Self-organized critical branching in systems that violate conservation laws

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Abstract. A non-conservative critical branching model is proposed to demonstrate that self-organized criticality (SOC) can occur in mean-field sandpiles that violate a conservation law. The critical state is characterized by avalanche sizes and lifetimes that obey an inverse power-law distribution with exponents $\tau_S = 3/2$ and $\tau_T = 2$, respectively. Criticality is achieved when the branching process is coupled to a background activity characterized by the spontaneous switching between refractoriness and quiescence among system components. The stationary state of the system is analysed mathematically and numerically, and is shown to exhibit a transition from a subcritical phase to a critical phase. SOC in sandpile models has been widely believed to occur only when grains are conserved during avalanches. However, such a conservation law is likely to be violated by open, non-equilibrium systems such as biological networks and socially interacting systems like animal groups. The model explores the role of dynamic synapses and synaptic plasticity in maintaining criticality of cortical networks. These brain networks have been found to display neuronal avalanches that obey a power-law distribution. The non-conservative model also emulates the main features of the size distributions of free-swimming tuna schools and red deer herds. Demonstrating criticality in self-organizing systems that violate conservation laws enhances the predictive ability of the theory of SOC in the arena of biocomplexity.
1. Introduction

Self-organized criticality (SOC) has been a popular theory of complexity even after almost 20 years since its conception. The sandpile model which was originally proposed by Bak, Tang and Wiesenfeld has served as a prototype of SOC behaviour [1]. The wide acceptance of the model lies in the simplicity of its definition, notwithstanding the intriguingly non-trivial consequences. The few algorithmic rules—which are easy to follow and write as a computer code—for generating scale invariance made the sandpile model an instant curiosity among physicists and mathematicians. To date, the seminal work by Bak et al [1, 2] has been cited in over 4700 scientific papers. Efforts at examining the model have been primarily focused on the mathematical aspects of its critical behaviour (formalism [3, 4], renormalization group [5, 6], universality class [7, 8]), its realm of validity (conditions for occurrence [9]), as well as its experimental substantiations focused primarily on granular systems [e.g. two-dimensional (2D) sand heaps] [10], and piles of rice [11]. The study of SOC by means of the sandpile model has, in point of fact, generated more questions than answers.

One fundamental question that has been raised is whether or not conservation of energy is a necessary requirement for SOC to emerge [9, 12, 13]. The issue of energy conservation in putative SOC models has been dealt with using two parallel approaches. On the one hand are models that define non-conservation of energy as the absence of conservation laws such as the forest-fire (FF) model [14]. On the other hand are models that identify non-conservation as the explicit violation of an existing conservation law such as the Olami–Feder–Christensen (OFC) model [12]. It is interesting to note that both these models were published in the same year in the same journal.

In contrast to the original sandpile model, the OFC model defines a fraction of the transported energy that is dissipated in each relaxation event—the forces are redistributed equally to four nearest-neighbours such that each neighbour receives a fraction $\alpha$ of the transmitted force.
If $\alpha < 0.25$ the model is non-conservative. Soon after scaling of the non-conservative OFC model was also reported, Klein and Rundle [15], noticing the behaviour of the exponential cutoff as a function of the system size, suspected the observed critical behaviour. A few years later, de Carvalho and Prado [16], revisiting the mean-field OFC model, found that it can achieve criticality only in the conservative case—that is for $\alpha = 0.25$. Christensen et al [17], repeating the analysis of de Carvalho and Prado [16], with the same set of parameters, attempted to refute this conclusion by asserting that numerical, rather than analytic, evidence does not rule out the possibility of criticality in the non-conservative case. This counterargument however was rather unconvincing and does not directly refute the fact that the OFC model analytically cannot achieve criticality in the violation of a conservation law.

The FF model has been purported to display SOC behaviour in the absence of a conservation law, rather than a violation of a conservation law as in the sandpile and OFC models. The secret to its ability to generate scale invariant distributions is a double time-scale separation [14] between three different processes: birth of trees at empty sites with rate $p$, lightning that strikes a tree with rate $f$, and spreading of fire from one tree to the next. Fire spreading occurs much faster than the rate at which new trees grow at empty sites, which in turn happens instantaneously compared to the rate at which lightning strikes trees. The model is said to be SOC when tree growth is so slow that fire burns down even before new trees grow at the edge of the firefront [18]. The dynamics of the system depends only on the ratio of $f/p$, but not on $p$ and $f$ separately. Using a renormalization group method, the nature of the FF model’s critical behaviour was explored and analytic results for 1D and 2D were derived [19, 20]. In the context of this method, SOC is interpreted as a critical phenomenon in which all parameters are irrelevant, such that the scale invariant dynamics corresponds to an attractive fixed point in the parameter (phase) space. However, the FF model’s critical state is associated with a repulsive fixed point, implying that the control parameter—the ratio $f/p$—is therefore relevant and must be fine-tuned to zero to display approximate critical behaviour. Put differently, the FF model exhibits ordinary critical phenomena [19].

Whether SOC indeed occurs for systems that violate a conservation law still remains an open question. In this paper, a critical branching model that exhibits SOC in the presence of violation of a conservation law in dynamical exchanges is presented. Previous results of a mean-field sandpile model that employs branching processes are first described and summarized in section 2. In section 3 the non-conservative critical branching model is described and its mathematical analysis is presented. The results of numerical simulations of the model are discussed in the first part of section 4. The second part presents experimental data for neuronal avalanches, free-swimming tuna, and red deer that illustrate the significance of the model in explaining and emulating size distributions of natural systems. A conclusion and summary of findings are given in section 5.

2. Self-organized branching process (SOBP)

2.1. Formulation and results of the mean-field model

The original sandpile model is complicated by the presence of spatial correlations. Mathematical analysis of the critical behaviour of the model was therefore not straightforward and it centred primarily on scaling arguments to explain discrepancies to the expected power-law distribution [21, 22]. This is where mean-field theory [23] comes in handy. By taking away the spatial
correlations, the sandpile model is reformulated in terms of densities and averages, making stochastic analyses much easier. In simulating mean-field versions of the sandpile model, the random-neighbour approach is suitable [24]. In the random-neighbour approach, each site is assigned a randomly chosen nearest-neighbour that is not necessarily situated contiguously with the site. Other mean-field techniques such as Bethe lattices [25] have also been applied to the analysis of sandpile models, particularly in solving for critical exponents.

In the mean-field theory, an avalanche which triggers subsequent activity or dies out, in an uncorrelated fashion, is treated as a branching process. SOC can therefore be directly related to the critical behaviour of branching processes, for which the theory is well established [26]. However, criticality of a branching process can be arrived at by the fine-tuning of a control parameter—the branching parameter—to its critical value of 1. The branching parameter quantifies the average number of descendants in the next generation that each ancestor would have. If this parameter is less than 1, the branching process dies out after a finite number of generations. If it is more than 1, the branching process can generate an infinite number of descendants with a nonzero probability. A branching parameter that is equal to 1 thus defines a balance between extinction and explosion. The presence of this relevant control parameter in the branching process seems to contradict the very idea of self-organization. But this apparent paradox has been resolved through a mean-field model, known as the SOBP proposed by Zapperi et al [27].

The sandpile model is driven by the injection of energy (in the form of grains) from an external source. Sites in the system store the added energy. As stored energy reaches a threshold at a certain site, it relaxes by dissipating the stored energy to nearest neighbours. Relaxation of a single site triggers relaxation in other sites. Collective relaxation initiated by a single site is what is referred to as the avalanche. The SOC state is where avalanche sizes and lifetimes are distributed as a power-law. For the sandpile to achieve SOC, it is crucial for stored energy to be ultimately expelled out of the system through boundaries to prevent it from reaching a frozen state and to keep it hovering around the critical state. Hence, the role of boundary conditions is essential to the sandpile model’s critical behaviour. In the SOBP model, since there is no concrete embodiment of spatial dimensions, the boundary condition has been elegantly implemented by simply limiting the maximum number \( n \) of generations of relaxation events that can occur during an avalanche. In this way, energy is dissipated out of the system by excited sites of the \( n \)th generation that relax in a single avalanche event.

The SOBP model employs the same rules as the Manna version of the sandpile model. Sites may either be inactive (state 0), active (state 1), or excited (state 2). A total of \( N = 2^{n+1} - 1 \) sites comprise the sandpile and it is constantly exposed to a slow driving field that puts in additional grains. The density of active sites, \( p \), varies in time. If the addition of a single grain results in an active site becoming excited, the site relaxes by distributing grains to its two nearest neighbours. The neighbours are chosen randomly among \( N - 1 \) other sites, which implements the random-neighbour scheme for mean-field models. This puts off any spatial correlation between a site and its neighbourhood, and minimizes memory effects. By examining the continuum time limit, the authors of the SOBP model found that the sandpile self-organizes to a critical state that is characterized by \( p = p_c = 1/2 \). The avalanche size and duration obey a power-law distribution with exponents \( \tau_S = 3/2 \) and \( \tau_T = 2 \), respectively. Numerically, the avalanche distributions have an exponential cutoff because of the finite size of the system. But as \( n \gg 1 \), the cutoff approaches \( \infty \). The most significant insight that the SOBP model has contributed to SOC theory is its elucidation that the density \( p \) of active sites serves as the order parameter of...
mean-field sandpile models. Through this order parameter, an understanding of how sandpile models approach criticality has been achieved [27].

2.2. Non-conservation in the SOBP model

The local dynamical rules of a critical sandpile model is such that the number of grains (or amount of energy) transferred from one site to another is conserved. In other words, no grain is destroyed or created during the relaxation process except at the boundaries. In [28] the SOBP model is generalized to a case wherein the possibility that grains will be destroyed during relaxation is allowed. A dissipation parameter $\epsilon \geq 0$ defines the degree of non-conservation of the system. Grains are lost—absorbed or outwardly dissipated—during transfer with probability $\epsilon$. Thus, $\epsilon = 0$ describes a conservative system and any non-zero $\epsilon$ corresponds to a non-conservative system.

It was concluded that any $\epsilon > 0$ destroys the criticality of the SOBP model [28]. The critical value of $p$ is now $p_c = 1/2(1 - \epsilon)$, which is always greater than $1/2$ for any $\epsilon > 0$. However, the sandpile self-organizes to a stationary state wherein $p = 1/2$ for any value of $\epsilon$. Hence, the system is always subcritical for any degree of non-conservation. The avalanche size distribution in particular has a cutoff size that scales as $s_{\text{cutoff}} \sim 2\epsilon^{-2}$, which diverges to $\infty$ as $\epsilon \to 0$.

In the model we propose, the sandpile achieves criticality for $\epsilon \in [0, \frac{1}{2}]$, contrary to the conclusion of [28]. Outward dissipation of grains due to violation of the conservation law is compensated by an internal background activity, which drives the system to self-organise and maintain at a critical state, as will be described in section 3.

3. Non-conservative critical branching model

3.1. Motivations

Open systems far from equilibrium are not constrained by conservation of energy. Exposure to the environment can influence their design that allows them to operate amidst energy losses. In particular, biological systems may have evolved towards designs, such as dynamical motifs in dissipative biological networks [29, 30], that enable them to maintain biocomplexity.

Recently it has been observed that neocortical networks exhibit neuronal avalanches [31], much like the ones observed in sandpile models. The size and duration of these avalanches also obey power-law trends that are consistent with those derived for mean-field critical branching processes. These neuronal networks self-organize to a critical state albeit the propagation of action potentials from one neuron to the next is inherently non-conservative [32]. It is yet unclear what underlies the maintenance of the critical state in these biological systems. Exploration of mechanisms that may be responsible for the experimentally observed criticality of neuronal avalanches is an important step to understanding information processing and memory storage of the neocortex inside animal brains.

Animal groups also exemplify systems that are non-conservative because the behaviour and decisions of animals are usually ‘self-driven’ [33]. In animal systems, population dynamics is closely tied with social grouping behaviour through the paradigm which asserts that group size affects reproductive behaviour in animals. A population ecology theory has been put forward by Sutherland [34] which states that individual (grouping) behaviour of animals ultimately influences the temporal fluctuations in the population. This idea is supported by a recent study
in which the role played by social grouping behaviour on the population dynamics of Serengeti lions has been explored [35]. The authors have attributed the ‘saltatory’ changes (sudden leaps to new equilibrium values) of the lion population to stochastic group formation and recruitment. The ‘saltatory’ population dynamics tends to support a ‘sandpile avalanche’ picture of animal grouping.

3.2. Framework

Inspired by biocomplexity, our model deviates from the original sandpile formulation in that grains can be spontaneously created or annihilated in ‘storage’ sites. This framework takes on a more dynamical ‘sandpile’ system, for which sites are interpreted as excitable agents. Energy assumes the form of a stimulus—for instance, an action potential in the case of neuronal networks or an environmental trigger in the case of animal systems—that is stored and integrated by an agent. The build-up of stored stimuli inside an agent ultimately induces a response that consequently dissipates the stimulus through neighbouring agents or directly towards the environment. Stimulus propagation corresponds to the avalanches or ‘relaxation events’ in the sandpile picture.

In accordance with studies of excitable media [36, 37], each agent in the system may be in any of three states: ‘quiescent’ (state 1), ‘excited’ (state 2) and ‘refractory’ (state 0). By storage and integration of stimulus, a refractory agent turns quiescent and a quiescent agent becomes excited. An excited agent stores enough stimulus to exceed its threshold and fires a response in order to relax back to a quiescent or a refractory state. The response of the excited agent may initiate a train of subsequent excitations of other quiescent agents. When this happens, an avalanche occurs. What is not defined in the framework of ordinary sandpile models is the possibility that apart from excitation within an avalanche, a quiescent agent can spontaneously become refractory and vice versa. This independent process is what we consider as ‘background activity.’

3.3. Critical SOBP that violates a conservation law

A total of \( N = 2^{n+1} - 1 \) excitable agents composes the population, where \( n \) corresponds to the maximum number of generations of excitation allowed in one single avalanche—the boundary condition. The model has no explicit dependence on spatial dimensions, which makes it suitable to describe distributed networks, as well as socially interacting systems made up of components that are constantly in motion such as animal groups. The mean-field nature of the model also does not require a physical boundary. Fish schools, for instance, traverse a vast oceanic space. The population dynamically reconfigures the landscape of agent states in the absence of an avalanche. A quiescent agent turns refractory with a probability \( \lambda \), whereas a refractory agent becomes quiescent with a probability \( \eta \). The dynamic reconfiguration takes place on the same timescale as the flux of stimulus from the environment. The density \( q \) of quiescent agents in the population at a particular time also corresponds to the probability that a stimulus from the environment initiates excitation, because only quiescent agents get excited. Once an excited agent emerges, an avalanche ensues. The excited agent relaxes by dissipating its stored stimulus to other agents in the population. The avalanche occurs much faster compared to the reconfiguration process and the flux of stimulus from the environment. This timescale separation is indeed a key element in sandpile models to attain criticality [38].
Table 1. Transition rules of the non-conservative branching model with corresponding transition probabilities. The central digits of the avalanche rules correspond to the excited agent and the flanking digits are the two random neighbours. The sum of transition probabilities for the avalanche and non-conservation rules is \( q \), which is the probability that an agent had been excited to initiate the avalanche.

| Process | Rule | Transition probability |
|---------|------|------------------------|
| Background activity | \( 1 \rightarrow 0 \) | \( \lambda q \) |
| | \( 0 \rightarrow 1 \) | \( \eta(1 - q) \) |
| Avalanche (branching process) | \( 121 \rightarrow 202 \) | \( \alpha q^3 \) |
| | \( 021 \rightarrow 102 \) | \( 2\alpha q^2(1 - q) \) |
| | \( 020 \rightarrow 101 \) | \( \alpha q(1 - q)^2 \) |
| | \( 121 \rightarrow 112 \) | \( \beta q^3 \) |
| | \( 021 \rightarrow 012 \) | \( 2\beta q^2(1 - q) \) |
| | \( 020 \rightarrow 011 \) | \( \beta q(1 - q)^2 \) |
| Non-conservation (dissipation/absorption) | \( 2 \rightarrow 0 \) | \( \epsilon q = (1 - \alpha - \beta)q \) |

An excited agent randomly stimulates at most two other agents in the population. With a probability \( \alpha \) the excited agent becomes refractory by transferring 2 units of stimuli to two random neighbours. With a probability \( \beta \) the excited agent becomes quiescent by dissipating only 1 unit of stimulus to one random neighbour. By incorporating a probability \( \epsilon = 1 - \alpha - \beta \) that an excited agent entirely relaxes to a refractory state by outwardly dissipating (or inwardly absorbing) 2 units of stimuli without subsequently stimulating other agents, the transfer rule becomes non-conservative. The conservation law is violated for \( \epsilon > 0 \).

The non-conservative transfer rule is repeated until no more excited agents remain—when the population has entirely relaxed. There is however a limit \( n \) to the number of transfer generations that take place during an avalanche. At the \( n \)th generation of transfer, any remaining excited agents dissipate (or absorb) stimuli. The processes described are summarized in table 1 as a list of transition rules.

By taking \( q \) as a continuous dynamical variable and using table 1, the density of quiescent agents satisfies the stochastic dynamical equation

\[
\frac{dq}{dt} = (1 - q)\eta - q\lambda + A(q; \alpha, \beta) + \frac{\xi(q)}{N}.
\]  

The noise term \( \xi/N \) arises from the model’s stochasticity. It takes account of fluctuations around average values assumed to hold in the mean-field calculations and appropriately vanishes in the limit of large \( N \). The term \( A(q; \alpha, \beta) \) represents the effect of the avalanche on the density \( q \). Following closely [28], this avalanche term is

\[
A = \frac{1}{N} \left\{ 1 - ((2\alpha + \beta)q)^n - \frac{\epsilon q}{1 - (1 - \epsilon)q} \left[ 1 + \frac{1 - ((2\alpha + \beta)q)^{n+1}}{1 - (2\alpha + \beta)q} - (2((2\alpha + \beta)q)^n) \right] \right\}.
\]  

The first term inside the curly brackets of (2) represents the one unit of external stimulus received by a quiescent agent, consequently becoming an excited agent. The second term represents the
average amount of stimuli dissipated or absorbed by agents stimulated at the \( n \)th generation. The third term represents the average quantity of stimuli lost due to non-conservation that occurs with probability \( \epsilon = 1 - \alpha - \beta \).

In order to reduce the number of parameters in (1), a relation is defined such that

\[
\frac{\lambda}{\eta} = 2\alpha + \beta - 1,
\]

which effectively couples the background activity to the avalanche (branching process). Equation (3) is a phenomenological assumption whose underlying physics can be interpreted for a particular system under scrutiny. In the case of cortical networks for instance, (3) is related to the stochastic effects of excitatory and inhibitory post-synaptic potentials on a neuron’s membrane potential and this is explored with more detail in a subsequent work. The assumption of (3) also parallels the work of Pruessner and Jensen [39], which is derived from the FF model [14] and the Zhang model [22].

The number of parameters of (1) can further be reduced by using the definition \( \epsilon = 1 - \alpha - \beta \) and then taking \( \beta = 0 \) without loss of generality. Effectively, only two parameters determine the dynamic behaviour of the model, namely \( \eta \) and \( \epsilon \). Equation (3) is defined only for \( 0 \leq \lambda/\eta \leq 1 \). For \( \lambda/\eta > 1 \), the number of quiescent agents gets depleted in time (\( q \to 0 \)), hence, criticality cannot be sustained. Moreover, the model can only show criticality if \( \epsilon \in [0, \frac{1}{2}] \) because the critical value of the density \( q \) is greater than 1 if \( \epsilon > \frac{1}{2} \) [28], so that the system would always be sub-critical.

In order to show that the non-conservative branching model exhibits SOC, the critical state must be an attractive fixed point in the order parameter space [19], as will be discussed in section 4.

3.4. Analytic results

From table 1, a branching probability \( \pi_k \) can be defined as

\[
\pi_k = \alpha q \delta_{k,2} + \beta q \delta_{k,1} + [1 - (1 - \epsilon)q] \delta_{k,0},
\]

where \( k \) denotes the number of agents stimulated by an excited agent: \( k = 2 \) with probability \( \alpha q \), \( k = 1 \) with probability \( \beta q \), and \( k = 0 \) with probability \( [1 - (1 - \epsilon)q] \), which is an accrued effect of non-conservation and the case wherein a refractory agent, rather than a quiescent agent, is charged by external stimulation. The branching process is critical if the branching parameter \( \sigma = \sum_k k \pi_k = 1 \) [26], and consequently the critical value of \( q \) is \( q_c = (2\alpha + \beta)^{-1} \). From (4) the generating function for the avalanche size distribution is derived

\[
F(\omega) = \frac{1 - b\omega - \sqrt{1 - 2b\omega + a\omega^2}}{2\alpha q\omega},
\]

where \( \omega \) is a complex variable, \( a = \beta^2 q^2 - 4\alpha q [1 - (1 - \epsilon)q] \) and \( b = \beta q \). The avalanche size distribution \( P(s) \) is related, by definition, to the generating function in series form

\[
F(\omega) = \sum_{s=1}^{\infty} P(s) \omega^s.
\]
Expansion of (5) around the singularity \( \omega = 0 \) and its subsequent comparison with (6) gives the solution for \( P(s) \). A closed form for the solution is tedious to calculate in general, hence a recurrence relation for the avalanche size distribution is deduced

\[
P(s) = \frac{(2s - 1)bP(s - 1) - (s - 2)aP(s - 2)}{s + 1},
\]

subject to the following end conditions: \( P(0) = 0 \) and \( P(1) = (b^2 - a)/4a \). Equation (7) describes a power-law with exponent \( \tau_s = 3/2 \) for large \( s \) if the relation \( a = 2b - 1 \) is satisfied. This relation can be written as a function

\[
Q(q) = \beta^2 q^2 - 4\alpha q [1 - (1 - \epsilon)q] - 2\beta q + 1,
\]

the root of which is \( q = q_c \).

For completeness, the non-conservative branching model should properly reduce to the conservative SOBP case. This can be shown from (3) by letting \( \lambda, \eta \rightarrow 0 \) simultaneously and rewriting the right-hand side in terms of \( q_c \). Consequently, this leads to the condition that \( 1 - q_c \rightarrow q_c \), which implies \( q_c \rightarrow \frac{1}{2} \). This is exactly what the conservative SOBP predicts (see section 2).

4. Results and discussion

The stationary properties of the model are examined by means of a well-established geometrical theory of fixed points [40]. Nonlinear differential equations such as (1) may be analysed graphically in terms of vector fields. In this framework, \( dq/dt \) is interpreted as a ‘velocity vector’ at each possible value of \( q \). This is convenient to illustrate by plotting (1) versus \( q \) as shown in figure 1, which is a type of plot known as the ‘phase portrait’ [40]. The fixed point \( q^* \) is the value of \( q \) at which \( dq/dt = 0 \). The trajectory of the vector around the neighbourhood of this fixed point is directed to the right where \( dq/dt > 0 \) and to the left where \( dq/dt < 0 \). This means that if \( dq/dt \) is increasing around its neighbourhood the fixed point is said to be repulsive or unstable. Any degree of perturbation can dislodge the state of the system away from a repulsive fixed point. On the other hand, if \( dq/dt \) is decreasing around its neighbourhood the fixed point is said to be attractive or stable. Linearization of (1) also gives

\[
\lim_{q \rightarrow q^*} \frac{\partial}{\partial q} \frac{dq}{dt} < 0.
\]

These observations imply that after perturbation the state of the system would be attracted back to the fixed point. In the language of nonlinear dynamics, a stable fixed point is a ‘dynamical attractor’ of the system. Dynamical attractors represent steady-state or stationary solutions of dynamical equations.

Figure 1 shows the phase portraits of a non-conservative system with \( \epsilon = 0.25 \) and \( \eta = 0.03125 \) for different sizes \( N = 2^{n+1} - 1 \). The values of \( q \) where \( dq/dt = 0 \) are the fixed points \( q^* \). These fixed points are attractive because the curves are monotonically decreasing. Also illustrated in figure 1 is the function \( Q(q) \) defined in (8) which appears as a parabola. It has a unique root that corresponds to the value \( q_c \) for which the branching process is critical. For \( n = 4 \) and 8, \( q^* < q_c \), which implies that the stationary state of the non-conservative system...
Figure 1. Phase portrait of a non-conservative system with $\epsilon = 0.25$ and $\eta = 0.03125$ for different values of $n$. The root of $dq/dt$ corresponds to the fixed point value $q^*$ of $q$. The solid (red) curve is the function $Q(q)$ defined in (8) with root at the critical point $q_c = 2/3$. For $n \geq 16$, $q^* = q_c$, which indicates that the non-conservative system evolves towards its critical state by self-organization.

is sub-critical. For $n \to \infty$, $q^* = q_c$ but at $n = 16$, the fixed point $q^*$ already coincides with the critical point $q_c$. This implies that the non-conservative system self-organizes towards a critical state even for a finite system. The rapid approach of $q^*$ towards $q_c$ from $n = 8$ to $n = 16$ and the absence of any perceptible difference between $q^*$ and $q_c$ from $n = 16$ to $n \to \infty$ is suggestive of a phase transition.

Indeed, as shown in figure 2 a phase transition is apparent. Figure 2 plots $q^*$ against the quantity $\eta N$ for two non-conservative systems with $\epsilon = 0.25$ and $\epsilon = 0.45$ at different values of $n$. The data points collapse along the same curve for each value of $\epsilon$, which indicates universal behaviour in the variation of $q^*$ with $\eta N$. A vertical line separates the two phases: sub-critical phase ($q^* < q_c$) and critical phase ($q^* = q_c$). Non-conservative systems are considered to be at the critical phase for $\eta N \sim 10^3$. Thus, the product of the probability that refractory agents become quiescent $\eta$ and the system size $N$ serves as an indicator of SOC behaviour in non-conservative systems. As expected, the critical behaviour for an infinite system occurs for virtually any value of $\eta$. However, as $\eta \to 0$, where $q^* \to \frac{1}{2}$, the non-conservative system behaves sub-critically. This is in accordance with the conclusions from a study of the non-conservative SOBP model [28]. The phase transition essentially shows that neither $\epsilon$ nor $\eta$ are relevant control parameters of critical behaviour if the system is large enough. This is in stark contrast with FF models, which necessitate the fine-tuning of control parameters even for an infinite system in order to display critical behaviour [19]. Furthermore, FF models become critical in the imposed absence of a conservation law. On the other hand, the non-conservative branching model presented here displays SOC in the presence of violation of a conservation law.

Figure 3 illustrates the steady-state distributions $P(s)$ and $P(T)$ of avalanche sizes and lifetimes, respectively, of a non-conservative system with $\epsilon = 0.2$, for two different boundary
Figure 2. The fixed point value $q^*$ for two degrees of non-conservation $\epsilon = 0.25$ (open polygons) and $\epsilon = 0.45$ (filled polygons), and corresponding critical values, $q_c = 0.667$ and $q_c = 0.909$, respectively. Data points for $q^*$ versus $\eta N$, corresponding to different values of $n$, collapse to the same curve. A transition occurs between a sub-critical phase ($q^* < q_c$) and a critical phase ($q^* = q_c$). The phases are separated by a solid (black) vertical line. Starting at $\eta N \sim 10^3$ the non-conservative system is considered to be in the critical phase.

sizes: $n = 16$ and $n = 183$. The distributions corresponding to $n = 183$ are offset for clarity. $P(s)$ is a power-law spanning roughly three orders of magnitude with exponent $\tau = 3/2$ for $n = 183$, which unequivocally demonstrates the criticality of the model despite non-conservation. The fat exponential tail of $P(s)$ is merely an artifact of the imposed finiteness of the system (both in size and duration of observation), appropriately vanishing in the limit $n \to \infty$ [27]. The inset graph in figure 3 is the distribution $P(T)$ of avalanche lifetime $T$, which is the number of stimulation generations that take place before the avalanche dies out. The distribution also obeys a power-law with exponent $\tau_T = 2$, in agreement with previous mean-field results [27, 28].

Therefore, non-conservative systems do display SOC behaviour for a wide range of parameter values: $\epsilon \in [0, \frac{1}{2}]$ and $\eta > 0$. This is different from previous investigations of SOC in non-conservative systems, which rather concluded SOC behaviour in non-conservative systems to occur only for limiting values of the parameters [14], or for a narrow range of parameters [12]. Furthermore, the proposed background activity in our non-conservative critical branching model seems to be a natural element in biological systems that display complexity. In the following section, we illustrate the enhancement of the predictive ability of SOC theory for biocomplexity by emulating experimental results for neuronal avalanches in sliced cortical networks [31], and for group size distributions of animals in motion such as free-swimming tuna [41] and red deers in a forest reserve in Poland [42].
4.1. Neuronal avalanches in cortical networks

Living cortical networks have recently been shown to display SOC behaviour. Beggs and Plenz [31] experimentally demonstrated that the propagation of spontaneous activity in the form of local field potentials (LFPs) in slices of rat neocortex occurs in the form of ‘neuronal avalanches.’ The size and lifetime distribution of these avalanches obey power-laws with exponents \( \tau_S = 3/2 \) and \( \tau_T = 2 \), respectively. These are unsurprisingly consistent with mean-field values because the authors have observed that the propagation of LFPs does not occur in a spatially contiguous manner [31]. This implies that each neuron can be thought to have random neighbours. However, in contrast to sandpile models, which are stochastic, neuronal avalanches happen in repeating spatio-temporal patterns that the authors suggest as a mechanism for information processing and memory storage [43].

To prove that the cortical system indeed behaves critically, the authors quantified the branching parameter as the ratio between the number of neurons that fire an LFP and the number of neurons that subsequently get stimulated by the LFP. The value of the branching ratio has been measured to be close to 1, which is the value that makes the branching process critical [26]. The authors assumed that the intensity of LFP measured during an avalanche is directly proportional to the number of neurons that synchronously fire the action potential. To measure LFP they used an array of 60 microelectrodes. The size of the avalanche corresponds to the number of microelectrodes that detect LFP. The power-law distribution of neuronal avalanche sizes is characterized by a cutoff size which increases as the number of microelectrodes in the array increases.

Figure 3. Typical avalanche size distribution \( P(s) \) of a non-conservative system with \( \epsilon = 0.2 \) and boundary sizes: \( n = 16 \) (○) and \( n = 183 \) (○). \( P(s) \) scales as a power-law with exponent \( \tau_S = 3/2 \). The scaling regime broadens when \( n \) is increased. The exponential fat tail is an artifact of finite \( n \). The inset graph illustrates the distribution \( P(T) \) of avalanche lifetimes \( T \), which is the number of stimulation generations before the avalanche dies out: \( n = 16 \) (■) and \( n = 183 \) (○). Power-law scaling of \( P(T) \) with exponent \( \tau_T = 2 \) also broadens by increasing \( n \).

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is increased. A phenomenological model has been proposed to emulate the size distribution of neuronal avalanches [44], but this model fails to elucidate synaptic mechanisms that bring about and sustain the branching process. Moreover, it remains unknown whether repeating activity patterns of \textit{in vivo} cortical networks are neuronal avalanches.

The propagation of LFP cannot be assumed to be conservative. Experimentally it has been observed that signal propagation between cortical neurons in the neocortex indeed violates a conservation law. The spike number—the number of peaks in the action potential—is not conserved during transmission [32]. Moreover, microelectrode recordings in synaptically connected pairs of neurons reveal the presence of synaptic transmission failures wherein action potentials from the pre-synaptic neuron do not trigger release events in the post-synaptic neuron [45]. But if transmission is non-conservative the signals would dramatically attenuate thereby rendering most output synapses inactive (refractory); the signal would consequently die out after a few transmission steps. The neuronal avalanche distribution would therefore exhibit a characteristic scale and thus the cortical network would be sub-critical. This scenario apparently disagrees with the results of Beggs and Plenz [31].

Recently it has been proposed that dynamic synapses may give rise to criticality of neuronal avalanches [46]. Dynamic synapses, through the combined effects of synaptic plasticity mechanisms of depression and facilitation [46], have been found to be important in keeping the critical balance between cortical excitation and inhibition to foster a stable state bordering inactivity and epileptiform activity [47]. The stability of the activity of \textit{in vivo} cortical neurons indicates that firing rates of both inhibitory and excitatory neurons are dynamically self-adjusted under sustained activation [45]. Anatomically, excitatory synapses dominate inhibitory ones in the neocortex [45]. A mean-field analysis has explored the significance of dynamic synapses in the synchronisation of a globally coupled network of integrate-and-fire neurons [48]. There is also evidence that synaptic background activity in the form of membrane potential fluctuations enhances the sub-threshold signal detection capability of cortical networks [49].

In the framework of our non-conservative model, the role of dynamic synapses and synaptic plasticity is played by the background activity. The spontaneous switching between refractory and quiescent states of neurons dynamically adjusts the levels of cortical excitation and inhibition. Figure 4 shows the size distribution of neuronal avalanches, with data taken from [44], and of a non-conservative system with $\epsilon = 0.25$ and $\eta N \approx 3670$. The non-conservative system comprises $N = 131\,071$ neurons with $\alpha = 0.5$ and $\beta = 0.25$. Refractory neurons spontaneously become quiescent with a probability $\eta = 0.025$. Because neuronal avalanche size is measured in terms of the number of microelectrodes that detect LFP [31], rescaling is done from LFP intensity (in $\mu$V) to the number of microelectrodes, such that each microelectrode resolves about $4 \, \mu$V of LFP. Thus, the avalanche sizes from the simulation of the model is rescaled by the same factor of $\frac{1}{4}$ to fit the data. Figure 4 also shows the steady-state density of quiescent neurons that corresponds to the critical value $q_c = 0.8$ (inset graph). This density value is consistent with the findings of Vogels and Abbott [32] that firing of active potentials due to stimulation occurs only $80\%$ of the time in cortical networks. At the critical state, the density $q$ hovers around $q_c$. In addition, the non-conservative model also fits the exponential tail of the neuronal avalanche size distribution. This exponential tail arises from the experiment because of the finite number of microelectrodes used to detect LFP. When the number of microelectrodes is increased, the exponential tail also moves to the right. This is also consistent with the feature of the avalanche size distributions generated by the model as $N$ is increased.
4.2. Group sizes of animals in motion

Animal groups can suitably be described by mean-field models because animals are constantly in motion with speeds that allow them to cover vast areas of territory. Mean-field models have been used to simulate collective behaviour of animals [33] such as fishes schooling in the ocean [41]. Groups of animals in motion can also be characterized as non-conservative systems because animal behaviour is ‘self-driven’ [33], which means that animals can decide to absorb stimuli that they receive from other animals, rather than respond to it. This mechanism of animal behaviour has been utilized in stochastic agent-based models of animal grouping based on behavioural mimicry [50, 51].

Data sets of group-size distributions are available for free-swimming tuna (Thunnus albacares, Katsuwonus pelamis and T. obesus) [41], and for red deer (Cervus elaphus) in a forest reserve in Poland [42]. The data sets are based on long-term sighting observations: 7 years (1976–1982) for tuna and 17 years (1986–2003) for red deer.

Mean-field description of free-swimming tuna is appropriate because of the considerable variance in the locations that tuna fish reach owing to swimming speeds in the order of 1 m s$^{-1}$ [41]. The total number of tuna observed is estimated to be around $N = 5488$ by integrating the fitting function used in [41] from 1 to $\infty$. In the non-conservative model we use $n = 11$ or a total of $N = 4095$ agents. It is assumed that individual fish move in a certain direction.
Figure 5. Size distribution of free-swimming tuna schools [41] (filled, black circles), and of a non-conservative system with $\epsilon = 0.15$ and $\eta N = 409.5$ taken after $2^{15}$ time steps (solid, blue curve). Also shown is the size distribution of avalanches from a SOBP model [28] (dashed, red curve), with the same value of $q_c = 0.952$ as the non-conservative system. Inset graph shows the evolution of $q$ with time exhibiting ‘saltatory’ fluctuations especially at the rising portion of the curve. The steady-state value of $q$ is less than $q_c$ (dashed, blue line), implying that the non-conservative system is sub-critical.

when they observe other fish doing the same action. When fish observe other fish, stimulus is transferred. But an individual fish can choose not to respond to the stimulus. Fish in a group are thus behaviourally synchronized due to transfer of group-forming stimulus from one fish to another. Thus, grouping dynamics of fish may be interpreted as an avalanche.

During the transfer of group-forming stimulus, a fish can subsequently stimulate other fish with a total probability of 0.85. Thus, the degree of non-conservation is $\epsilon = 0.15$. Refractory (inactive) fish spontaneously activate and become quiescent with a probability of $\eta = 0.1$. Hence, $\eta N = 409.5$, which suggests that the non-conservative system is in a sub-critical phase based on figure 2. The experimental data for fish school size distribution is plotted in figure 5. Avalanche size distribution of the non-conservative model is plotted as well and fits the data more satisfactorily compared to an equivalent SOBP model (figure 5: dashed, red curve). Also shown is the evolution of the density of quiescent fish with time (inset graph), displaying saltatory fluctuations especially on the rising portion of the graph. The density reaches a steady state value that is less than the critical value (figure 5: dashed, blue line), which confirms that the non-conservative system indeed self-organizes to a sub-critical state. This explains the remarkable exponential tail of the school size distribution. The sub-critical behaviour may simply be brought about by an insufficient number of fish in the population. The number of fish may dramatically have been reduced by an excessive catch.

The red deer (C. elaphus) has been studied for a span of 17 years from August 1986 to December 2003. Deer group sizes were observed for three seasons each year (autumn, winter and summer). The size distribution varies by season because of several factors such as snow
Figure 6. Cumulative size distribution of red deer groups observed in a forest reserve in Poland [42] (filled, black circles), and of a non-conservative system with $\epsilon = 0.25$ and $\eta N = 10.23$ taken after $2^{17}$ time steps (solid, blue curve). Shown as well is a cumulative size distribution of avalanches generated by a SOBP model [28] (dashed, red curve) with the same value of $q_c = 0.952$ as the non-conservative system. Inset graph depicts the evolution of $q$ with time. The steady state of $q$ is much less than $q_c$ (dashed, blue line), implying that the non-conservative system self-organizes to a sub-critical state.

Figure 6 illustrates the cumulative size distribution of red deer groups for all summer seasons from 1986 to 2003, and of a non-conservative model with $\epsilon = 0.25$. Group-forming stimulus is transferred from one deer to another with a total probability of 0.75. Refractory individuals spontaneously become quiescent at a rate $\eta = 0.01$ such that $\eta N = 10.23$. The inset graph of figure 6 depicts the evolution of the density $q$ of quiescent agents with time. The steady-state value of $q$ is much less than the critical value $q_c$, which implies that the non-conservative system self-organizes to a sub-critical state. Sub-criticality is evident in the significant exponential truncation of the deer group size distribution in the experimental data. Also plotted in figure 6 is the avalanche size distribution of an equivalent SOBP model with the same value of $q_c$. The sub-critical behaviour displayed by red deer grouping may be attributed to the high-rate of predation by wolves and the prevalence of hunting. These factors considerably reduce the red deer population in the forest park in Poland [42], thereby curtailing the chance of observing SOC.
The sub-critical behaviour of both tuna fish schools and red deer groups in terms of the size distribution of group sizes demonstrates that the violation of conservation laws in biological systems is the rule rather than the exception. Therefore an SOC model that works even for non-conservative systems is a crucial step in understanding mechanisms for which open, non-equilibrium systems are able to maintain themselves at the critical state and display complexity despite energy losses.

5. Summary and conclusion

SOC has been demonstrated to occur in mean-field sandpiles that violate a conservation law during dynamical transfer through a proposed non-conservative critical branching model. The critical state of a non-conservative system is possible when a background activity consisting of the spontaneous switching between refractory and quiescent agent states is coupled to the branching process. The model exhibits a transition from a sub-critical to a critical phase depending on the value of the product between the probability $\eta$ that refractory agents turn quiescent and the system size $N$. For a wide range of parameter values, $\epsilon \in [0, \frac{1}{2}]$ and $\eta > 0$, a non-conservative system with large enough size can exhibit SOC.

Energy dissipation in SOC is a fundamental issue because most real-world complex adaptive systems (such as the ecosystem or the neocortex) are not isolated—they constantly interact with their environment. Understanding real-world complex systems necessitates the accurate description of the role of energy dissipation in their dynamics. Our proposed background activity seems to be a natural feature in systems that exhibit biocomplexity.

The model has been used to explore the role of dynamic synapses and synaptic plasticity in maintaining cortical networks at the critical state, which has been suggested to be important to the brain’s ability to process information and store memory. The model has also been able to emulate the main features of the group size distributions of free-swimming tuna and red deer. An understanding of SOC in systems that violate conservation laws essentially enhances the predictive ability of SOC theory in the field of biocomplexity.

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