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Functional optimization in complex excitable networks

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Abstract — We study the effect of varying wiring in excitable random networks in which connection weights change with activity to mold local resistance or facilitation due to fatigue. Dynamic attractors, corresponding to patterns of activity, are then easily destabilized according to three main modes, including one in which the activity shows chaotic hopping among the patterns. We describe phase transitions to this regime, and show a monotonous dependence of critical parameters on the heterogeneity of the wiring distribution. Such correlation between topology and functionality implies, in particular, that tasks which require unstable behavior —such as pattern recognition, family discrimination and categorization— can be most efficiently performed on highly heterogeneous networks. It also follows a possible explanation for the abundance in nature of scale-free network topologies.

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Excitable systems allow for the regeneration of waves propagating through them, and may thus respond vigorously to weak stimulus. The brain and other parts of the nervous system are well-studied paradigms, and forest fires with constant ignition of trees and autocatalytic reactions in surfaces, for instance, also share some of the basics [1–5]. The fact that signals are not gradually damped by friction in these cases is a consequence of cooperativeness between many elements in a nonequilibrium setting. In fact, the systems of interest may be viewed as large networks whose nodes are "excitable". This, which admits various realizations, typically means that each element has a threshold and a refractory time between consecutive responses, a behavior that impedes thermal equilibrium.

Brain tasks may ideally be reproduced in mathematical neural networks. These consist of neurons —often simplified as binary variables which in practice suffices to dig out the main effects of cooperation¹— connected by edges representing synapses [7–9]. Assuming edges weighted according to a prescription (e.g., [10]) which in a sense saves information from a set of given patterns of activity, these patterns become attractors of the phase-space dynamics. Therefore, one may interpret that the system shows retrieval of the stored patterns, known as

associative memory. Actual neural systems do much more than just recalling a memory and staying there, however. That is, one should expect dynamic instabilities or other destabilizing mechanism. This expectation is reinforced by recent experiments suggesting that synapses undergo rapid changes with time which may both determine brain tasks [6,11–13] and induce irregular and perhaps chaotic activity [14,15].

One may argue that the observed rapid changes (which have been described [6,12,13] as causing "synaptic depression" and/or "facilitation" on the time scale of milliseconds — i.e., much faster than the plasticity process in which synapses store patterns) may simply correspond to the characteristic behavior of single excitable elements. Furthermore, a fully connected network which describes cooperation between such excitable elements has recently been shown to exhibit both attractors and chaotic instabilities [16]. Here, we extend and generalize this study to conclude on the influence of the excitable network topology on dynamic behavior. We show, in particular, an interesting correlation between certain wiring topology and optimal functionality.

Consider N binary nodes $(s_i = \pm 1)$ —we expect our main result to occur also for more complex nodes—and the adjacency matrix, $\epsilon_{ij} = 1, 0$, which indicates the existence or not of an edge between nodes i, j = 1, 2, ..., N. Let a set of M patterns, $\xi_i^{\nu} = \pm 1$, $\nu = 1, ..., M$ (which we generate here at random), and

¹Several studies have already shown that binary neurons may capture the essence of cooperation in many more complex settings. See, for instance, [6] in the case of integrate and fire neuron models of pyramidal cells.

assume that they are "stored" by giving each edge a base weight $\overline{\omega_{ij}} = N^{-1} \sum_{\nu} \xi_i^{\nu} \xi_j^{\nu}$. Actual weights are dynamic, however, namely, $\omega_{ij} = \overline{\omega_{ij}} x_j$, where x_j is a stochastic variable. Assuming the limit in which this varies in a time scale infinitely smaller than the one for node dynamics, we may consider a stationary distribution such as $P(x_j|S) = q\delta(x_j - \Xi_j) + (1-q)\delta(x_j - 1)$, $S = \{s_j\}$, for instance. This amounts to assume that, at each time step, every connection has a probability q of altering its weight by a factor Ξ_j which is a function (to be determined) of the local field at j, defined as the net current arriving to j from other nodes. This choice differs essentially from the one in ref. [16], where q depends on the global degree of order and Ξ_j is a constant independent of j.

Assume independence of the noise at different edges, and that the transition rate for the stochastic changes is

$$\frac{\bar{c}(S \to S^i)}{\bar{c}(S^i \to S)} = \prod_{j/\epsilon_{i,i}=1} \frac{\int \mathrm{d}x_j P(x_j|S) \Psi(u_{ij})}{\int \mathrm{d}x_j P(x_j|S^i) \Psi(-u_{ij})},$$

where $u_{ij} \equiv s_i s_j x_j \overline{\omega_{ij}} T^{-1}$, $\Psi(u) = \exp\left(-\frac{1}{2}u\right)$ to have proper contour conditions, T is a "temperature" or stochasticity parameter, and S^i stands for S after the change $s_i \to -s_i$. (For a description of this formalism and its interpretation, see [17].) We define the effective local fields $h_i^{\text{eff}} = h_i^{\text{eff}}(S, T, q)$ via $\prod_j \varphi_{ij}^-/\varphi_{ij}^+ = \exp(-h_i^{\text{eff}} s_i/T)$, where $\varphi_{ij}^{\pm} \equiv q \exp(\pm \Xi_j v_{ij}) + (1-q) \exp(\pm v_{ij})$, with $v_{ij} = \frac{1}{2} \epsilon_{ij} u_{ij}$. Effective weights ω_{ij}^{eff} then follow from $h_i^{\text{eff}} = \sum_j \omega_{ij}^{\text{eff}} s_j \epsilon_{ij}$. To obtain an analytical expression, we linearize around $\overline{\omega_{ij}} = 0$ (a good approximation when $M \ll N$), which yields

$$\omega_{ij}^{\text{eff}} = [1 + q(\Xi_j - 1)]\overline{\omega_{ij}}.$$

In order to fix Ξ_j here, we first introduce the overlap vector $\overrightarrow{m} = (m^1, \cdots m^M)$, with $m^{\nu} \equiv N^{-1} \sum_i \xi_i^{\nu} s_i$, which measures the correlation between the current configuration and each of the stored patterns, and the *local* one $\overrightarrow{m_j}$ of components $m_j^{\nu} \equiv \langle k \rangle^{-1} \sum_l \xi_l^{\nu} s_l \epsilon_{jl}$, where $\langle k \rangle$ is the mean node connectivity, *i.e.*, the average of $k_i = \sum_j \epsilon_{ij}$. We then assume, for any $q \neq 0$, that the relevant factor is $\Xi_j = 1 + \zeta(h_j^{\nu})(\Phi - 1)/q$, with

$$\zeta(h_j^{\nu}) = \chi^{\alpha}/(1+M/N) \sum_{\nu} |h_j^{\nu}|^{\alpha},$$

where $\chi \equiv N/\langle k \rangle$ and $\alpha > 0$ is a parameter. This comes from the fact that the field at node j may be written as a sum of components from each pattern, namely, $h_j = \sum_{\nu}^M h_j^{\nu}$, where

$$h_j^{\nu} = \xi_j^{\nu} N^{-1} \sum_i \epsilon_{ij} \xi_i^{\nu} s_i = \chi^{-1} \xi_j^{\nu} m_j^{\nu}.$$

Our choice for Ξ_j , which amounts to assume that the "fatigue" at a given edge increases with the field at the

preceding node j (and allows to recover the fully connected limit in [16] if $\alpha = 2$), finally leads to

$$\omega_{ij}^{\text{eff}} = [1 + (\Phi - 1)\zeta_j(\overrightarrow{m_j})]\overline{\omega_{ij}}.$$

Varying Φ one sets the nature of the weights. That is, $0 < \Phi < 1$ corresponds to resistance (depression) due to heavy local work, while the edge facilitates, i.e., tends to increase the effect of the signal under the same situation for $\Phi > 1$. (The action of the edge is reversed for negative Φ). We performed Monte Carlo simulations using standard parallel updating with the effective rates $\bar{c}(S \to S^i)$ computed using the latter effective weights.

It is possible to solve the single pattern case (M=1)under a mean-field assumption, which is a good approximation for large enough connectivity. That is, we may substitute the matrix ϵ_{ij} by its mean value over network realizations to obtain analytical results that are independent of the underlying disorder. Imagine that each node hosts k_i half-edges according to a distribution p(k), the total number of half-edges in the network being $\langle k \rangle N$. Choose a node i at random and randomly join one of its half-edges to an available free half-edge. The probability that this half-edge ends at node j is $k_i/(\langle k \rangle N)$. Once all the nodes have been linked up, the expected value (as a quenched average over network realizations) for the number of edges joining nodes i and j is $\overline{\epsilon_{ij}} =$ $k_i k_j / (\langle k \rangle N)$ (see footnote 2). Using the notation $\eta_i \equiv \xi_i s_i$, we have $m_j = \chi \langle \eta_i \epsilon_{ij} \rangle_i = \frac{\chi}{N} \sum_i \eta_i \epsilon_{ij}$. Because node activity is not statistically independent of connectivity [20], we must define a new set of overlap parameters, analogous to m and m_j . That is, $\mu_n \equiv \langle k_i^n \eta_i \rangle_i / \langle k^n \rangle$ and the local versions $\mu_n^j \equiv \chi \langle k_i^n \eta_i \epsilon_{ij} \rangle_i / \langle k^n \rangle$. After using $\epsilon_{ij} = \overline{\epsilon_{ij}}$, one obtains the relation $\mu_n^i = \langle k^{n+1} \rangle k_i \mu_{n+1} / (\langle k^n \rangle \langle k \rangle^2)$. Inserting this expression into the definition of μ_n , and substituting $\langle s_i \rangle = \tanh[T^{-1}h_i^{eff}(S)]$ (for very large N), standard mean-field analysis yields

$$\mu_n(t+1) = \frac{1}{\langle k^n \rangle} \langle k^n \tanh M_{T,\Phi}(k,t) \rangle_k,$$

where the last quantity is defined as

$$M_{T,\Phi} = \frac{k}{TN} \left[\mu_1(t) + (\Phi - 1) \frac{\langle k^{\alpha+1} \rangle}{\langle k \rangle^{\alpha+1}} |\mu_1(t)|^{\alpha} \mu_{\alpha+1}(t) \right].$$

This is a two-dimensional map which is valid for any random topology of distribution p(k). Note that the macroscopic magnitude of interest is $\mu_0 = m \equiv |\overrightarrow{m}|$.

A main consequence of this is the existence of a critical temperature, T_c , under very general conditions, e.g., for many different network connectivities. More specifically, as T is decreased, the overlap m describes a second-order

²Assuming one edge at most between any two nodes, $\epsilon_{ij} = 0, 1$, the value will be slightly smaller, but it is easy to prove that this is also a good approximation for $k_i, k_j \ll N$. If more than one edge is permitted, which is more realistic, this result is exact for any random network, and it agrees (for a power law distribution with $\gamma = 3$) with the one obtained in [18] for an evolving network [19].

phase transition from a disordered or, say, "paramagnetic" phase to an ordered ("ferromagnetic") phase which exhibits associative memory. The mean-field temperature signaling this transition is

$$T_c = \langle k^2 \rangle (\langle k \rangle N)^{-1}.$$

On the other hand, the map reduces to $\mu_n(t+1) = \text{sign}\{\mu_n(t)[1+(\Phi-1)\langle k^{\alpha+1}\rangle/\langle k\rangle^{\alpha+1}]\}$ for T=0. This implies the existence at $\Phi=\Phi_0$, where

$$\Phi_0 = 1 - \langle k \rangle^{\alpha + 1} / \langle k^{\alpha + 1} \rangle,$$

of a transition as Φ is decreased from the ferromagnetic phase to a new phase in which periodic hopping between the attractor and its negative occurs. This is confirmed by the Monte Carlo simulations for M>1, namely, the hopping is also among different attractors for finite T. The simulations also indicate that this transition washes out at low enough finite temperature. Instead, Monte Carlo evolutions show that, for a certain range of Φ values, the system activity then exhibits chaotic behavior.

The transition from ferromagnetic to chaotic states is a main concern hereafter. Our interest in this regime follows from several recent observations concerning the relevance of chaotic activity in a network. In particular, it has been shown that chaos might be responsible for certain states of attention during brain activity [21,22], and that some network properties such as the computational capacity [23] and the dynamic range of sensitivity to stimuli [24] may become optimal at the "edge of chaos" in a variety of settings.

We next notice that the critical values T_c and Φ_0 only depend on the moments of the generic distribution p(k), and that the ratio $\langle k^a \rangle / \langle k \rangle^a$, a > 1, is a convenient way of characterizing heterogeneity. We studied in detail two particular types of connectivity distributions with easily tunable heterogeneity, namely, networks with $\langle k \rangle N/2$ edges randomly distributed with p(k) such that the heterogeneity depends on a single parameter. Our first case is the bimodal distribution, $p(k) = \frac{1}{2}\delta(k - k_1) + \frac{1}{2}\delta(k - k_2)$ with parameter $\Delta = (k_2 - k_1)/2 = \langle k \rangle - k_1 = k_2 - \langle k \rangle$. Our second case is the *scale-free* distribution, $p(k) \sim k^{-\gamma}$, which does not have any characteristic size but k is confined to the limits, k_0 and $k_m \leq \min(k_0 N^{\frac{1}{\gamma-1}}, N-1)$ for finite N (see footnote 3). Notice that the network in this case gets more homogeneous as γ is increased⁴, and that this kind of distribution seems to be most relevant in nature [19,20,25,26]. In particular, it seems important to mention that the functional topology of the human brain, as defined by correlated activity between small clusters of neurons, has been shown to correspond to this case with exponent $\gamma \simeq 2$ [27]. (It has not yet been possible to

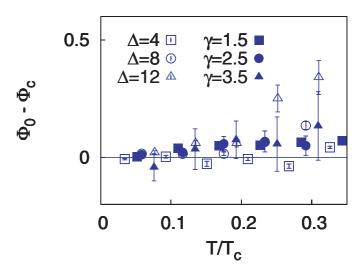


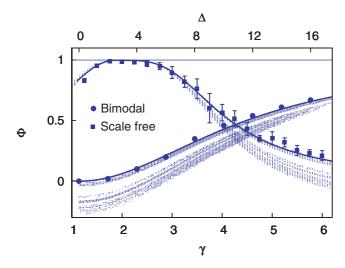
Fig. 1: The temperature dependence of the difference between the values for the fatigue at which the ferromagnetic-periodic transition occurs, as obtained analytically for T=0 (Φ_0) and from MC simulations at finite T (Φ_c). The critical temperature is calculated as $T_c = \langle k^2 \rangle (\langle k \rangle N)^{-1}$ for each topology. Data are for bimodal distributions with varying Δ and for scale-free topologies with varying γ , as indicated. Here, $\langle k \rangle = 20$, N=1600 and $\alpha=2$. Standard deviations, represented as bars in this graph, were shown to drop with $N^{-1/2}$ (not depicted).

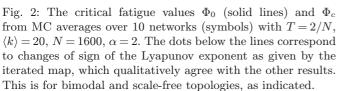
ascertain the brain's *structural* topology experimentally, but there is some evidence that function reflects structure at least to some extent [28]. Furthermore, it has been suggested, based on indirect methods, that the structural connectivity of cat and macaque brains, at the level of brain areas, may indeed be scale free [29] —and in any case displays significantly higher heterogeneity than that of, say, Erdős-Rényi random graphs.)

We obtained the critical value of the fatigue, $\Phi_c(T)$, from Monte Carlo simulations at finite temperature T. These indicate that chaos never occurs for $T \gtrsim 0.35T_c$. On the other hand, a detailed comparison of the value Φ_c with Φ_0 —as obtained analytically for T=0— indicates that $\Phi_c \simeq \Phi_0$. Figure 1 illustrates the "error" $\Phi_0 - \Phi_c(T)$ for different topologies. This shows that the approximation $\Phi_c \simeq \Phi_0$ is quite good at low T for any of the cases examined. Therefore, assuming the critical values for the main parameters, T_c and Φ_0 , as given by our map, we conclude that the more heterogeneous the distribution of connectivities of a network is, the lower the amount of fatigue, and the higher the critical temperature, needed to destabilize the dynamics. As an example of this interesting behavior, consider a network with $\langle k \rangle = \ln(N)$, and dynamics according to $\alpha = 2$. If the distribution were regular, the critical values would be $T_c = \ln(N)/N$ (which goes to zero in the thermodynamic limit) and $\Phi_0 = 0$. However, a scalefree topology with the same number of edges and $\gamma = 2$ would yield $T_c = 1$ and $\Phi_0 = 1 - 2(\ln N)^3/N^2$ (which goes to 1 as $N \to \infty$).

³Though the minimum connectivity is 1, we shall assume $k_0 \ge 2$, which reduces the probability of disconnection.

⁴The distribution is truncated and therefore not strictly scale free for $\gamma < 2$. However, nature shows examples for which γ is slightly larger than 1, so that we consider the whole range here.





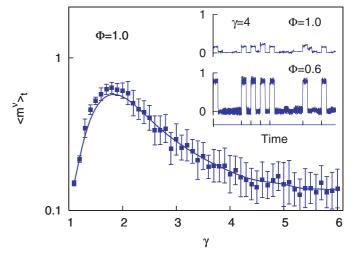


Fig. 3: Network "performance" (see the main text) against γ for scale-free topology with $\Phi=1$, as an average over 20 network realizations with stimulation every 50 MC steps for 2000 MC steps, $\delta=5$ and M=4; other parameters as in fig. 2. Inset shows sections of typical time series of m^{ν} for $\gamma=4$; the corresponding stimulus for pattern ν is shown below.

Figure 2 illustrates, for two topologies, the phase diagram of the ferromagnetic-chaotic transition. Most remarkable is the plateau observed in the edge-of-chaos or transition curve for scale-free topologies around $\gamma \simeq 2$, for which very little fatigue, namely, $\Phi \lesssim 1$ which corresponds to slight depression, is required to achieve chaos. The limit $\gamma \to \infty$ corresponds to $\langle k \rangle$ -regular graphs (equivalent to $\Delta = 0$). If γ is reduced, k_m increases and k_0 decreases. The network is truncated when $k_m = N$. It follows that a value of γ exits at which k_0 cannot be smaller, so that k_m must drop to preserve $\langle k \rangle$. This explains the fall in Φ_c as $\gamma \to 1$.

Assuming that the "ferromagnetic phase" here corresponds to a $synchronous\ state$, our results are in qualitative agreement with the ones obtained recently for coupled oscillators [30,31]. As a matter of fact, the range of coupling strengths which allow for stability of synchronous states in these systems has been shown to depend on the spectral gap of the Laplacian matrix [32], implying that the more heterogeneous a topology is, the more easily activity can become unstable. It should be emphasized, however, that the dynamics we are considering here does not come within the scope of the formalism used to derive these results, since activity at node i depends on the local field at node j.

As a further illustration of our findings, we monitored the performance as a function of topology during a simulation of pattern recognition. That is, we "showed" the system a pattern, say ν chosen at random from the set of M previously stored, every certain number of time steps. This was performed in practice by changing the field at each node for one time step, namely, $h_i \to h_i + \delta \xi^{\nu}$, where δ measures the intensity of the input signal. Ideally,

the network should remain in this configuration until it is newly stimulated. The performance may thus be estimated from a temporal average of the overlap between the current state and the input pattern, $\langle m^{\nu} \rangle_{time}$. This is observed to simply increase monotonically with Δ for the bimodal case. The scale-free case, however, as illustrated in fig. 3, shows how the task is better performed the closer to the edge of chaos the network is. This is because the system is then easily destabilized by the stimulus while being able to retrieve a pattern with accuracy. Figure 3 also shows that the best performance for the scale-free topology when $\Phi=1$, i.e., in the absence of any fatigue, definitely occurs around $\gamma=2$.

The model network above is one of the simplest relevant situations one may conceive. In particular, as emphasized above, we are oversimplifying actual nodes as binary variables. However, our assumption of dynamic connections which depend on the local fields in such a simple scenario happens to show that a close relation may exist between topological heterogeneity and function, thus suggesting this may indeed be a relevant property for a realistic network to perform efficiently certain high-level functions. In a similar way to networks shown previously to be useful for pattern recognition and family identification [33], our system retrieves memory patterns with accuracy in spite of noise, and yet it may easily destabilize itself to change state in response to an input signal —without requiring an excessive fatigue for the purpose. There is a correlation between the amount Φ of fatigue and the value of γ for which performance is maximized. One may argue that the plateau of "good" behavior shown around $\gamma \simeq 2$ for scale-free networks with $\Phi \lesssim 1$ (fig. 2) is a possible justification for the supposed tendency of certain systems in nature to evolve towards this topology. It may also serve as a hint when implementing artificial networks.

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