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Dissipative self-organized branching in a dynamic population

Dranreb Earl Juanico, Christopher Monterola, and Caesar Saloma*
National Institute of Physics, University of the Philippines, Diliman, Quezon City 1101, Philippines

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We study a locally nonconservative self-organized branching process (SOBP) in an open system of excitable agents exhibiting spontaneous excitation and deexcitation. The SOBP achieves criticality even in the absence of energy conservation as the population relaxes to a stable state with no overexcited agent. Criticality is widely thought to happen only in a locally conservative SOBP. Our model explains the observed characteristic size in the size distribution of tuna fish schools and the neuronal avalanches in cortical networks.

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INTRODUCTION

Self-organized criticality (SOC) is a powerful concept that is now widely used to explain scaling phenomena in several interesting physical systems. The sandpile model of Bak, Tang, and Wiesenfeld [1] is the earliest implementation of SOC. It stimulated research activity in both experiment (e.g., Oslo rice pile experiment [2], real sandpiles [3]) and theory (e.g., critical exponents [1], SOC-generating rules [4–6]). The role of energy conservation during dynamical exchanges is essential to our understanding of how SOC emerges in a system. The prevailing consensus seems that relaxation processes toward SOC require local conservation at least on the average.

Explorations of the possibility of SOC in nonconservative models have remained relevant since locally nonconservative self-organized synchronization is found in many important real-world biological and social systems [7]. Recent examples are the coordinated cell-wide oscillations in the mitochondrial energy state of heart cells [8], the synchronous diving behavior of Adelie penguins (*Pygoscelis adeliae*) [9], and the synchronization of opinion dynamics [10]. Synchronization is achieved via self-organization and has been attributed to locally nonconservative mechanisms. Mitochondrial networks achieve phase synchronization via the transport of reactive oxygen species through lossy inner-membrane anion channels [8].

The incorporation of any degree of dissipation into the relaxation rules was demonstrated to lead to a subcritical steady state where the power-law behavior of the avalanche (size and lifetime) distributions is followed by a significant drop-off at a characteristic size and duration [12]. An unstable active site relaxes with probability ϵ by dissipating the grains out of the system and the self-organized branching process (SOBP) becomes critical only at $\epsilon=0$. SOC is therefore possible only in systems with a locally conservative relaxation process.

In the Olami-Feder-Christensen (OFC) model, earthquakes are locally nonconservative, displaying SOC [5]. Criticality is deduced from the power law distribution of earthquake intensities and analyzed by Bröker and Grassberger [13] and Chabanol and Hakim [14]. They argued that the mean-field OFC model could exhibit true criticality only in a conservative relaxation process. Carvalho and Prado [7] sustained the claim after analyzing the branching rate of the original OFC model. Thus, the issue of SOC without energy conservation needs further study and elucidation.

Here, we demonstrate the possibility of SOC in a locally nonconservative system of excitable agents whose "population" dynamics unfolds by spontaneous excitation and deexcitation. SOC is established by a matching condition between the population dynamics and the relaxation process. It is achieved even when the relaxation is locally nonconservative—energy is gained from or dissipated to the environment during population branching. Our model could explain the observed size distribution of tuna fish schools. The population dynamics described here is also consistent with the synaptic background activity in cortical networks [15] displaying neuronal avalanches during action potential transmission [16].

SOBP IN A DYNAMIC POPULATION

Consider a system of excitable agents in a lattice with open boundaries. The system with an inherent demographic activity is constantly exposed to an external stimulus. Under excessive stimulation, it relaxes by redistributing or dissipating the energy surplus, effectively synchronizing the behavior of a certain number of agents. The relaxation is akin to the Manna toppling rules [4] in an "infinite" lattice (mean-field approximation). At an arbitrary time t, an agent can be in any of three mutually exclusive discrete states: understimulated (US, state $z=0$), amply stimulated (AS, $z=1$), or overstimulated (OS, $z=2$). An AS agent responds without affecting others to an external stimulus, while an OS agent responds by expending excess energy, subsequently exciting either one or two other agents with probabilities β and α, respectively. In the latter case, the OS agent spends enough excess energy to deexcite itself completely ($z:2\rightarrow0$). In the former, the OS agent deexcites only partially ($z:2\rightarrow1$). The neighboring agent(s) that is excited by the OS agent is randomly selected. We also allow the possibility ($\alpha+\beta<1$) that an OS agent can expend its excess energy to deexcite itself completely without affecting any of its neighbors. The expended energy is dissipated out of the system in a manner consistent with the dissipation mechanism reported in [12].

The population relaxes and relieves itself of the excess energy from an initially OS agent by a series of agent deexcitations over time. In a relaxed system, all agents are either

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*Electronic address: csaloma@nip.upd.edu.ph

US or AS only. An avalanche refers to a cluster of agents that are synchronized behaviorally by a single stimulus, and the avalanche size is equal to the cumulative number of excited agents. Following the approach in [12], we impose a boundary condition that puts an upper bound n to the number of excitation events that occur during the system relaxation process. The relaxation dynamics can be mapped to an equivalent branching tree consisting of $N=2^{n+1}-1$ nodes.

By interpreting the system as a population of excitable agents, we can define a background demographic activity that is driven by the spontaneous excitation of US agents and deexcitation of AS agents. The stochastic background proceeds much more slowly than the relaxation dynamics itself—a scheme resembling the time-scale separation in forest-fire models but without the externally driven stochastic background (e.g., lightning).

Let $p=p(t)$ denote the fraction of AS agents and N the total number of agents. Initially, the lattice is populated entirely by US agents $[p(0)=0]$. At any later time, a US and an AS agent are spontaneously excited and deexcited with probability $\eta\,(z:0\rightarrow 1)$ and $\lambda\,(z:1\rightarrow 0)$, respectively. Concurrently, an OS agent can emerge with a probability p (mean-field approximation) due to the continuous flux of external stimuli. OS agents are produced only from AS agents, i.e., $z:1\rightarrow 2$. A dynamical equation for p is

$$\frac{dp}{dt}=(1-p)\eta-p\lambda+\Theta(p;\alpha,\beta,n)+\frac{\xi(p,t)}{N}, \tag{1}$$

where Θ is the relaxation term that considers the change in the number of AS agents remaining after a relaxation or synchronization event, and ξ/N denotes the fluctuations around average values assumed to hold in the calculation of Θ. The noise term ξ/N vanishes as the system size N increases. Following the analysis in [12], Θ is derived from the following relation:

$$N\Theta(p;\alpha,\beta,n)=1-\sigma(p)^n-\frac{(1-\alpha-\beta)p}{1-(\alpha+\beta)p}\times\left(1+\frac{1-\sigma(p)^{n+1}}{1-\sigma(p)}-2\sigma(p)^n\right), \tag{2}$$

where $\sigma(p)=(2\alpha+\beta)p$ is the branching parameter, which has a critical value of 1. Consequently, the critical value of p is $p_c=(2\alpha+\beta)^{-1}$.

We prove that, even without energy conservation, a system can still display SOC. Local energy nonconservation is implemented by allowing $\alpha+\beta<1$. The coupling of the background demographic stochasticity (λ and η) with the branching relaxation dynamics (α and β) permits a nonconservative system to achieve criticality. We defined an ansatz matching condition:

$$\lambda/\eta=2\alpha+\beta-1. \tag{3}$$

The steady state of Eq. (1) is first studied at the fixed point $p=p^*$. We show that the matching condition leads to a steady state $p^*=p_c$. The first two terms of Eq. (1) add up to zero as the third term $\Theta\rightarrow 0$ at the matching condition where $p_c=(2\alpha+\beta)^{-1}$ and $p^*=p_c$. The last term vanishes as $N\rightarrow\infty$.

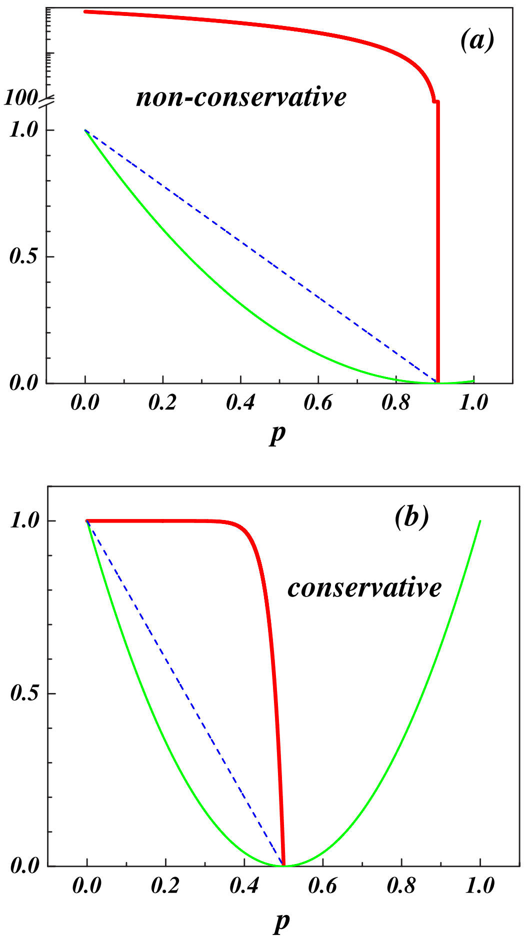

FIG. 1. (Color online) Plots of Ndp/dt (red, thick solid line), $Q(p)$ (green, solid line), and $R(p)$ (blue, dashed line) vs density p of AS agents: (a) $\alpha=0.3$, $\beta=0.5$, $\eta=2^{-4}$, $\lambda=(2\alpha+\beta-1)\eta$; (b) $\alpha=1.0$, $\beta=0.0$, $\eta=0$. Curves intersect at $p=p_c$.

Figure 1 plots the behavior of Ndp/dt vs p against the critical constraint functions $Q(p)=\beta^2p^2-4\alpha p[1-(\alpha+\beta)p]-2\beta p+1$, and $R(p)=1-(2\alpha+\beta)p$. Using the standard generating function approach [17], we derive a power law solution to the recurrence relation and obtain a cluster size distribution $P(s)$ of the form

$$P(s)=\frac{b(2s-1)P(s-1)-a(s-2)P(s-2)}{s+1}. \tag{4}$$

The system is critical when $p^*=p_c$, implying that the Ndp/dt, $Q(p)$ and $R(p)$ plots intersect at the origin only at $p^*=p_c$. A locally nonconservative system ($\alpha=0.3$, $\beta=0.5$) satisfies such a condition if λ/η satisfies the matching condition [see Fig. 1(a)]. For comparison, the corresponding case for a truly conservative system is presented in Fig. 1(b). For a nonconservative system that is driven by a stochastic background, the steady state becomes critical ($p^*=p_c$) only when the spontaneous excitation rate η exceeds a threshold value η_{th}. Note that $\eta_{th}\rightarrow 0$ when $n\rightarrow\infty$.

Figure 2 illustrates a continuous phase transition from a subcritical to a critical steady state for a nonconservative system ($\alpha=0.55$ and $\beta=0$). Even if the relaxation dynamics

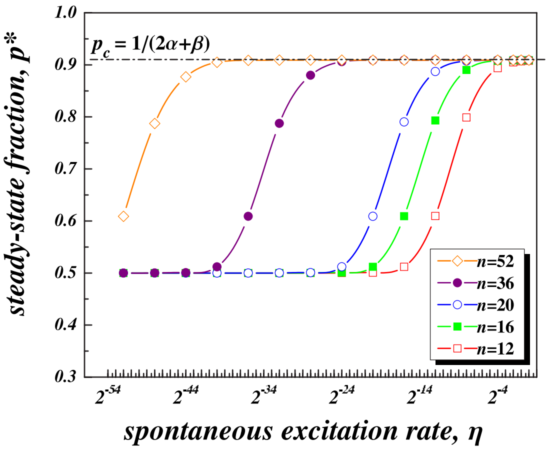

FIG. 2. (Color online) Steady-state density p^* of AS agents vs η for different n (lattice size=$2^{n+1}-1$, α=0.55, β=0). System is subcritical if $\eta < \eta_{th}$ where $\eta_{th} \rightarrow 0$ with increasing n. Above $\eta = \eta_{th}$, $p^* \rightarrow p_c$.

is inherently nonconservative, the threshold spontaneous excitation rate steers the stochastic background that matches the relaxation dynamics at λ/η=0.1 and propels the system toward SOC. The existence and necessity of η_{th} indicates a nonlinear dependence of p^* on η.

We validate the predicted criticality by examining the scaling properties of the cluster size distribution $P(s)$ and the relaxation time distribution $P(T)$. Figure 3 shows that both obey a power law for a nonconservative system (α=0.3, β=0.5) satisfying Eq. (3) with $\eta > \eta_{th} \sim 2^{-5}$ for n=16 (case I). On the other hand, scaling vanishes if $\eta < \eta_{th}$ even when Eq. (3) is satisfied (case II). It also vanishes when Eq. (3) is not satisfied at all (case III).

We recall that, in forest-fire models, relaxation dynamics is coupled with a stochastic background. However, the background source is external while the driving rates must satisfy the double limits $\lambda, \eta \rightarrow 0$ and $\lambda/\eta \rightarrow 0$ to display criticality. In our model, the stochastic background is inherent in the system while the driving rates only need to satisfy Eq. (3) and $\eta > \eta_{th}$ for any system (conservative or nonconservative) to display criticality.

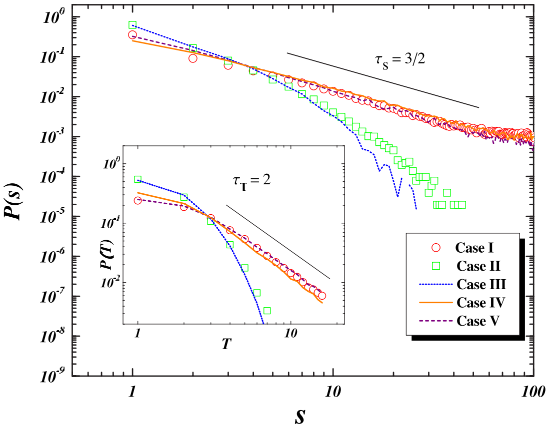

FIG. 3. (Color online) $P(s)$ plots for nonconservative system (n=16, 2^{17} iterations, α=0.3, β=0.5) with stochastic background: $\eta > \eta_{th}$ (I), $\eta < \eta_{th}$ (II) where Eq. (3) is satisfied and (III) where Eq. (3) is unsatisfied. Also shown is a conservative system (α=1, β=0) with (IV) and without background (V).

CONSERVATIVE SOBP WITHOUT BACKGROUND

Ours is a generalization of the SOBP model of SOC. We now show that it reduces consistently to a conservative system in the absence of a stochastic demographic background. We rewrite Eq. (3) in terms of $p_c = (2\alpha+\beta)^{-1}$, and obtain $\lambda/\eta = p_c^{-1}(1-p_c)$. The background is then switched off by letting $\lambda \rightarrow 0$ and $\eta \rightarrow 0$ simultaneously. The process leads to the limit $1-p_c \approx p_c \rightarrow 1/2$, which is satisfied only if α=1 and β=0. The result is exactly the same as the mean-field result of [11]. The limit $p_c \rightarrow 1/2$ is also evident in Fig. 2 as $\eta \rightarrow 0$.

A conservative SOBP also corresponds to Eq. (4) with b =0. The resulting analytic solution for $P(s)$ holds only for odd values of size s [18], because a grain is unable to leave a toppling site (β=0). In contrast, our model enables a $P(s)$ solution to hold for all s values by allowing not only the possibility that an OS agent deexcites completely (with probability α), but also the likelihood that it deexcites only partially (with probability β).

Figure 3 plots the $P(s)$ produced by our model for three possible η values relative to η_{th} (cases I, II, and III) in a stochastic background. Also shown is the corresponding performance of a conservative system (α=1, β=0) with (case IV) and without (case V) background.

FISH SCHOOL SIZE SCALING

Bonabeau *et al.* [19] formulated a mean-field model of animal aggregation (e.g., fish schools) that interplayed aggregation and splitting. Fish schooling is an interesting manifestation of avalanche dynamics in ecology [20,21]. Fishes aggregate when searching for food, protecting themselves from predators, or when migrating to more favorable habitats.

Our model could explain the behavior of the observed fish school size distribution. At least for fish populations, we can define an effective "excitation" rate η by accruing the change due to actual birth and immigration, and an effective "deexcitation" rate λ that arises from actual death, emigration, predation, and fish catch.

Two (or more) fish engaging in the same activity (e.g., foraging) trigger the rest of the population, eventually stimulating a large number of other fishes to follow suit. Such behavioral synchronization is a possible progenitor of schooling [20]. Synchronization propagates like a wave front, closely resembling an avalanche. Thus, fish schooling may be interpreted as a relaxation process with a stochastic demographic background. Allelomimesis is a possible catalyzing biomechanism for synchronization. It is a possible means for survival [22] and a suitable mechanism [23] for scaling in different animal and human group size distributions [24]. Behavioral synchronization is naturally noisy since fishes emigrate out of the school (to forage) or compete and eliminate each other over a limited food resource. Hence, the relaxation process as a means for behavioral synchronization is inherently nonconservative. Recently, we showed that animals exhibit a strong tendency to copy conspecific behavior [23,24], justifying the locally nonconservative nature of behavioral synchronization.

The tuna fish school size distribution $P(s)$ behaves as a power law with $\tau_s = 3/2$ [19]. However, closer examination reveals that $P(s)$ also exhibits a characteristic scale with a characteristic size. In Bonabeau *et al.*'s model, the truncation of $P(s)$ is attributed to a splitting parameter σ which limits the fish school lifetime due to break-up. Here, we attribute the characteristic scale to a large λ value owing, for instance, to a rapid mortality rate due to (1) catch loss or predation $[\lambda/\eta > (2\alpha+\beta-1)]$, or (2) subthreshold spontaneous excitation (at rate η) that disables the capability of stochastic background to steer the relaxation process toward criticality.

Figure 4 compares the measured school size distribution with the model prediction. The size distribution exhibits subcriticality due to the mismatch between the stochastic demographic background and the relaxation dynamics (i.e., $\lambda/\eta = 0.25 > 2\alpha+\beta-1 = 0$).

ENERGY NONCONSERVATION IN CORTICAL NETWORKS

We also mention the experiments of Beggs and Plenz [16], which reported the spreading of local field potential activity in cortical networks reminiscent of SOC sandpile avalanches. Vogels and Abbott [25], and Galarreta and Hestrin [26] showed that neural activity propagation does not conserve the information content in action potentials. The synchronization of a large number of firing neurons is not possible unless an underlying background activity keeps the network at the critical state.

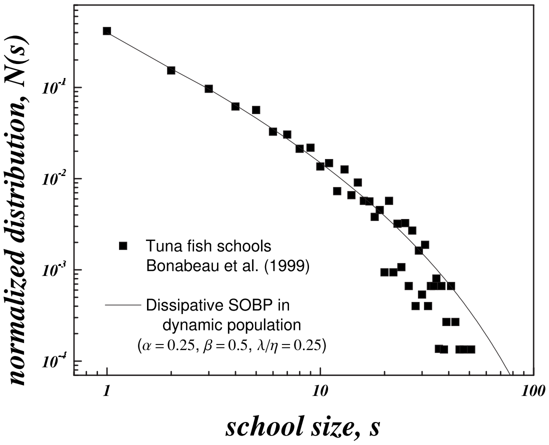

FIG. 4. Tuna fish school size distribution vs model prediction ($\alpha=0.25$, $\beta=0.5$, $\lambda/\eta=0.25$). Exponential tail indicates subcriticality due to high deexcitation probability ($\lambda = 0.25\eta$).

We have described a locally nonconservative SOBP in a dynamic population of excitable agents that could exhibit spontaneous excitation and deexcitation. The SOBP could achieve criticality even without energy conservation as the population relaxes to a stable state. Until now, criticality is widely thought to happen only in a locally conservative SOBP. Our model explains the observed tuna fish school size distribution including the existence of a characteristic size.

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