Effective And Optimal Storage of Memory Patterns With Variable Coding Levels

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Abstract

This paper studies the storage of memory patterns with varying coding levels (fraction of firing neurons within a pattern) in an associative memory network. It was previously shown that effective memory storage (that scales with the network's size) requires that the synaptic modification rule used during learning explicitly depends on the coding level of the stored memory patterns. We show that the memory capacity of networks storing variably coded memory patterns is inherently bounded and does not scale with the network's size. These results question the biological feasibility of associative memory learning that uses synaptic level information only. However, we show that applying a neuronal weight correction mechanism that uses local neuronal level information, provides effective memory capacity even when the coding levels vary considerably. Using neuronal weight correction yields near optimal memory performance even with non-optimal synaptic learning rules. These findings provide further support to the idea that neuronal level normalization processes play an important role in governing synaptic plasticity and may be crucial for learning in the nervous system.

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1 Introduction

During the last decade various associative memory models have shown that neural networks are capable of storing memories via Hebbian synaptic changes. However, a major caveat of all Hebbian synaptic learning rules is their explicit dependency on the coding level of the stored memory patterns (the fraction of firing neuron in the pattern). This information about the patterns' coding level is a global, network-level, property, and is unlikely to be available at the synaptic level. For example, the optimal learning rule for hetero-associative memory networks [Dayan and Willshaw, 1991], the covariance learning rule (first proposed by [Sejnowski, 1977]), depends on the coding level of both the input and output patterns. We have recently shown [Chechik *et al.*, 1999a] that this coding level dependency is a more general property of Hebbian synaptic learning rules. Namely, any Hebbian learning rule must explicitly depend on the coding level of the stored memory patterns, otherwise the network memory capacity is drastically reduced to one that does not scale with the network's size. We have then shown that effective memory storage that scales with the network's size is obtained even for synaptic learning rules that do not utilize explicit coding level information if appropriate neuronal level remodeling of synaptic efficacies is employed.

Our previous work [Chechik *et al.*, 1999a] has focused on the special case where all memory patterns stored in the network have the same coding level. When dealing with a noisy biological system, the coding level dependency naturally raises the question of storing memory patterns with a variety of coding levels. Could the brain effectively store such memory patterns within the same network? Could effective memory storage be obtained using local information only? Could this be accomplished via a single learning rule that does not critically depend on the patterns' coding levels?

In the current article we answer these questions by analyzing the memory performance of a network that stores memory patterns with varying coding levels. We show that the coding level variability leads to three problems that limit the memory storage capacity of the network: non-zero synaptic mean, non-zero postsynaptic covariance, and non-optimal neuronal threshold. These problems reduce the network memory capacity from an *effective* capacity that scales linearly with the network's size to a bounded memory capacity that does not scale with the size of the network. We then show that a simple normalization process at the neuronal level results in a vanishing synaptic mean and postsynaptic covariance, and that the addition of global inhibition may replace the optimal threshold. These mechanisms qualitatively improve the network memory capacity: instead of the bounded memory capacity obtained when using Hebbian learning rules only, they provide linear memory capacity even when storing patterns whose coding levels are highly variable.

Neuronal normalization mechanisms have already been shown to play an important role in the process of self-organization of neural networks and in preventing the problem of synaptic runaway in unsupervised learning [Miller and MacKay, 1994, Oja, 1982]. The current article shows that it is a specific form of neuronal level normalization that is required to enable effective memory storage of variably coded noisy patterns via associative memory learning.

The next section describes the model and section 3 analyses the problems encountered when storing memory patterns with varying coding levels. Section 4 describes a neuronal weight correction mechanism that addresses these problems, and presents analytical and simulations results. Assuming the operation of this neuronal correction mechanism, section 5 derives optimal learning rules as a function of the coding levels' distribution. Our results are then discussed in section 6.

2 The Model

We analyze a model of auto-associative memory network with binary firing $\{0,1\}$ neurons. M uncorrelated memory patterns are stored in an N-neuron network, forming attractors of the network's dynamics. Memory pattern ξ^μ $(1 \leq \mu \leq M)$ has *coding level* p_μ (that is, there are $\mathbf{1}^T\xi^\mu = p_\mu N$ firing neurons out of the N neurons). The updating rule for the state X_i^t of neuron i at time t is

$$X_i^{t+1} = \theta(f_i) \ , \quad f_i = \frac{1}{N}\sum_{j=1}^{N} W_{ij}X_j^t - T \quad , \tag{1}$$

where f_i is the neuron's input field, T is the neuronal threshold, and $\theta(f) = \frac{1+sign(f)}{2}$. The synaptic weight W_{ij} between the jth (presynaptic) neuron and the ith (postsynaptic) neuron is determined by a synaptic learning rule that depends on the neurons' activity in each of the M stored memory patterns

$$W_{ij} = \sum_{\mu=1}^{M} (\xi_i^\mu - a)(\xi_j^\mu - a) \quad . \tag{2}$$

where a is a parameter of the learning rule. In the case of a *homogeneous coding level*, that is when all memories share exactly the same coding level, a is optimally set to their coding level and the model reduces to the model analyzed by [Tsodyks and Feigel'man, 1988]. This learning rule was proved to be optimal for the homogeneous coding case by [Dayan and Willshaw, 1991]. The overlap m^μ (or similarity) between the current network's activity pattern X and the memory ξ^μ serves as a measure of memory performance (retrieval acuity) and is defined in terms of the coding level p_μ as

$$m^\mu = \frac{1}{p_\mu(1-p_\mu)N} \sum_{j=1}^{N} (\xi_j^\mu - p_\mu) X_j \quad , \tag{3}$$

3 Analysis

To analyze the network's memory performance we derive the signal-to-noise ratio of the neuronal input field, a the primary determinant of retrieval capacity [Meilijson and Ruppin, 1996]. Restricting attention, without loss of generality, to the retrieval of memory pattern ξ^1, the network is initialized in a state X generated independently of the other memory patterns. This state is assumed to have activity level p_1 (thus equal to the coding level of ξ^1), and overlap $m_0^1 = \frac{(1-p_1-\epsilon)}{(1-p_1)}$ with ξ^1, where $\epsilon = P(X_i = 0|\xi_i^1 = 1) = (\frac{1-p_1}{p_1})P(X_i = 1|\xi_i^1 = 0)$. Denoting $W_{ij}^* = W_{ij} - (\xi_i^1 - a)(\xi_j^1 - a)$, the conditional mean of the neuronal input field is

$$\begin{aligned} E\left[f_i|\xi_i^1\right] &= E\left[\frac{1}{N}\sum_{j=1}^{N} W_{ij}X_j|\xi_i^1\right] - T = \qquad (4) \\ &= E\left[\frac{1}{N}\sum_{j=1}^{N}(\xi_i^1 - a)(\xi_j^1 - a)X_j|\xi_i^1\right] + E(W_{ij}^*)E(X_j|\xi_i^1) - T = \\ &= (\xi_i^1 - a)(1-a)P(X_j = 1|\xi_j^1 = 1)P(\xi_j^1 = 1) + \end{aligned}$$

$$+(\xi_i^1 - a)(0-a)P(X_j = 1|\xi_j^1 = 0)P(\xi_j^1 = 0) + p_1 \sum_{\mu=2}^{M} (p_\mu - a)^2 - T =$$

$$= \quad (\xi_i^1 - a)(1-a-\epsilon)p_1 + p_1 \sum_{\mu=2}^{M} (p_\mu - a)^2 - T \quad ,$$

and its variance is

$$\begin{aligned} V\left[f_i\right] &= V\left[\frac{1}{N}\sum_{j=1}^{N} W_{ij}X_j\right] \approx V\left[\frac{1}{N}\sum_{j=1}^{N} W^*_{ij}X_j\right] = \\ &= \frac{1}{N}V\left[W^*_{ij}X_j\right] + COV\left[W^*_{ij}X_j, W^*_{ik}X_k\right] = \\ &= \frac{1}{N}p_1\, V\left[W^*_{ij}\right] + p_1^2\, COV\left[W^*_{ij}, W^*_{ik}\right] \quad . \end{aligned} \tag{5}$$

The signal-to-noise ratio of the neuron's input field is thus

$$\frac{Signal}{Noise} = \frac{E(f_i|\xi_i^1 = 1) - E(f_i|\xi_i^1 = 0)}{\sqrt{V(f_i)}} \approx \frac{(1-a-\epsilon)p_1}{\sqrt{\frac{1}{N}p_1 V\left[W_{ij}\right] + p_1^2 COV\left[W_{ij}, W_{ik}\right]}}. \tag{6}$$

Therefore, for large enough networks the noise term in the neuronal input field is dominated by the postsynaptic covariance $COV\left[W_{ij}, W_{ik}\right]$ between the efficacies of the incoming synapses. To obtain the signal-to-noise ratio as a function of the distribution of the coding levels $\{p_\mu\}_{\mu=1}^{M}$, we calculate the relevant moments of the synaptic weights' distribution

$$E(W_{ij}) = \sum_{\mu=1}^{M} E\left[W^\mu_{ij}\right] = \sum_{\mu=1}^{M} (p_\mu - a)^2 \quad , \tag{7}$$

$$\begin{aligned} V(W_{ij}) &= \sum_{\mu=1}^{M} V\left[W^\mu_{ij}\right] = \sum_{\mu=1}^{M} E\left[(W^\mu_{ij})^2\right] - E^2\left(W^\mu_{ij}\right) = \\ &= \sum_{\mu=1}^{M} p_\mu(1-p_\mu)\left[p_\mu(1-p_\mu) + 2(p_\mu - a)^2\right] \quad , \end{aligned} \tag{8}$$

and

$$\begin{aligned} COV \quad & \left[W_{ij}, W_{ik}\right] = \\ \approx & \sum_{\mu=1}^{M} E\left[(\xi_i^\mu - a)^2(\xi_j^\mu - a)(\xi_k^\mu - a)\right] - \sum_{\mu=1}^{M} E^2\left[(\xi_i^\mu - a)(\xi_j^\mu - a)\right] = \\ = & \sum_{\mu=1}^{M} p_\mu(1-p_\mu)(p_\mu - a)^2 \quad . \end{aligned} \tag{9}$$

Substituting Eqs. (7)-(9) in the signal-to-noise ratio (Eq. 6) one obtains

$$\frac{Signal}{Noise} \approx \sqrt{\frac{N}{M}} \frac{(1-a-\epsilon)\sqrt{p_1}}{\sqrt{\frac{1}{M}\sum_{\mu=1}^{M} p_\mu^2(1-p_\mu)^2 + (2+Np_1)\frac{1}{M}\sum_{\mu=1}^{M} p_\mu(1-p_\mu)(p_\mu - a)^2}}. \tag{10}$$

This signal-to-noise calculation yields an important conclusion: When all the p_μ are equal and equal to a, the last term of the denominator vanishes and the signal-to-noise ratio remains constant as M grows linearly with N. In this case *effective learning* is obtained, i.e., the network's memory capacity grows linearly with the network's size. However, if some of the p_μ's differ from each other, then for every a the noise term grows linearly with N, resulting in a bounded memory capacity that does not scale with the size of the network. Thus, **unless all memory patterns share the same coding level and the learning rule is properly adjusted to this coding level, the memory capacity of the network is inevitably bounded**. In this case the network's memory capacity mainly depends on the coding level a used in the learning rule, and on the variance of the actual coding levels $\{p_\mu\}_{\mu=1}^{M}$ of the stored memory patterns.

The above signal-to-noise analysis assumes that the neuronal threshold is optimally set to maximize memory retrieval. Such optimal setting requires that the threshold be set to

$$\begin{aligned} T^{Optimal}(\xi^1) &= \frac{E(f_i|\xi_i^1=1)+E(f_i|\xi_i^1=0)}{2} \\ &= (\frac{1}{2}-a)(1-a-\epsilon)p_1 + p_1\sum_{\mu=1}^{M}(p_\mu-a)^2 \end{aligned} \tag{11}$$

during the retrieval of the memory pattern ξ^1 [Chechik *et al.*, 1998]. The optimal threshold thus depends both on the coding level of the retrieved pattern p_1 and on the variability of the coding levels p_μ. These parameters are global properties of the network that may be unavailable at the neuronal level, making optimal setting of the threshold biologically implausible.

To summarize, the signal-to-noise analysis reveals three problems that prevent effective memory storage of patterns with varying coding levels using a single synaptic learning rule. First, the mean synaptic efficacy is no longer zero, and depends on the coding level variability (Eq. 7). Second, the correlation between incoming synaptic efficacies is non-zero (Eq. 9); this correlation results in a positive postsynaptic covariance $COV(W_{ij}, W_{ik})$, that bounds the memory capacity of the network. Third, the optimal neuronal threshold explicitly depends on the coding level of the stored memory patterns (Eq. 11). It is important to note that these problems are inherent to all Hebbian additive synaptic learning rules, since these must explicitly depend on the coding level of the stored memory patterns to obtain effective memory storage [Chechik *et al.*, 1999b].

To demonstrate the effects of these problems on the network's memory performance we have stored memory patterns with coding levels that are normally distributed around a, in a network that uses the optimal learning rule for coding level a (Eq. 2). The neuronal threshold was also set to its optimal value for the mean coding level a (Eq. 11). The memory capacity of such networks as a function of the network size is depicted in Figure 1, for various values of coding level variability. Clearly, even small perturbations from the mean coding level a result in considerable deterioration of memory capacity. Moreover, this deterioration becomes more pronounced for larger networks, revealing a bounded network memory capacity.

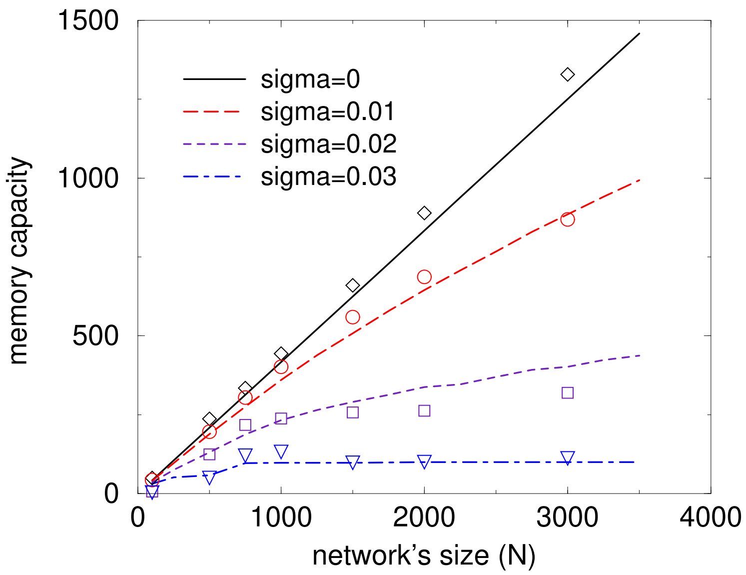

Figure 1: Memory capacity as a function of network's size for various coding level distributions. Memory capacity is measured as the number of memory patterns that can be stored in the network and then retrieved almost correctly (with an average overlap greater than $m = 0.95$) when the network is presented with a degraded pattern ($\epsilon = 0.18$ that results in an average initial overlap of $m_0 = 0.8$). Coding levels are normally distributed $p_\mu \sim N(a, \sigma^2)$ with mean of $a = 0.1$ and standard deviations of $\sigma = 0, 0.01, 0.02, 0.03$.

4 Effective Memory Storage

The above results show that current Hebbian learning alone cannot provide effective memory storage (where the memory capacity grows linearly with network's size) unless all patterns share exactly the same coding level. How then can noisy biological networks store memories effectively? We now turn to describe a mechanism that compensates for coding level variability and provides successful memory storage of such patterns.

4.1 Neuronal Weight Correction

We analyze a neuronal level process that is basically similar to the normalization process first proposed by [von der Malsburg, 1973] to operate during cortical self-organization. In this process, as a synapse is modified during learning, its postsynaptic neuron additively modifies all its synapses to maintain the sum of their efficacies at a baseline zero level. As this **neuronal weight correction** is additive it can be performed either "online" after each memory pattern is stored or "offline" at a later time after several memories have been stored.

We have previously shown that the joint operation of neuronal weight correction over a linear Hebbian learning rule is equivalent to the use of another Hebbian learning rule that has both zero synaptic mean and zero post-synaptic covariance (see [Chechik *et al.*, 1999a] for details). In the case of variable coding levels discussed here, the application of neuronal weight correction combined with the learning rule of (Eq. 2) results in the same synaptic matrix as when storing memory patterns via the learning rule

$$W_{ij} = \sum_{\mu=1}^{M} (\xi_i^\mu - a)(\xi_j^\mu - p_\mu) \quad . \tag{12}$$

To see this, consider the synaptic efficacy changes that follow the storage of one memory pattern with coding level p_μ (using Eq. 2), and focus on a synapse Wij between two firing neurons ($\xi_i = 1, \xi_j = 1$): Following learning with Eq. 2, the synaptic strength is first increased by $(1-a)(1-a)$. Then, when other synapses of the same postsynaptic neuron are strengthened, the synapse W_{ij} weakens by $\frac{1}{N}(1-a)(1-a)$, and when other synapses weaken, the synapse W_{ij} is strengthened by $\frac{1}{N}a(1-a)$. As there are $p_\mu N$ such strengthening events and $(1-p_\mu)N$ weakening events, the total change in synaptic strength is $(1-a)(1-p_\mu)$. A similar calculation for synapses between quiescent and firing neurons completes the learning rule of Eq. (12).

This formalization of neuronal weight correction operating on one learning rule as equivalent to storage with another learning rule, enables us to calculate the memory performance of networks that undergo neuronal weight correction using a conventional signal-to-noise analysis as in Eqs. (7)-(9). These calculations yield synaptic mean

$$E(W_{ij}) = 0 \quad , \tag{13}$$

variance

$$V(W_{ij}) = \sum_{\mu=1}^{M} p_\mu^2 (1-p_\mu)^2 + \sum_{\mu=1}^{M} (p_\mu - a)^2 p_\mu (1-p_\mu) \quad , \tag{14}$$

and postsynaptic covariance

$$COV\left[W_{ij}, W_{ik}\right] = 0 \quad , \tag{15}$$

resulting in a signal-to-noise ratio

$$\frac{Signal}{Noise} = \sqrt{\frac{N}{M}} \frac{(1-a-\epsilon)\sqrt{p_1}}{\sqrt{\frac{1}{M}\sum_{\mu=1}^{M} p_\mu^2 (1-p_\mu)^2 + \frac{1}{M}\sum_{\mu=1}^{M} p_\mu (1-p_\mu)(a-p_\mu)^2}} \quad . \tag{16}$$

A comparison of Eq. (16) with Eq. (10) readily shows that the dependence of the noise term on the networks' size (evident in Eq. 10) is now eliminated. Thus, a neuronal mechanism that maintains a fixed sum of incoming synapses effectively calibrates to zero the synaptic mean and postsynaptic covariance, providing a memory storage capacity that grows linearly with the size of the network. This is achieved without the need to explicitly monitor the actual coding level of the stored memory patterns.

4.2 Global Inhibition Networks

The neuronal weight correction mechanism solves two of the three problems of storing memory patterns with variable coding level, setting to zero the synaptic mean and postsynaptic covariance. But even after neuronal weight correction is applied the optimal threshold is

$$T^{Optimal}(\xi^1) = (\frac{1}{2} - p_1)(1 - a - \epsilon)p_1 \quad , \tag{17}$$

retaining a dependence on the coding level of the retrieved pattern. We suggest that this difficulty may be partially circumvented by replacing the neuronal threshold with a global inhibitory term. To this end, Eq. (1) is substituted with

$$X_i^{t+1} = \theta(f_i) \ , \quad f_i = \frac{1}{N}\sum_{j=1}^{N}(W_{ij} - I)X_j^t = \frac{1}{N}\sum_{j=1}^{N} W_{ij}X_j^t - \frac{I}{N}\sum_{j=1}^{N} X_j^t \quad , \tag{18}$$

where I is the global inhibition term set to $I = (\frac{1}{2} - a)(1 - a - \epsilon)$. Since $E[X_j] = p_\mu$, the mean neuronal field in a network that uses global inhibition of this form is corresponds to a network that uses a neuronal threshold with $T = (\frac{1}{2} - a)(1 - a - \epsilon)p_1$. In the case of small p_1 this yields a fair approximation to the field of a neuron that uses the optimal threshold (Eq. 17).

To demonstrate the beneficial effect of neuronal weight correction and activity-dependent inhibition, we turn again to store memory patterns whose coding levels are normally distributed as in Figure 1 using the learning rule of Eq. (2). Figure 2 compares the memory capacity of networks with and without neuronal weight correction and activity-dependent inhibition. The memory capacity is also compared to the case were all memories share exactly the same coding level (dot-dashed line), showing that the application of neuronal weight correction and activity-dependent inhibition (long dashed line) successfully compensates for the coding level variability, obtaining almost the same capacity as the capacity achieved with a homogeneous coding level.

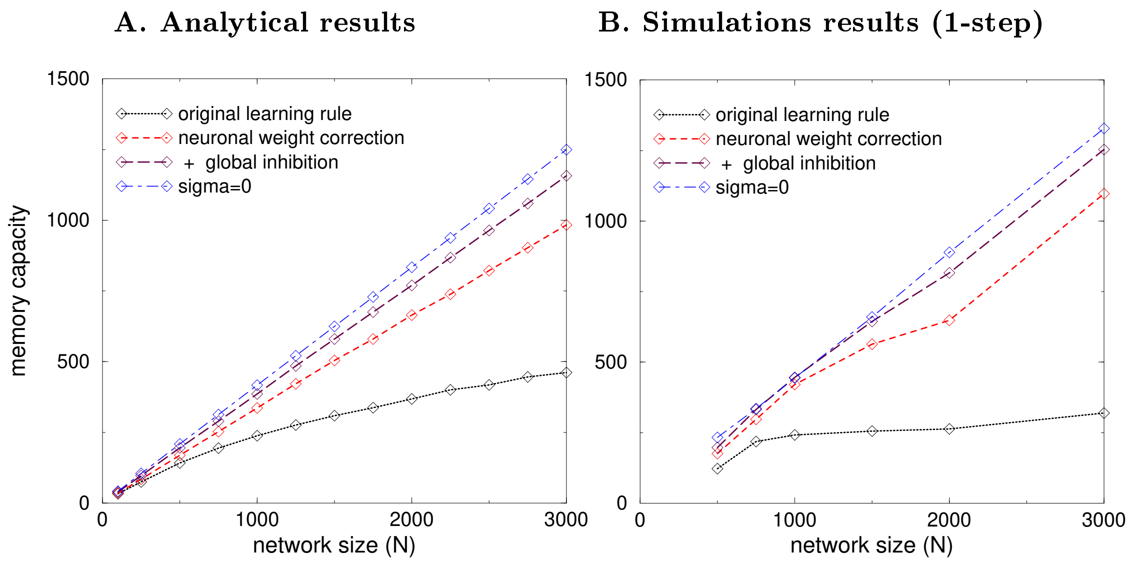

Figure 2: Memory capacity as a function of the network's size when storing patterns with normally distributed coding levels $p_\mu \sim N(0.1, 0.02)$ using the original learning rule of Eq. (1). The four curves correspond to the following cases: no correction at all (solid line), neuronal weight correction (dashed line), neuronal weight correction with activity dependent inhibition (long dashed line), and homogeneous coding - all patterns share exactly the same coding level (dot dashed line). **A**. Analytical results, **B**. Simulations results of a network performing one step of the dynamics.

Figure 3 plots the network's memory capacity as a function of the coding level variability. While the original learning rule provides effective memory storage only when coding levels are close to the mean, the application of neuronal correction mechanism provides effective memory storage even when storing an ensemble of patterns with high variability of coding levels. The addition of activity-dependent inhibition is mainly needed when the coding level variability is very high.

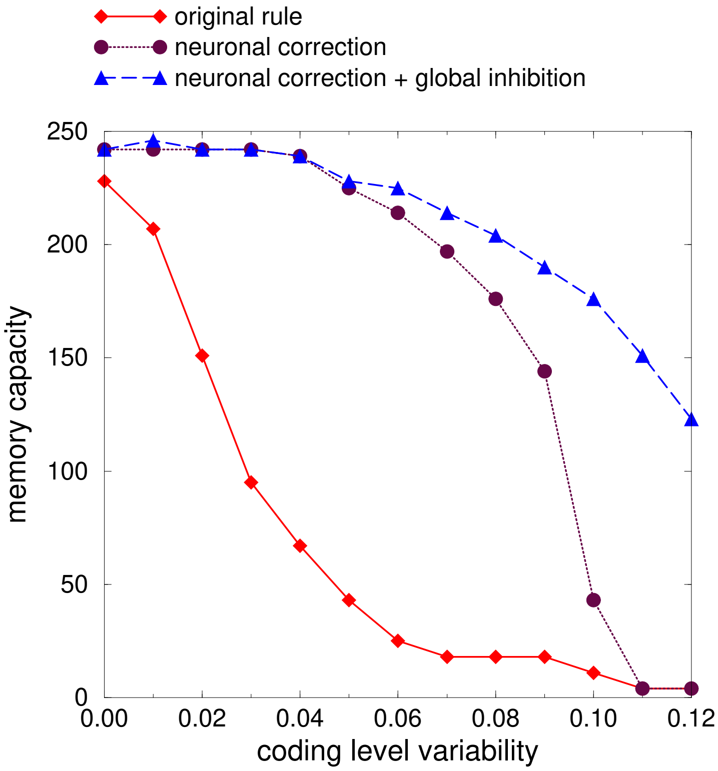

Figure 3: Memory capacity as a function of coding level variability of the stored memory patterns. Memory storage was obtained using the original learning rule of Eq (1) with $a = 0.1$, but actually storing patterns with normally distributed coding levels $p_\mu \sim N(0.1, \sigma^2)$, for several values of the standard deviation σ. Simulation parameters: $N = 1000$, $\epsilon = 0.18$ yielding m_0=0.8 on average.

Memory patterns that differ by their coding level also differ by their retrieval acuity. Figure 4 plots the retrieval acuity of memory patterns stored in the same network as a function of their coding level, showing that lower coding levels results in lower retrieval acuity. This phenomenon results from the dependency of the signal-to-noise term on the coding level of the retrieved pattern (Eq. 16): Patterns with lower coding levels have a lower signal-to-noise ratio, resulting in a lower retrieval acuity.

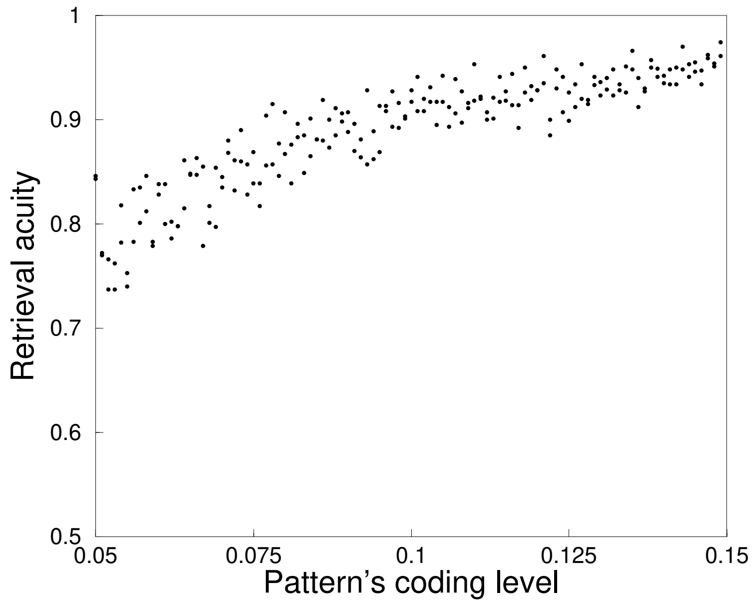

Figure 4: Retrieval acuity of patterns as a function of their coding level. 600 patterns are stored in a 1000-neurons network using the learning rule of Eq. (1) with $a = 0.1$, followed by the application of neuronal weight correction. The coding levels of the pattern are uniformly distributed with $p_\mu \sim U(0.05, 0.15)$.

5 Optimal Memory Storage

The above results show that neuronal weight correction must be applied when the coding level is heterogeneous. We now turn to study the effects of the underlying synaptic rule on the network memory performance when neuronal weight correction is applied. To obtain a yardstick for comparing various learning rules, we derive the rule that (together with neuronal weight correction) maximizes the network memory performance.

Following the arguments used to derive Eq. (12), the family of learning rules resulting from the application of neuronal weight correction can all be written in the form

$$W_{ij} = \sum_{\mu=1}^{M} (\xi_i^\mu - \Delta)(\xi_j^\mu - p_\mu) \quad , \tag{19}$$

where the parameters Δ determines the learning rule (for example, in the case of Eq. (12) we have $\Delta = a$). Note that a single parameter is needed to describe all effective learning rules as these rules are defined by four parameters that satisfy three constraints: The synaptic mean and postsynaptic covariance are zero, and the learning rules can be arbitrarily scaled if the neuronal threshold is properly set [Chechik *et al.*, 1999a]. Following an analysis similar to Eqs. (4)-(10) the signal-to-noise ratio of this learning rule is

$$\frac{Signal}{Noise} \approx \sqrt{\frac{N}{M}} \quad (1-p_1-\epsilon)\sqrt{p_1} \quad \frac{1}{\sqrt{\frac{1}{M}\sum_{\mu=1}^{M} p_\mu(1-p_\mu)(\Delta-p_\mu)^2}}. \tag{20}$$

The signal-to-noise ratio is separated to a product of three terms: one that depends on the memory load only, another that depends on the coding level p_1 of the retrieved pattern and a third one that depends on the learning rule parameter Δ and the coding level distribution. To optimize with regard to Δ, rewrite the denominator of this last term in the form

$$\begin{aligned}(Noise)^2 \quad \propto \quad & \sum_{\mu=1}^{M} p_\mu(1-p_\mu)\left[\Delta - \frac{\sum_{\mu=1}^{M} p_\mu^2(1-p_\mu)}{\sum_{\mu=1}^{M} p_\mu(1-p_\mu)}\right]^2 + \\ & + \sum_{\mu=1}^{M} p_\mu^3(1-p_\mu) - \frac{(\sum_{\mu=1}^{M} p_\mu^2(1-p_\mu))^2}{\sum_{\mu=1}^{M} p_\mu(1-p_\mu)} \quad ,\end{aligned} \tag{21}$$

to see that the optimal Δ (that minimizes the noise term) is determined by the first three moments of the coding level distribution

$$\Delta^{Optimal} = \frac{\sum_{\mu=1}^{M} p_\mu^2(1-p_\mu)}{\sum_{\mu=1}^{M} p_\mu(1-p_\mu)} \quad . \tag{22}$$

This optimal Δ value can also be written as $\Delta^{Optimal} = \sum_{\mu=1}^{M} p_\mu[\frac{p_\mu(1-p_\mu)}{\sum_{\mu=1}^{M} p_\mu(1-p_\mu)}]$ showing that the parameter Δ is an average of p_μ with regard to the distribution function $q_\mu = \frac{p_\mu(1-p_\mu)}{\sum_{\mu=1}^{M} p_\mu(1-p_\mu)}$. In the case of homogeneous coding level, $q_\mu = \frac{1}{M}$ and we obtain $\Delta^{Optimal} = \frac{1}{M}\sum_{\mu=1}^{M} p_\mu$, corresponding to the covariance learning rule (Eq. 2), known to be optimal for this case [Dayan and Willshaw, 1991]. However, for any heterogeneous distributions with $p_\mu < 0.5$, $\Delta^{Optimal} > \frac{1}{M}\sum_{\mu=1}^{M} p_\mu$, and the underlying learning rule is inherently different from the covariance rule.

The above analysis pertains to learning rules that result from the combined action of the underlying synaptic learning rule and neuronal weight correction. For each Δ there is a three dimensional family of learning rules that are transformed by neuronal weight correction into the optimal learning rule (Eq. 19, 22). These rules should only satisfy the following constraint (if the neuronal threshold is properly set):

$$\frac{\Delta(\xi_i=1,\xi_j=1)-\Delta(\xi_i=1,\xi_j=0)}{\Delta(\xi_i=0,\xi_j=1)-\Delta(\xi_i=0,\xi_j=0)} = \frac{(1-\Delta^{Optimal})}{(-\Delta^{Optimal})} \tag{23}$$

where $\Delta(\xi_i, \xi_j)$ is the additive change to the synaptic efficacy following some combination of pre (ξ_j) and post (ξ_i) synaptic activities. It should be stressed that while optimal learning requires the above constraint, all additive learning rules are transformed into effective rules via the application of neuronal weight correction [Chechik *et al.*, 1999a].

To quantify the effect of the underlying learning rule, we have compared the network memory performance of networks as a function of the learning rule parameter Δ, for various coding levels distributions. These simulations show that the superiority of the optimal learning rule over other effective rules is small, improving memory capacity by few percents only. In particular, the covariance learning rule, that uses only the first moment of the coding levels distribution approximates well the optimal learning rule (that uses the first three moments). **These results thus show that neuronal weight correction achieves almost-optimal memory performance even with non optimal synaptic learning rules**.

6 Discussion

We have analyzed associative memory networks that store memory patterns with variable coding levels. Our analysis shows that three problems limit the memory storage capacity of such networks: non-zero mean synaptic value, non-zero postsynaptic covariance and inadequate neuronal threshold. We then presented a neuronal weight correction mechanism that zeroes the postsynaptic covariance and synaptic mean. This weight correction mechanism provides an effective memory capacity that scales linearly with the network's size, while only a bounded number of memory patterns can be stored without such mechanism. When neuronal weight correction is applied the underlying synaptic learning rule itself has only a slight effect on memory performance. In particular, a learning rule that uses only mean coding level information, successfully approximates the optimal learning rule and provides almost optimal memory capacity.

These results suggest that the storage of patterns with variable coding levels in biological memory networks cannot be restricted to the use of synaptic level information only but must also use neuronal-level information. Indeed, there is increasing evidence that neuronal level normalization processes shape the synaptic efficacies in an activity dependent manner (e.g. [Turrigano *et al.*, 1998]). [van Ooyen, 1994, Miller, 1996] provide a review of mechanisms that perform normalization of synaptic efficacies in a manner that conserves the total synaptic weight of the postsynaptic neuron. In a previous paper [Chechik *et al.*, 1999a] we have computationally studied one of these mechanisms, *Neuronal Regulation* [Horn *et al.*, 1998b, Horn *et al.*, 1998a] and showed that this mechanism zeroes the postsynaptic covariance. The results of the current article, showing that the postsynaptic covariance is the term that limits the memory capacity in face of coding level variability, suggest that neuronal regulation is essential in the more general case of effective storage of patterns with coding level variability.

The need to store memory patterns with highly variable coding levels arises when considering possible realizations of human memory systems. It has been suggested that human memory is organized in a hierarchy of memory modules, where lower-level modules represent simple features and concepts and higher level modules bind them into more complex entities (e.g. [Damasio, 1989, Moll *et al.*, 1994]). Within this framework, neurons in a binding module should respond to patterns that are the combination of several features. However, as the number of features combined into a concept may vary considerably, the binding neurons must be able to correctly respond to memory patterns with high variation in their coding level. Our results, described within the framework of an auto-associative memory, pertain also to this hetero-associative memory task. Neuronal weight correction may hence be a universal mechanism that is necessary to provide effective hierarchical memory storage, involving both auto and hetero associative memory networks.

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