample is shown in fig. A1.

It is apparent that most of the hidden units develop interesting internal representations which can be interpreted as simple detectors for edges of parts of single digits. Both experiments also show the presence of a small fraction of extremely noisy features (that usually become irrelevant since the threshold of the corresponding neuron raises in order to inhibit its activation during the dynamics).
Figure A2. Generation of samples. The two series of plots show the probability of obtaining an active state for the visible neurons after 100 time-steps of the dynamics, starting from 8 different initial states. 

a. Samples generated in the first experiment, where the TAP approximation was employed in the clamped limit with no inhibition.

b. Samples generated in the second experiments, where the correlation where registered during the time evolution of the network, and where finite time dependent fields, constrained synapses and the “winner-takes-all” inhibition scheme where considered. The superior smoothness of the samples from the first experiment is also due to the choice of a higher temperature in the dynamics ($\beta_1 = 2$ against $\beta_2 = 30$, see Methods).

Generative tasks

A better way of assessing the quality of the internal representation of the learned dataset in the two experiments is to test the generative properties of the networks. As shown in fig. A2, we obtained some visible configurations from the steady-state distribution of the models, generated according to the information learned from the training images. The steady-state distribution is reached by the dynamical evolution of the network when starting from a visible neuronal state induced by one of the learned images. In order to initialize the network, visible neurons are clamped with a very strong field ($\lambda^\text{ext} = 50$) in the direction the image and of the correct label for an initial period of 30 time steps. The field on the first 784 neurons is then removed, while the visible neurons receiving the supervised stimulus are maintained clamped, and the network is left evolving for some iterations. Keeping the output labels clamped only mildly encourages the network to produce new samples from the same category, and this small signal does not have a major effect.

Alternatively the networks can be asked to generate the correct label of a test image, presented to the network with a clamping signal. In the first experiment, the output of the network was read directly from the magnetizations obtained at convergence of the TAP equations iterative procedure, by simply picking the maximum magnetization between the ones corresponding to the visible neurons associated to the label of each category. This network was able to reach a generalization error rate of 2.76%. This result is far from state-of-the-art classification performance (around 0.3% [53]), but is remarkably low if one takes into account the highly noisy environment and the small size of the network. In the second experiment, the magnetizations were instead explicitly registered during the dynamical evolution of the network. In this case, the performance declined to a 7.74% generalization error rate. This result is nevertheless of interest, considering that the entire learning process was done without a clear supervised signal and that the system was subject to a number of biological requirements restraining the computational performance of the network.