Self-organization of heterogeneous topology and symmetry breaking in networks with adaptive thresholds and rewiring

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Abstract – We study an evolutionary algorithm that locally adapts thresholds and wiring in Random Threshold Networks, based on measurements of a dynamical order parameter. If a node is active, with probability $p$ an existing link is deleted, with probability $1-p$ the node’s threshold is increased, if it is frozen, with probability $p$ it acquires a new link, with probability $1-p$ the node’s threshold is decreased. For any $p < 1$, we find spontaneous symmetry breaking into a new class of self-organized networks, characterized by a much higher average connectivity $K_{\text{evo}}$ than networks without threshold adaptation ($p=1$). While $K_{\text{evo}}$ and evolved out-degree distributions are independent from $p$ for $p<1$, in-degree distributions become broader when $p \to 1$, indicating crossover to a power law. In this limit, time scale separation between threshold adaptions and rewiring also leads to strong correlations between thresholds and in-degree. Finally, evidence is presented that networks converge to self-organized criticality for large $N$, and possible applications to problems in the context of the evolution of gene regulatory networks and development of neuronal networks are discussed.

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Introduction. – Interaction networks in nature often exhibit highly inhomogeneous architectures. Examples are scale-free degree distributions in protein networks [1] and metabolic networks [2], mostly accompanied by intricate second-order regularities as, for example, community structure [3]. The emergence of these properties often is explained by means of intuitive topology-based models, e.g. preferential attachment [4] or node duplications [5]. Real networks, however, are characterized not only by an evolving topology, but also by evolution of function, conveniently abstracted in terms of dynamics, i.e. the flow of information or matter on these networks. So far, only few studies explicitly consider the more general case of co-evolution between network dynamics and topology [6–9].

One example is the question how networks may evolve topologies that optimize biologically relevant parameters, e.g. flexible adaptation with respect to changing environments, or insensitivity against random perturbations of topology or dynamics (robustness) [10]. In this context, Kauffman introduced random Boolean networks (RBN) to study the dynamics of gene regulatory networks from a global perspective [11,12]. It was shown that RBN undergo a order-disorder transition at a critical wiring density (connectivity) $K_c = 2$ [11–14]; similar results were established for random threshold networks (RTN), which constitute a sub-class of RBN [15–19]. It has been postulated that evolution should drive dynamical networks towards this “edge of chaos” to optimize adaptive flexibility and robustness [11,12,20]. Interestingly, in recent years experimental evidence has accumulated that information processing networks in biological organisms indeed operate close to criticality. In particular, gene regulatory networks of several organisms have been shown to exhibit critical dynamics [21–23], similar results were established for neuronal networks in the brain [24,25]. Since, in all these systems, there generally exists no central control instance that could continuously adjust global system parameters to poise dynamics at the critical state, we have to postulate that there are simple, local adaptive mechanisms that are capable of driving global dynamics to a state of self-organized criticality. However, for many years no such mechanism able to generate critically connected networks could be provided.

To address this problem, a RTN-based model was proposed, linking rewiring of network nodes to local
measurements of a dynamical order parameter, e.g. the average activity (magnetization) [7]. It was shown that this simple, local adaptive mechanism leads to a global self-organized critical state in the limit of large system sizes $N$. Subsequently, this principle was generalized to networks of noisy neurons [8] and to RBN with evolvable logical functions [9]. Interestingly, finite-size networks in these models evolve a broadly distributed heterogeneous in-degree connectivity [9,26]. Still, these topological heterogeneities are smaller than those observed in real-world networks, presumably because dynamical elements were assumed to be homogeneous with respect to their dynamical behavior. While this assumption leads to elegant models, it is quite unrealistic, as it becomes apparent e.g. in the frequent occurrence of canalizing functions in gene regulatory networks, with strong impact on dynamics in RBN models [27]. Recent studies have shown that partial canalization completely dominates the space of all possible Boolean functions, in particular, for higher $k$ [28]; this can implicitly result in a rewiring in models that evolve the functions of the nodes [29,30]. Considering the accumulating experimental evidence of both close-to-criticality and heterogeneous architecture of information processing networks in nature, for instance in gene regulatory networks [21–23,31,32] and neuronal networks in the nervous system [24,25,33], it is fascinating to speculate about a mechanism that might explain both observations: coevolution of local structural-dynamical heterogeneity and global homeostasis by local dynamical rules. For this purpose, we introduce a minimal model linking regulation of activation thresholds and rewiring of network nodes in RTN to local measurements of a dynamical order parameter. A new control parameter $p \in [0,1]$ determines the probability of rewiring vs. threshold adaptations: If a node is active, with probability $p$ an existing link is deleted, with probability $1-p$ the node’s threshold is increased, if it is frozen, with probability $p$ it acquires a new link, with probability $1-p$ the node’s threshold is decreased. We show that the symmetry of the evolutionary attractor for $p = 1$ (no threshold adaptations, rewiring only) is broken spontaneously for any $p < 1$. This new dynamical fixed point, that potentially constitutes a new universality class of self-organized networks, exhibits a much higher average connectivity $\overline{K}_{\text{exo}}$, compared to $p=1$ networks, however, with a value $\overline{K}_{\text{exo}}$ that is insensitive to $p$. In-degree distributions become very broad, suggesting a crossover to a distribution with a power law tail $\sim k^{-3/4}_i$ for $p \to 1$. Further, we establish the emergence of strong correlations between in-degree and thresholds in this limit, while for small $p$, correlations are weak. This indicates that an adaptive time scale separation, with rare events of dynamical diversification and frequent rewiring, can lead to emergence of highly inhomogeneous topologies, without the need for network growth (as, for example, in preferential attachment models). Evidence is presented that networks with $p < 1$ converge to a critical state for large $N$, however, with a finite-size scaling significantly different from the one found for the case $p = 1$, and problems associated to the identification of criticality in this new class of densely wired coevolutionary adaptive networks are discussed. Finally, we discuss how the adaptive principles working in this model might apply to gene regulatory networks in living organisms and neuronal networks in the nervous system.

**Dynamics.** – We consider a network of $N$ randomly interconnected binary elements with states $\sigma_i = \pm 1$. For each site $i$, its state at time $t+1$ is a function of the inputs it receives from other elements at time $t$ (synchronous updates):

$$\sigma_i(t+1) = \begin{cases} +1 & \text{if } f_i(t) > 0, \\ -1 & \text{else}, \end{cases}$$

with

$$f_i(t) = \sum_{j=1}^{N} c_{ij} \sigma_j(t) + h_i. \quad (2)$$

The interaction weights $c_{ij}$ take discrete values $c_{ij} = \pm 1$, with $c_{ij} = 0$ if site $i$ does not receive any input from element $j$. Thresholds $h_i$ may vary from node to node, taking integer values $h_i \leq 0$ (see footnote 1). In the following discussion, adaptive changes will be applied to the absolute value $|h_i|$, keeping in mind that the sign of $h_i$ is always negative.

As a dynamical order parameter, we define the average activity $A(i)$ of a site $i$

$$A(i) = \frac{1}{\tau_i+1} \sum_{t=T_i}^{T_i+\tau} \sigma_i(t). \quad (3)$$

Notice that a frozen site, i.e. a site that does not change its state, has $|A(i)| = 1$, whereas an active site has $|A(i)| < 1$.

**Topology evolution.** – Let us now discuss a particular evolutionary scheme that couples local adaptations of both the number of inputs and of thresholds to a site’s average activity. Since the switching dynamics of nodes is governed by the deterministic rule eq. (1), it can be modified only by adaptations of $c_{ij}$ or $h_i$ in eq. (2), by either changing the values of the existing non-zero weights $c_{ij}$, by setting a weight that was zero previously to $c_{ij} = \pm 1$, or by incrementing/decrementing $h_i$. If node $i$ is frozen, it can increase the probability to change its state by either setting a zero weight to $c_{ij} = \pm 1$, thereby increasing its number of inputs $k_i \to k_i + 1$, or by making its threshold $h_i \leq 0$ less negative, i.e. $|h_i| \to |h_i| - 1$. If $i$ is active, it can reduce its activity by adapting either setting one of its existing non-zero inputs to $c_{ij} = 0$, i.e. $k_i \to k_i - 1$, or by increasing its threshold $|h_i| \to |h_i| + 1$. This adaptive scheme is realized in the following algorithm.

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1We chose $h_i \leq 0$ to ensure that thresholds make activation, i.e. $\sigma_i = +1$, more difficult.
anewinputfromarandomlychosensite
j
to
1
threshold
(seealsofig.1):

Fig.1:Left:withprobability
p
active
nodes
lose
one
of
their
inputs,
with
probability
1 − p
they
increase
their
(threshold)
threshold
|h_i|
. Right: with probability
p
frozen nodes acquire
a new input from a randomly chosen site
j,
changing
\(c_{ij} = 0\)
to
\(c_{ij} = \pm 1\).
With probability
1 − p,
the
(threshold)
threshold
|h_i|
is decremented instead.

(see also fig. 1):

1) Create a random network with average connectivity
\(\bar{K}_{ini} > 0\) and average threshold
\(\bar{h}_{ini} = 0\).
Each of the
\(N \cdot \bar{K}_{ini}\) interaction weights is randomly initialized to
\(c_{ij} = +1\) or
\(c_{ij} = -1\) with equal probability.

2) Select a random initial state
\(\bar{h}_{ini} = (\sigma_1, \ldots, \sigma_N)\).

3) Iterate network dynamics for
T
time steps.

4) Select a network site
i
at random and measure its
average activity
\(A_i\) over the last
\(T/2\) updates.

5) Adapt input number
k_i
and
threshold
\(h_i\) in the following way:
   - If
\(|A_i| < 1\)
, then with probability
p
remove
one input
\(c_{ij}\) randomly selected from the
\(k_i\) inputs,
i.e.
set
\(c_{ij} = 0\).
With
probability
1 − p,
adapt
\(|h_i| \rightarrow |h_i| + 1\).

   - If
\(|A_i| = 1\)
, then with probability
p
add a new input
\(c_{ij}\) from a randomly selected site
j,
assigning
\(c_{ij} = +1\) or
\(c_{ij} = -1\) with equal probability.
With probability
1 − p,
adapt
\(|h_i| \rightarrow |h_i| - 1\).
If
\(h_i = 0\), let its value unchanged.

6) Go back to step 3).

If the control parameter
p
takes values
p > 1/2,
rewiring of nodes is favored, whereas for
p < 1/2
threshold adaptations are more likely. Notice that the model introduced in [7] is contained as the limiting case
\(p = 1\)
(rewiring only and
\(h_i = \text{const} = 0\) for all sites). Notice that adaptation of interaction weights
\(c_{ij}\) in step 5) conserves the initial symmetry of the weight distribution, i.e.
\(c_{ij}\) takes the values
+1
and
−1
with equal probability
\(p = 1/2\).

The number of dynamical updates
\(T\) in step 3) of the algorithm was set to
\(T = 200\) in simulations, i.e.
the average activity was measured over the last
\(T/2 = 100\) dynamical updates, after a transient of
100 updates. The transient before activity measurement ensures a proper decoupling from initial conditions, while averaging of
\(A(i)\) over
100 updates is enough to provide the typical switching behavior of
\(i\) and a decent time scale separation between fast switching dynamics and slow topology adaptation\(^2\).

However, simulations show that the results are not very sensitive to the choice of
\(T\), only for very small values
\(T < 10\) we see differences, e.g. convergence to a slightly lower average connectivity.

Results. – After a large number of adaptive cycles, networks self-organize into a global evolutionary steady state.
An example is shown in fig. 2 for networks with
\(N = 512\): starting from an initial value
\(\bar{K}_{ini} = 1\), the networks’ average connectivity
\(\bar{K}\) first increases, and then saturates around a stationary mean value
\(\bar{K}_{evo}\); similar observations are made for the average threshold
\(\bar{h}\) (fig. 2, lower panel). The non-equilibrium nature of the system manifests itself in limited fluctuations of both
\(\bar{K}\) and
\(\bar{h}\) around
\(\bar{K}_{evo}\) and
\(\bar{h}_{evo}\). Regarding the dependence of
\(\bar{K}\) with respect to
\(p\), we make the interesting observation that it changes non-monotonically. Two cases can be distinguished: when
\(p = 1\),
\(\bar{K}\) stabilizes at a very sparse mean value
\(\bar{K}_{evo}\), e.g. for
\(N = 512\) at
\(\bar{K}_{evo} = 2.664 \pm 0.005\).
When
\(p < 1\), the symmetry of this evolutionary steady state is broken. Now, \(\bar{K}\) converges to a much higher mean value
\(\bar{K}_{evo} \approx 43.5 \pm 0.3\) (for
\(N = 512\), however, the particular value which is finally reached is independent of
\(p\).

The latter observation is made rigorous from measurements of
\(\bar{K}_{evo}\) for different
\(N\) over
10^6 evolutionary steps,

\(^2\)Since in each evolutionary step one node is rewired, this time scale separation is at the order of
\(N \cdot T\).
Fig. 3: Upper four curves: evolutionary mean values $\bar{K}_{\text{evo}}$ of the average connectivity, as a function of $p$; system sizes from top to bottom: $N = 512$, $N = 256$, $N = 128$ and $N = 64$. Lower four curves: the same for the evolutionary mean values $|\bar{h}_{\text{evo}}|$ of the average absolute threshold. Statistics was taken over $10^6$ evolutionary steps, after a transient of $4 \cdot 10^6$ steps.

| $p$ | $|\bar{h}_{\text{evo}}|$ |
|-----|------------------|
| 0.2 | 100              |
| 0.3 | 50               |
| 0.4 | 25               |
| 0.5 | 15               |
| 0.6 | 10               |
| 0.7 | 5                |
| 0.8 | 2                |
| 0.9 | 1                |
| 1   | 0                |

Fig. 4: Line-pointed curves: in-degree distributions of evolved networks; data points only: the corresponding out-degree distributions $\langle k \rangle$: $p = 0.3$, $p = 0.5$, $p = 0.8$, $p = 0.95$, $p = 0.99$. Statistics was gathered over $10^6$ evolutionary steps, after a transient of $4 \cdot 10^6$ steps. Networks had size $N = 512$. The dashed line has slope $-3/4$.

Fig. 5: Average number $\langle k_{\text{in}} \rangle$ of inputs for a given node in evolving networks, as a function of the respective nodes (absolute) threshold $|h|$. Statistics was taken over $10^6$ rewiring steps, after a transient of $4 \cdot 10^6$ steps. For all values $p < 1$, a clear positive correlation between $k_{\text{in}}$ and $|h|$ is found.

after systems have reached the steady state. While $K_{\text{evo}}$ obviously depends on the system size $N$, curves are very flat with respect to $p$ (fig. 3, upper four curves); the same holds for $|h_{\text{evo}}|$ (fig. 3, lower four curves). On the other hand, convergence times $T_{\text{con}}$ needed to reach the steady state are strongly influenced by $p$: $T_{\text{con}}(p)$ diverges when $p$ approaches 1 (compare fig. 2 for $p = 0.99$). We conclude that $p$ determines the adaptive time scale. This is also reflected by the stationary in-degree distributions $p(k_{\text{in}})$ that vary considerably with $p$ (fig. 4); when $p \to 1$, these distributions become very broad. The numerical data suggest that a power law

$$ \lim_{p \to 1} p(k_{\text{in}}) \propto k_{\text{in}}^{-\gamma} $$

with $\gamma \approx 3/4 \pm 0.03$ is approached in this limit (cf. fig. 4, dashed line). At the same time, it is interesting to notice that the evolved out-degree distributions are much narrower and completely insensitive to $p$ (fig. 4, data points without lines).

How can one understand the emergence of broad in-degree distributions with increasing $p$? Evidently, lifetimes of both low thresholds $|h_{\text{in}}| < 0$ and high thresholds $|h_{\text{in}}| > 0$ become long for $p \to 1$. Since sites with low thresholds tend to be active and hence, on average, lose links, while sites with high thresholds tend to freeze and hence, on average, acquire new links, we would indeed expect that $p(k_{\text{in}})$ is broadened for $p \to 1$. On the other hand, for $p \to 0$, frequent adaptive changes of thresholds prevent long sequences of both frozen or highly active states, and hence make emergence of strong local wiring heterogeneities less probable. If this idea is correct, we would expect that, in the limit $p \to 1$, the in-degree of sites should exhibit a strong positive correlation to their thresholds, while for $p \to 0$ these correlations should be less pronounced. This is indeed exactly what we observe. For $p = 0.99$, the average in-degree $\langle k_{\text{in}} \rangle$ of a given node, as a function of its threshold $|h|$, shows a steep increase, while the corresponding curve is relatively flat for $p = 0.3$ (fig. 5).

An interesting question is whether the networks with $p < 1$ still approach a self-organized critical state for large $N$, as it was found for the case $p = 1$ [7]. Since networks now evolve more densely wired, non-trivial topologies, this question has to be answered by application of a dynamical criterion. For this purpose, we studied damage spreading: after each adaptive step, dynamics was run from an initial system state $\vec{\sigma}$ and again from a direct neighbor state $\vec{\sigma}'$ differing in one bit; after $t = 200$ updates, the Hamming distance $d$ between both trajectories was measured and the average fraction of damaged nodes $\bar{y}(t) := d/N$ was determined. Figure 6 shows $\bar{y}$, averaged over $10^6$ evolutionary steps, as a function of $N$. We find that the finite networks investigated here are all supercritical, however, $\bar{y}$ decreases monotonically with $N$. 

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critical state with a sparse average connectivity (no threshold adaptation) networks evolve as self-organized.

Notice, however, that convergence is logarithmic, whereas chaotic to frozen dynamics is approached for large $N$. The averaged scaling behavior can be fit by

$$y(N) \approx a \cdot [\ln(N)]^{-\beta},$$  \hspace{1cm} (5)

with $a = 0.77 \pm 0.02$ and $\beta = 0.917 \pm 0.01$. This dependence indicates that $y = 0$, i.e., the critical transition form chaotic to frozen dynamics is approached for large $N$. Notice, however, that convergence is logarithmic, whereas for $p = 1$ power laws were found [7,9]. Again, this indicates that $p < 1$ networks evolve to a new dynamical fixed point different from the case $p = 1$, and hence may constitute a new universality class.

**Discussion.** To summarize, we studied a model of network evolution that couples both rewiring of inputs and adaptation of activation thresholds to local measurements of a dynamical order parameter. A control parameter $p$ determines the probability of threshold adaptations vs. link rewiring. While for $p = 1$ (rewiring only, no threshold adaptation) networks evolve a self-organized critical state with a sparse average connectivity $K_{con} \approx 2$, for any $p < 1$ (both rewiring and threshold adaptation) networks evolve a significantly more dense wiring, with broad heterogeneous in-degree distributions exhibiting a crossover to a power law $\sim k^{-3/4}$ for $p \rightarrow 1$. In this limit, time scale separation between rare threshold adaptations and frequent rewiring leads to emergence of strong correlations between thresholds and in-degree. Hence, a new dynamical fixed point of adaptive network evolution has been found that is fundamentally different from networks without threshold adaptation ($p = 1$) and may correspond to a new universality class. We presented evidence that, in the limit of large $N$, networks logarithmically approach a self-organized critical state. A detailed characterization of the critical state for this new class of more densely wired, self-organized networks in the limit $N \rightarrow \infty$ is difficult and remains to be done in future work.

Our model presents a novel mechanism leading to co-evolution of topological and dynamical heterogeneity with robust homeostatic regulation, the latter reflected e.g. by the insensitivity of the evolved average connectivity with respect to $p$. This combination of properties is rather remarkable and may play a decisive role in information processing networks in nature for maintaining both a close-to-critical state and diversity of structure and dynamics; hence, it is interesting to speculate that similar mechanisms might be at work in the evolution of biological networks. Let us briefly discuss this for gene regulatory networks and neuronal networks.

Recent experimental results provide evidence that gene regulatory networks of eukaryotic cells operate close to criticality [21–23], exhibiting a stunning degree of structural diversity [31] and interactions that can change in response to diverse stimuli [32]. The paradigm of activity-dependent rewiring, that can be paraphrased in this context as frozen genes acquire new inputs (functions), active (chaotic) genes lose inputs, provides a simple coevolutionary adaptive scheme [34] for the evolution of a self-organized critical state in regulatory networks. While this model correctly captures topological properties of regulatory networks in simple organisms, e.g. bacteria [26,35], it does not reproduce the structural diversity observed in regulatory networks of eukaryotes. In this paper, we showed that coevolution of dynamical diversity, abstracted in terms of threshold adaptations, with dynamical rewiring can lead to emergence of such non-trivial topologies, reflected e.g. in the observed crossover to power law distributed connectivities for $p \rightarrow 1$. It is interesting to note that diversity of dynamical mechanisms in gene regulation has primarily evolved in eukaryotes, for example in the context of RNA-based regulation [36] that complements protein-based circuits, and epigenetic reprogramming through DNA methylation [37].

Indications for critical behavior were found also in neuronal networks in the brain [24,25]. Activity-dependent neural development [33,38,39] is a candidate mechanism for emergence of criticality from local dynamical rules capable to regulate crucial global parameters, e.g. the average wiring density, without global knowledge about the system state. Coevolution of global homeostasis with structure dynamics diversity is found, for example, in the distribution of dendritic spines, with an almost constant average density despite a broad lifetime distribution of individual spines [33]. Interestingly, the activity-dependent adaptation of wiring and thresholds in our model leads to a similar emergence of both local heterogeneity and global homeostasis. While the current model certainly strongly simplifies the complexity of real dynamical networks, these two examples demonstrate that its evolutionary principles might well apply to different classes of adaptive systems in nature.

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