

Excitable Networks: Nonequilibrium Criticality and Optimum Topology*

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Abstract

Excitable media may be modeled as simple extensions of the Amari–Hopfield network with dynamic attractors. Some nodes chosen at random remain temporarily quiet, and some of the edges are switched off to adjust the network connectivity, while the weights of the other edges vary with activity. We conclude on the optimum wiring topology and describe nonequilibrium phases and criticality at the edge of irregular behaviour.

Keywords: Dynamical memories, silent neurons, criticality, optimum network topology

1 Introduction and Model Details

Understanding the fundamentals of how high-level brain functions result from the cooperation between many neurons and synapses dates back to McCulloch and Pitts [McCulloch & Pitts, 1943] who implemented pioneering ideas of the 1906 Nobel laureate Ramón y Cajal. Oversimplified mathematical models such as the Amari–Hopfield or neural network [Amari, 1972, Hopfield, 1982, Amit, 1989] typically consisting of binary variables, which represent the neurons, connected by edges, which represent the synapses, are relevant with this aim. Assuming inhomogeneous time-independent connection strengths as in the Hebb prescription [Hebb, 1949], which in a sense stores information from a set of given

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patterns of activity, these become attractors of dynamics, i.e., there is retrieval of stored patterns, known as “associative memory”.

Experiments suggest that this picture lacks essential features, however. One problem is that connections between neurons do not seem to be constant but undergo fast time changes—variously described as fluctuations on the time scale of milliseconds, *short-term* plasticity and synaptic *fatigue*, for instance. These changes during operation are expected to influence processing of information, and thus memory storage and retrieval, and simple modelling has in fact shown that they may induce dynamic instabilities and even chaos [Abbott *et al.*, 1997, Malenka & Nicoll, 1999, Pantic *et al.*, 2002, Marro *et al.*, 2008]. This is interesting because the activity of neural systems in nature does not permanently stay in a memory. Instead, irregular wandering among the stored patterns seems to occur during brain activity, e.g., olfactory processes in insects have been associated with heteroclinic paths of activity in the patterns space [Mazor & Laurent, 2005, Torres *et al.*, 2008]. In summary, the present situation is consistent with synaptic fluctuations, on one hand, and with dynamic instabilities leading to irregular behaviour [Sompolinsky *et al.*, 1988, Korn & Faure, 2003, Torres *et al.*, 2008], which is probably caused by these fluctuations, on the other, and none of these features is contained in the standard neural network.

Recent theoretical work [Marro *et al.*, 2008, 2007, Johnson *et al.*, 2008], whose review, discussion and extension is the purpose of this paper, suggests that simple extensions of the *standard model*—namely, the Amari–Hopfield network with a Hebbian learning rule [Amit, 1989]—inspired along lines recently indicated by neurobiology should help our understanding of many other complex situations as well. That is, some of the main features in an ideal brain might be common to a number of excitable systems, including different parts of the nervous system, forest fires, autocatalytic reactions in surfaces and food webs, for instance [Lindner *et al.*, 2004, Arenas *et al.*, 2008, Allesina *et al.*, 2008]. The most relevant fact to be noticed is that *excitability* causes a nonequilibrium condition in any setting of many interacting elements, and this is what, for example, impedes damping by friction of signals in certain media. It then follows that a class of systems should be viewed concerning cooperation as large networks of *effective* “excitable” nodes—in the sense that each acts in practice as having a threshold and a time lag between consecutive responses—connected by edges of varying strength. Suitable generalizations of the standard model should therefore describe the essential physics in a number of apparently diverse man-made and natural systems.

As a further step with such a motivation, we report here on how the dynamics depends on connectivity in a model of excitable media. In particular, we conclude on a relevant correlation between wiring topology and network functionality and, more specifically, on the optimal wiring to which a complex excitable network could evolve to meet certain productivity criteria or to improve performance. We also describe the nature of both the irregular wandering of the activity among the stored patterns and the system critical behaviour at the onset of this irregular behaviour in the resulting nonequilibrium steady states.

The model of interest generalizes the standard setting along three main lines:

(i) *Time dependent connections.* Let a set of nodes $\vec{\sigma} = \{\sigma_i = \pm 1\}$ and the *local field* at i , or net current from other nodes, $h_i = \sum_{j \neq i} w_{ij} x_j \sigma_j$ ($i, j = 1, \dots, N$). Here, $w_{ij} = N^{-1} \sum_{\nu} \xi_i^{\nu} \xi_j^{\nu}$ ($\nu = 1, \dots, P$) is the Hebbian weight, which involves given patterns of activity $\{\xi_i^{\nu}\}$ (with $\xi_i^{\nu} = \pm 1$) and x_i is a stochastic (*fatigue*, say) variable for the effect of short term plasticity. Assuming this varies in a time scale infinitely smaller than the one for the nodes, we shall consider a stationary distribution, namely, either [Johnson *et al.*, 2008]

$$P(x_j|\vec{\sigma}) = q\delta[x_j - \Xi_j(\vec{\sigma})] + (1 - q)\delta(x_j - 1), \quad (1)$$

(where $\delta(x)$ is the Dirac delta function) which amounts to assume that, at each time step, every connection has a probability q of altering its weight by a factor $\Xi_j(\vec{\sigma})$ which is a function of the field at j , or else [Marro *et al.*, 2008]

$$P(x_j|\vec{\sigma}) = \zeta_j(\vec{\sigma})\delta(x_j - \Phi) + [1 - \zeta_j(\vec{\sigma})]\delta(x_j - 1). \quad (2)$$

The *noise parameter* Φ describes resistance or *depression*, e.g., due to heavy local work when $0 < \Phi < 1$, while the edge facilitates, i.e., tends to increase the effect of the signal under the same situation for $\Phi > 1$, and the action of the edge is reversed for negative Φ .

The consideration of fast time-dependent variations of the connections as in the examples (1) and (2) generalizes the standard model in a non-trivial way. The result may be useful to describe the flow of food in trophic webs, the exchange of assets or information in social and communication networks, the number of transits and passengers in transport networks, and the constant variation of effective ionic interactions in spin glasses and other condensed systems due to reactions, diffusion and local rearrangements of ions and impurities [Torres *et al.*, 1998, Marro *et al.*, 2008], for instance.

(ii) *Wiring topology.* Let the topology matrix, $\epsilon = \{\epsilon_{ij} = 1, 0\}$, where the two values indicate the existence or not of an edge between nodes i, j , and define the *effective field* [Marro & Dickman, 1999] $h_i^{\text{eff}} = \sum_j w_{ij}^{\text{eff}} \sigma_j \epsilon_{ij}$ where, assuming (1), one may write that $w_{ij}^{\text{eff}} = [1 + (\Phi - 1)\tilde{\zeta}_j]w_{ij}$. Here, $\tilde{\zeta}_j$ denotes a function of the vector (to be interpreted as a local overlap) of components $m_j^{\nu} = \langle k \rangle^{-1} \sum_l \xi_l^{\nu} \sigma_l \epsilon_{jl}$ with $\langle k \rangle$ the mean node connectivity, i.e., the average of $k_i = \sum_j \epsilon_{ij}$. For the sake of concreteness, given that one may write that $h_j = \sum_{\nu} h_j^{\nu}$ with $h_j^{\nu} \equiv N^{-1} \langle k \rangle \xi_j^{\nu} m_j^{\nu}$, we are assuming for $q \neq 0$ that $\Xi_j = 1 + \tilde{\zeta}_j(\Phi - 1)/q$, with $\tilde{\zeta}_j = (N/\langle k \rangle)^{\alpha} / (1 + M/N) \sum_{\nu} |h_j^{\nu}|^{\alpha}$, $\alpha > 0$ [Johnson *et al.*, 2008]. This generalization of the model allows for the consideration of *forbidden links* [Allesina *et al.*, 2008] and, more generally, complex wiring topologies determined by the matrix ϵ and characterized by k_i . Two examples of these are the bimodal case

$$p(k) = \frac{1}{2}\delta(k - k_1) + \frac{1}{2}\delta(k - k_2), \quad (3)$$

and the “scale-free” case

$$p(k) \sim k^{-\gamma} \quad (4)$$

with $k \in [k_0, k_m]$ for finite N which is known to be particularly relevant in different natural contexts [Torres *et al.*, 2004, Eguíluz *et al.*, 2005, Boccaletti *et al.*, 2006].

(iii) *Quiet nodes.* At each time step, only the state of a fraction ρ of randomly chosen nodes will be updated, to describe from *parallel* ($\rho \rightarrow 1$) to *sequential* ($\rho \rightarrow 0$) updating. This is consistent with the expectation that certain nodes may be more active than others and some may even not be engaged at a given time in a given cooperative task —there is no need for a network to maintain *all* the nodes fully informed of the activity of *all* the others at *all* times. In fact, it has been observed that the network activity does not distribute uniformly in practice [Shoham *et al.*, 2006, Ergorov *et al.*, 2000, Azouz & Gray, 2000]. The observed fast-variations of the connections strength with time discussed in (i) could also be related with the existence of quiet nodes, which are also a concern in computer science [Korniss *et al.*, 2003], for instance. The existence of reticent nodes should probably be considered a main feature of excitable media in which elements, after responding to perturbation, are refractory to further excitation.

2 Some Results

The different model realizations which follow from the above setting may be handled analytically in a few cases, particularly, for $M = 1$ and fully-connected networks. More general behavior may be obtained by mean-field and other approximations, and also by performing direct simulation of the models in the computer using the Monte Carlo method. A systematic study of the resulting phenomenology, which is very varied and intriguing, is on the way. We summarize next, graphically a few main results.

For a given level Φ of synaptic fatigue, varying $\rho \in [0, 1]$ we observe different regimes, including cases in which the system activity moves, even irregularly or apparently chaotically, between the Hebbian attractors. This is illustrated in figure 1. A detailed scaling analysis of both the activity and h_i reveals some critical features. We illustrate this in figure 2 which shows relevant power spectra as dynamics is changed by varying ρ from a regular case with the familiar memory retrieval to a *chaotic phase* in which the system jumps irregularly between different memory states. That is, the spectra is —except for expected large frequency peaks— roughly constant around $\rho = 0.35$, which is near the edge of chaos but still in the memory phase, while it shows power-law behavior and other signatures of criticality within the chaotic window, namely, for $\rho > 0.35$ in this case.

For a better quantification of the varied emergent behaviour in the model, we have investigated further the space of relevant parameters (ρ, Φ). That is, for a given “temperature” $T \geq 0$, and number of patterns M , we monitored the standard order parameters which characterize *non-dynamical* phases, namely, the steady-state overlaps $\langle m^\nu(t) \rangle_t = \int_{t_0}^{t_0+\Delta t} m^\nu(t) dt$ and the spin-glass order parameter $Q = \langle \langle \sigma_i(t) \rangle_t^2 \rangle = \frac{1}{N} \sum_{i=1}^N \left(\frac{1}{\Delta t} \int_{t_0}^{t_0+\Delta t} \sigma_i(t) dt \right)^2$. The latter is plot-

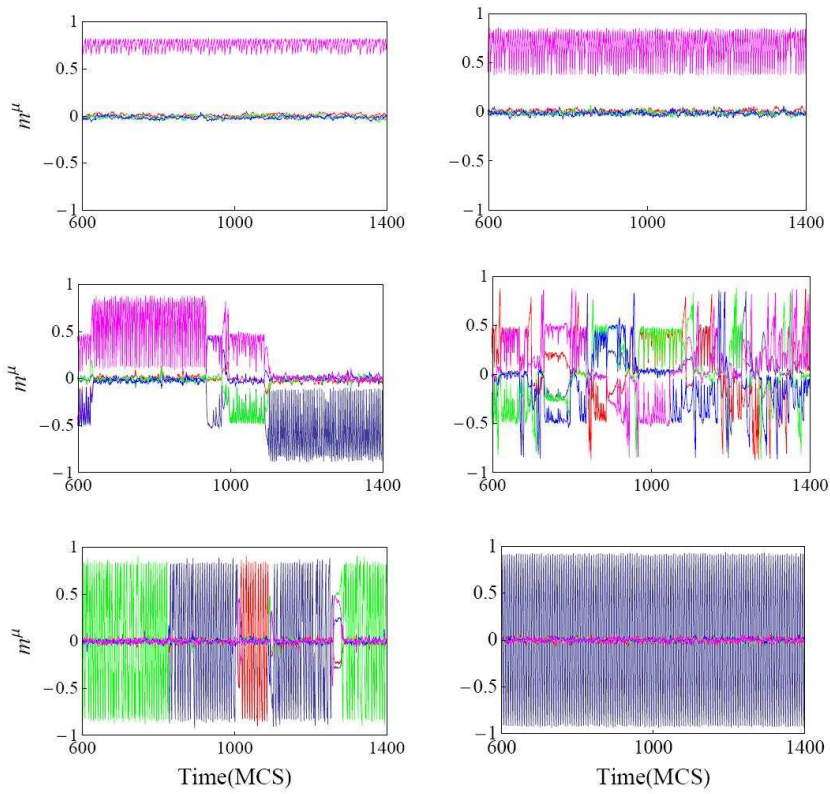


Figure 1: Time evolution of overlaps between the current activity and each of the stored patterns (different colours) for (top to bottom) $\rho = 0.1$ (left) and 0.35 (right) showing memory retrieval, $\rho = 0.4$ and 0.45 with two types of irregular jumping between patterns, and $\rho = 0.55$ (irregular) and 0.65 (regular) pattern-antipattern oscillations. This is for (1) with $\Phi = -0.5$, $N = 1600$ and $M = 5$ at low “temperature” (a measure of the level of stochasticity of the time evolution).

ted in figure 3A for a case which allows for an easy identification of the different relevant regimes. The fact is that non-dynamical phases, such as those associated with memory and spin-glass states have $Q \neq 0$, whereas all *dynamical phases*, defined as those in which neural activity is continuously wandering in a regular or chaotic way the different stored patterns, have $Q \approx 0$. Among the latter, as shown in figure 1, one can distinguish a phase where neural activity jumps chaotically between the basins of attraction of stored patterns (say Irregular Switching among Patterns or ISP phase), a phase with activity switching irregularly among different pattern-antipattern oscillations (Irregular Switching among Pattern Antipattern Oscillation or ISPAO phase), and a phase with the activity jumping periodically between pattern and antipattern states (Periodic

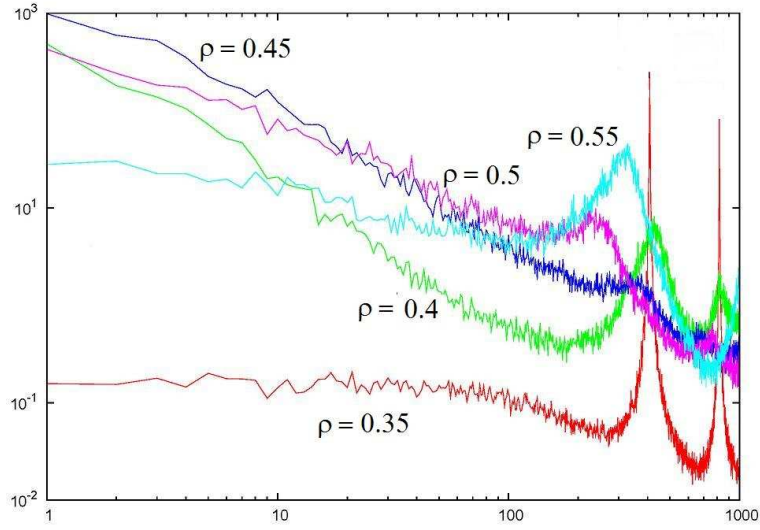


Figure 2: The power spectra of the local field $h_i(t)$ for different values of ρ , as indicated, as follows from Monte Carlo simulations.

Hopping or PH phase). The phase diagram, namely, the distribution of the different phases in the (ρ, Φ) space for $T = 0$ is schematized in figure 3B.

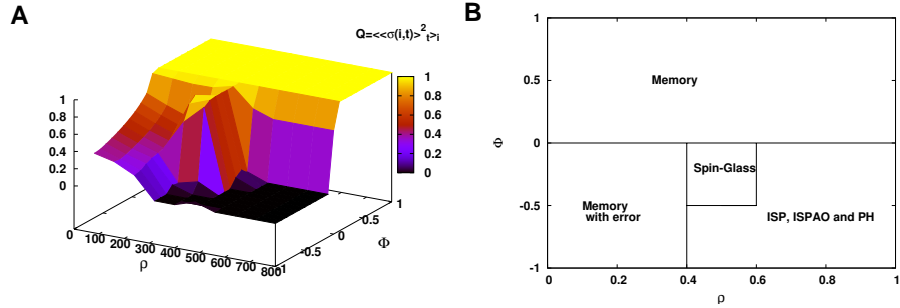


Figure 3: Panel A: Behaviour of the spin-glass order parameter Q as defined in the text, as a function of Φ and ρ for a network of $N = 800$ neurons, $M = 5$ stored patterns, and $T = 0$. Panel B: Schematized *phase diagram* with the observed memory and spin-glass phases and all the other dynamical regimes. The latter, namely, ISP, ISPAO and PH phases (as defined in the text) which have $Q = 0$, are localized in the region with $\Phi < 0$ and $\rho \in (0.3, 0.5)$.

Figure 4, on the other hand, illustrates the influence of the wiring topology on the resulting behavior our model. This shows that the scale-free topology

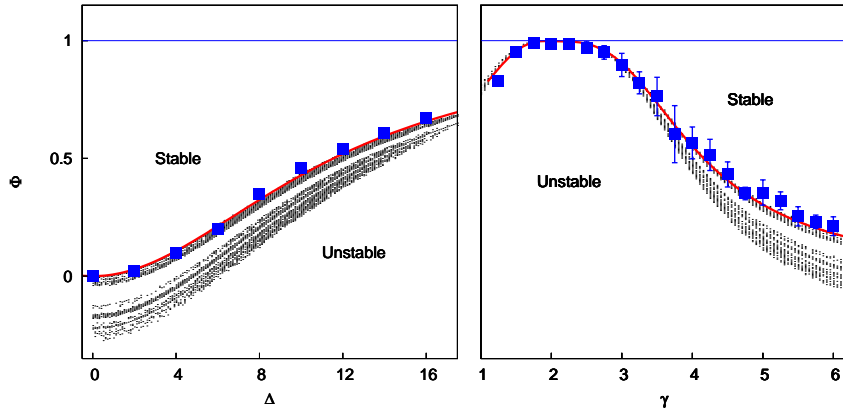


Figure 4: The critical fatigue Φ_c at which the phase changes from retrieval to jumping (red lines), in the case of a model with (1), is compared here when the connectivity is given by (3), left, with $\Delta = \frac{1}{2}(k_2 - k_1)$, and (4), right. Blue symbols corresponds to the critical line computed by MC simulations of the network with $N = 1600$ and mean connectivity $\langle k \rangle = 20$, and black dots correspond to values of the relevant parameters at which the Lyapunov exponent defining the collective dynamics of the network becomes positive. Other model parameters are $\rho = 1$, and $\alpha = 2$.

with $\gamma \simeq 2$ needs very little fatigue, namely, $\Phi \lesssim 1$, to achieve irregular behavior, which is the most efficient regime. For a practical illustration of the computational advantages of this result, we monitored the performance of a network during the pattern recognition process. In practice, we “showed” the system a pattern, say ν chosen at random from a set of M random patterns previously stored¹, every certain number of time steps. This was performed by changing the field at each node for one time step, namely, $h_i \rightarrow h_i + \zeta \xi^\nu$ where ζ is the amplitude of the stimulus. Ideally, the network should immediately acquire the configuration of the presented pattern ν and remain there until it is newly stimulated with a different pattern. The performance may thus be estimated from a temporal average of the overlap between the current state and the input pattern, $\langle m^\nu(t) \rangle_t$. With this criterion, we found that performance is best when the system is in the memory phase but close to the “edge of chaos” (though never exactly at this point, presumably because chaos is achieved through bifurcations). This is assumed to be due here to the fact that the condensed pattern is easily destabilised by the stimulus, while the system is able to remain in the new pattern after detecting it.

Figure 5 shows typical time series obtained during this task for a particular realization of a bimodal network with $\Delta = 10$ and different values of the fatigue

¹Pattern ν was also required to be different from whichever pattern was condensed — i.e., displayed the highest overlap — at the time of stimulation.

parameter Φ . Each of the three panels corresponds from top to bottom to $\Phi = 1$ for which the system is in a stable spin-glass state and there are no synaptic fluctuations, $\Phi = 0.5$, at which the system is in the memory phase but close to the edge of chaos, where the network is shown to respond optimally to the external signal, and $\Phi = 0$, at which the system is in the chaotic phase where it is sensitive to stimuli but not capable of retaining the network activity in a particular pattern. These results are in qualitative agreement with other models in which the “edge of chaos” is seen to optimize magnitudes such as computational capacity [Bertschinger & Natschläger, 2004] and dynamic range of sensitivity to stimuli [Assis and Copelli, 2008]. No doubt this intriguing model behaviour merits more detailed investigation.

Conclusions

In this work, we have analyzed the emergent properties of an extended version of the standard Amari-Hopfield neural network model, by considering realistic assumptions for synapse (the possibility of short-term plasticity) and neuron dynamics (the possibility of silent or quiet neurons) and network topology. Our analysis shows that these new features induce new phenology in the dynamical behavior of the network with the appearance of novel phases where the network is able to do different tasks. For instance, in some region of the parameter space, the network is able to efficiently retrieve the stored memories, as in a standard memory or ferromagnetic phase, and by slightly changing the relevant network parameters, the network activity can move to a dynamical phase which can be either, regular or chaotic, which is a positive feature. In the chaotic phase, the activity is able to dynamically retrieve for some period of time each one of the stored memories, which is positive for dynamical memory processing. Moreover, our analysis has shown that near the so called “edge of chaos”, the network activity becomes critical, that is, some relevant statistical properties of the dynamics show power-law distributions, as those observed in actual neural systems [Eguíluz *et al.*, 2005]. We have also explored the effect of network topology within these new phases. More precisely, we have shown that the heterogeneity of the network is important given that it enhances the dynamic performance.

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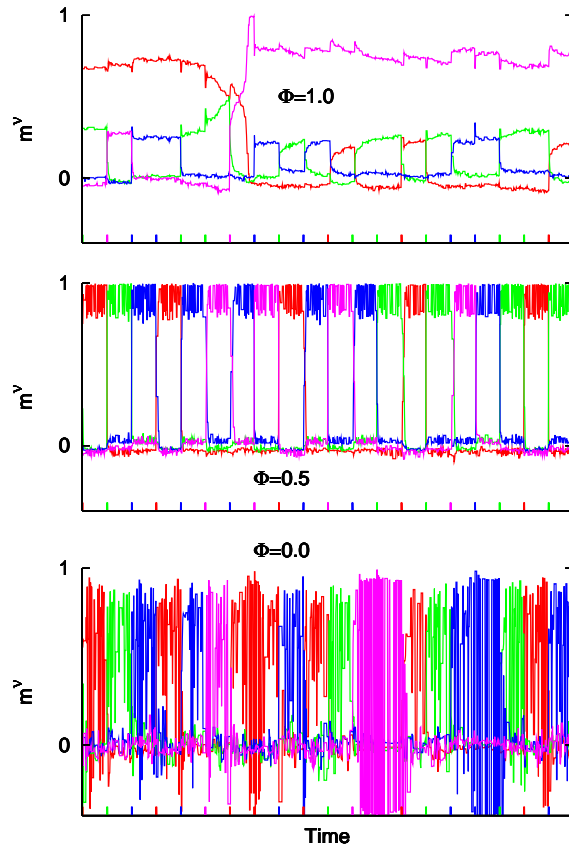


Figure 5: A pattern recognition process, as described in the main text, performed at different values of fatigue on a network with a bimodal random distribution with $\Delta = 10$. The overlaps for each of the $M = 4$ stored patterns are shown as coloured lines, while the stimuli are represented as appropriately coloured ticks. The top panel ($\Phi = 1$, i.e. static synapses) results in a performance of $\eta = 0.26$ (measured as the fraction of time that the network activity follows the stimulus); the middle panel ($\Phi = 0.5$) yields $\eta = 0.87$; and the bottom panel ($\Phi = 0.0$) has $\eta = 0.50$. In all cases, updating was $\rho = 0.5$ and $T = 0.08T_c$. Other parameters as in figure 4.

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