The organizing principles of neuronal avalanches: cell assemblies in the cortex?

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Neuronal avalanches are spatiotemporal patterns of neuronal activity that occur spontaneously in superficial layers of the mammalian cortex under various experimental conditions. These patterns reflect fast propagation of local synchrony, display a rich spatiotemporal diversity and recur over several hours. The statistical organization of pattern sizes is invariant to the choice of spatial scale, demonstrating that the functional linking of cortical sites into avalanches occurs on all spatial scales with a fractal organization. These features suggest an underlying network of neuronal interactions that balances diverse representations with predictable recurrence, similar to what has been theorized for cell assembly formation. We propose that avalanches reflect the transient formation of cell assemblies in the cortex and discuss various models that provide mechanistic insights into the underlying dynamics, suggesting that they arise in a critical regime.

Introduction

That memories, and indeed behaviors, are represented by the participation of distributed groups of neurons in a cell assembly [1,2] has been one of the most powerful and enduring ideas in neuroscience. The synchronization of neuronal activity observed during various cognitive and behavioral tasks has been proposed as one mechanism by which neuronal participation in a cell assembly might be identified [3,4]. Moreover, the propagation of synchrony in the form of 'synfire chains' [5] has been suggested as a theoretical construct for the dynamic selection of neuronal groups into cell assemblies [6,7]. However, the organization of the dynamics giving rise to cell assemblies has yet to be identified. If distributed patterns of synchronized neuronal activity are indeed the physical correlate of memories and behaviors [8,9], then cortical activity must produce these synchronized patterns in a dynamic regime that is highly flexible but yet enables a certain degree of predictability. Dynamics that give rise to cell assemblies would have to be capable of producing a rich diversity of patterns of various sizes, many of which must be stably reconstructed over time [10–14].

Here, we discuss recent findings on spontaneously arising synchronized activity patterns in superficial cortical layers – i.e. 'neuronal avalanches' [12,15,16], in the context of cell assembly formation. Although the definition of a 'cell assembly' has been associated with various mechanisms such as attractor neural networks, here we define a cell assembly as a group of neurons whose activity is transiently linked together by an active process intrinsic to the network. In addition, we define 'synchronized' simply as sufficiently temporally proximal so as to enable superposition in the extracellular field. We show that neuronal avalanches are attractive from a cell assembly perspective because of the large diversity of avalanche patterns found at many different scales, their stable recurrence in time with high precision and the interesting properties of their statistics that indicate rich internal dynamics with long-range correlations capable of complex outcomes. We further discuss how this form of activity could reflect a 'critical state' in the network, drawing from various models on complex systems dynamics.

Neuronal avalanches represent spatially irregular patterns of propagated synchrony

Neuronal avalanches are a previously unknown but robust form of synchronous activity in the cortex that was first measured in organotypic somatosensory cortex cultures from rat, grown on microelectrode arrays (MEA). The activity arose spontaneously after maturation of the cultures and depended on fast inhibition [15]. It was also found that neuronal avalanches could be induced in acute somatosensory and medial prefrontal cortex slices from adult rats with a combination of N-methyl-D-aspartate (NMDA) and dopamine or a dopamine D1 receptor agonist [15,16] (Figure 1a,b). In these experimental paradigms, the activity that was measured at each electrode was a local field potential (LFP). The MEA configuration used for these in vitro recordings was an 8 × 8 grid of electrodes, uniformly spaced at 200 μm, enabled measurements of nonoverlapping LFPs across ~2.6 mm² of cortex (Figure 1a). The LFP activity displayed frequent negative components which took the characteristic shape of a population spike: a sharp (10–50 ms) negative deflection often followed by a longer-lasting positive deflection, a feature largely restricted to the superficial layers of the cortex [16] (Figure 1a,b). The negative deflection of the LFP (nLFP) is of particular interest because, in vitro, where the thin tissue slice is submerged in grounded medium, it is likely
to represent the summation of local inward currents at high temporal resolution. Although the nLFP is composed of local synaptic inputs as well as spike activity, it nevertheless enables the occurrence and propagation of synchronized activity in a network to be easily monitored. By contrast, single-unit recordings, which capture only a fraction of the neurons participating in the nLFP, might be insufficient for this purpose [17].

Figure 1b shows an example of LFP activity recorded from an acute slice. Here, as in organotypic cortex cultures,
nLFPs appear to occur virtually simultaneously (i.e. within one to a few tens of milliseconds of one another) at various subsets of electrodes, separated by pauses. The fine temporal organization of these nLFPs, measured by the time of occurrence of their peaks (Figure 1d), reveals often disjointed patterns that are not confined in their spatial path and are therefore distinct from wave-like activity [12,15,16]. They also do not show any obvious temporal structure, such as an oscillation. How does one decide whether multiple nLFPs in the network belong to the same structure, such as an oscillation. How does one decide by what criteria they should be grouped? Cross-correlograms demonstrate that temporally proximal event, and by what criteria they should be grouped? Cross-correlograms demonstrate that temporally proximal event, and by what criteria they should be grouped?

Avalanches form highly diverse patterns on all spatial scales

To assess the diversity of neuronal avalanches, a simple measure would be the range of sizes of these avalanches, where size could be determined by the number of participating electrodes (i.e. cortex area) or the total sum of the nLFP peaks (Figure 1e). These sizes showed high diversity, characterized by a heavy-tail distribution, which, significantly, took on the form of a power law:

\[ P(s) \propto s^\alpha \]  

(Equation 1)

This equation states that the probability \( P \) of an avalanche size \( s \) is proportional to \( s \) to the power of a constant \( \alpha \), the power law exponent [15]. Significantly, this power law relationship describes the spatial rather than temporal organization of activity. Power laws have been found ubiquitously in the brain in the temporal organization of channel openings [22], the interval distributions (1/f) of transmitter release [23] and spike trains [24], as well as in the local amplitude fluctuations of the human electroencephalogram and magnetoencephalogram [25]. The relationship of these power laws to the power law in avalanche sizes that we describe here is as yet unclear. In the context of spatial organization, however, power laws have been associated with many complex systems, particularly those that involve highly interconnected systems and cascade behavior [20,26], and have several interesting implications.

Mathematically, the power law states that the relative occurrence of avalanches of different sizes \( s \) and \( k \cdot s \) (\( k = \) constant) is the same for every \( s \):

\[ \frac{P(k \cdot s)}{P(s)} = \left(\frac{ks}{s}\right)^\alpha = k^\alpha \]  

(Equation 2)

This scaling relationship is exemplified in Figure 2a by comparing the occurrences of events of size 2 versus size 4, to the number of occurrences of events of size 4 versus size 8, which in both cases is simply \( 2^\alpha \), a value independent of the size \( s \). This relationship, when viewed on a double-logarithmic scale, is characterized by a straight line with slope \( \alpha \) (Figure 2b), such that any size \( s \) and \( k \cdot s \) are always equidistant and therefore have a fixed relationship. This feature, called 'scale free' or 'scale invariant', is often associated with 'fractal' organization, where the relationship of pattern sizes to each other is apparent on every scale [27].

In neuronal avalanches, this fractal organization is shown by the robustness of the power law to various scaling operations. First, the power law characteristic of the distribution is robust to the choice of temporal scale – i.e. the value of \( \Delta t \) (Figure 3a). For a given interelectrode distance \( d \), relationship between the exponent and \( \Delta t \) was approximated as \( \alpha \propto \Delta t^{-0.16} \) (Figure 3b). When \( \Delta t \) was chosen as \( \Delta t_{avg} \), reflecting the average propagation time between pairwise active electrodes on the array, the power law exponent \( \alpha \) was \(-1.5\), regardless of the actual value of \( \Delta t_{avg} \) for each network, which varied from 2–6 ms.
Second, the power law and the value of its exponent $a = -1.5$ are robust to various choices in the spatial scale and spatial extent (Figure 3c,d). This was demonstrated by calculating the avalanche size distribution after systematically removing electrodes from the analysis so as to evaluate the dynamics arising in smaller and smaller areas of the cortex culture (Figure 3c) or at different interelectrode distances $d$ (Figure 3d). Another aspect of the scale invariance is revealed by the finding that activity initiated at every site has a similar probability of engaging other distant sites (Figure 3e). This previously unpublished analysis reveals that each spatial region (corresponding to the field of each electrode) initiated avalanches with sizes distributed according to the same power law (even though the frequency of initiations at individual sites varied).

A further implication of the power law concerns the maximal size of an event that is possible in the system. In theory, in an infinite system described by a power law with slope $a = 1.5$, large events are sufficiently probable, such that the system has no maximal size (i.e., tends to infinity), and a mean event size $E(s)$ does not exist:

$$E(s) = \int sP(s)ds = \int s \cdot s^{-1.5} ds$$

$$= \int s^{-0.5} ds = \int \frac{1}{s^{0.5}} ds \rightarrow \infty$$

(Equation 3)

Consequently, in a finite system such as the cortex, a power law with this exponent indicates that the underlying dynamics are only constrained by the size or physical borders of the system rather than by any intrinsic characteristic of the dynamics themselves. The implication is that activity originating at any site can potentially engage activity at any other site, demonstrating that every cortical site is correlated with every other cortical site over long periods of activity. This suggests that activation at any one site in the cortex, and, by implication, a particular input signal, has the potential to access information stored at any other site. The behavior can therefore be readily extrapolated to any scale, and the cut-off of the power law in any measurement (i.e., the maximal avalanche size where the probability drops to zero) reflects only how many

Figure 3. Avalanche sizes distribute according to a power law indicating scale invariant dynamics. (a) The distribution of avalanche sizes (where $s$ is expressed as number of electrodes) for different choices of $\Delta t$ (average from seven organotypic cortex cultures). The distribution follows a characteristic power law shape (straight line on a log–log scale) regardless of the choice of $\Delta t$, whereas the exponent $a$ varies systematically with $\Delta t$ for a given interelectrode distance $d$. (b) The power law exponent $a$ varies systematically with $\Delta t$ regardless of the size measure chosen (number of electrodes: square; summed nLFP amplitudes: circle). Choosing $\Delta t < \Delta t_{avg}$ results in a grouping of fewer nLFPs into avalanches, giving rise to a steeper slope on a log–log scale. By contrast, for $\Delta t > \Delta t_{avg}$, more nLFPs are combined, giving rise to a more shallow slope. At $\Delta t = \Delta t_{avg}$, $a = -1.5$ (gray; range for seven cultures). (c,d) The power law with exponent $a = -1.5$ is invariant to the choice of spatial scale. This is shown by its persistence when the analysis was restricted to smaller and smaller spatial extents of cortex ($c$; $\Delta t_{avg}$ constant) or when the interelectrode distance $d$ was increased by progressively eliminating electrodes from the analysis ($d$; $\Delta t_{avg}$ adjusted accordingly). In both cases, the measured range of the power law (where the distribution dropped off) was constrained only by the maximal number of electrodes in the analysis (average of seven cultures). (e) The avalanches initiated at each site distributed according to the same power law, with exponent $-1.5$ (shown in gray) indicating spatial homogeneity of the dynamics. Red and green indicate the two electrodes shown in those colors in the inset whereas black represents the average of all the electrodes. Data shown are of one representative organotypic culture. Panels a–d were adapted, with permission, from Ref. [15].
Electrodes were considered (Figure 3c,d). It is thus of interest to ask where the borders of these dynamics are drawn in the cortex. As mentioned earlier, this activity was found both in the medial prefrontal cortex and somatosensory cortex, and was largely restricted to the superficial layers. Furthermore, the avalanches frequently spanned the maximal cortical distance of the MEA of \(1.6 \text{ mm}\), which is generally beyond the width of a single cortical column. These features raise the exciting possibility that neuronal avalanches are a generalizable form of activity that arises in superficial layers and extends across multiple cortical columns to all regions of the cortex, giving rise to patterns that encompass distant regions of the cortex.

The engagement of even distant cortical regions in an avalanche is likely to be relatively fast. The distribution of avalanche lifetimes (i.e. the number of bins with width \(\Delta t_{\text{avg}}\) occupied by an avalanche) has been found to be a power law in the initial segment, with a slope of \(-2\), followed by a sharp exponential decay [15]. The steeper slope for lifetimes compared with avalanche sizes indicates that, as avalanches grow in size, their duration does not grow as much.

It is relevant to point out that epileptiform activity, which has also been shown to give rise to synchronized events that span large distances in the cortex [28], does not show a power law distribution in event sizes. Epileptiform bursts are thought to represent more uniform and stereotypical events [29,30]. Indeed, in the partially disinhibited slice model of epilepsy (i.e. reduced GABA\(_A\) inhibition), the power law was destroyed and the distribution of avalanche sizes became bimodal, indicating a relative preponderance of both small local events and large all-encompassing events [15,16,31].

**Avalanches can be stable and recur over hours**

The scale invariance of the avalanche dynamics, as described in Figures 2 and 3, indicates that diverse patterns arise at all scales, from every site in the superficial layers of the cortex. However, to be compatible with a cell assembly hypothesis, a proportion of these patterns must also be stable over time and be elicited by stimuli with some degree of reliability. The stimulus-dependent retrieval of particular patterns has yet to be assessed. However, the spontaneous retrieval (i.e. recurrence) of particular spatiotemporal avalanche patterns was tested in both

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**Figure 4.** Many avalanches are stable and recur over several hours. (a) Correlation matrix of 160 avalanches spanning four time bins (bin width, 4 ms) recorded over a 1 hour period in an organotypic cortex culture. Avalanches were sorted in order of similarity by a clustering algorithm, such that avalanches with high similarity or mutual correlation (blue) clustered along the diagonal. Self-similarity has been excluded from the matrix. Red regions along the diagonal indicate highly significant avalanche families. (b) Actual data (red circles) showed much higher correlations among avalanches, as compared with 50 sets of match-shuffled data (blue circles). (c) Examples of three pairs of avalanches that occurred several minutes apart, showing high spatiotemporal similarity. Avalanches are displayed as successive frames on the 8 × 8 MEA in time bins of width \(\Delta t_{\text{avg}}\). nLFPs are indicated by filled squares. nLFP amplitude is encoded using a gray scale. Largest amplitudes are indicated by black squares. Adapted, with permission, from Ref. [12].
organotypic cortex culture and in acute slice preparations [12,16]. This analysis showed that many complex spatio-temporal patterns did indeed recur with millisecond precision, often repeating even several hours apart. Figure 4a shows a comparison of correlations between 160 avalanches, spanning four time bins of length $\Delta t_{\text{avg}}$ that occurred over a time frame of one hour. The avalanches were sorted according to a clustering algorithm that progressively grouped avalanches with high similarity closer together, giving rise to ‘families’ of similar avalanches along the diagonal. To determine if the similarity over time of these avalanches was statistically significant, chance probabilities were constructed by a matched shuffling algorithm that destroyed the underlying spatial and temporal correlations but preserved the overall envelope of population activity, giving rise to an equivalent distribution of avalanche sizes. This procedure entailed shuffling individual nLFPs such that the temporal positions of active bins, as well as the overall rate of LFPs at each electrode, were preserved, whereas the number and position of active electrodes within individual time bins was altered. A comparison between the actual and shuffled data revealed that family size (i.e. the number of avalanches with high correlations grouped into a family by the clustering algorithm) was far larger than that found in random data [12,16] (Figure 4b). Some examples of pairs of highly similar avalanches from this dataset that occurred several minutes apart are shown in Figure 4c. Such self-similarity or pattern stability was found in the acute slice for up to an hour [16] – that is, as long as the activity was observed, and in organotypic cultures over much longer time frames of up to ten hours [12]. Thus, many avalanches represented spatiotemporal patterns to which the network returned repeatedly.

Avalanche formation and ‘criticality’

The unique implications of the power law distribution of avalanche size might be best appreciated by considering the mechanisms by which they have been found to arise in contrast to other distributions. The ubiquitous emergence of power law statistics in various complex systems (such as earthquakes, forest fires, biological taxa, personal income and the size of cities [26]) has led to a large body of theoretical work dedicated to understanding these mechanisms. Here, we discuss some of this work in the context of avalanche formation. An understanding of the dynamic process that leads to the formation of avalanches will be essential to uncover their role in the transmission and encoding of information.

When considering properties such as pattern diversity and the ability to create patterns across distant regions of the network, it is useful to first make the analogy to basic models in percolation theory [32], which study the conditions under which a giant or spanning cluster can form — that is, one that spans the maximal dimension of the system and therefore connects opposite sides. Typical percolation models are constructed on an $N \times N$ lattice and are defined by the probability $P$ of random site occupation (Figure 5). In these models, it is found that below a particular ‘critical’ probability of occupation or linkage $P_c$, the probability of the existence of a spanning cluster is 0 and the size of clusters (i.e. contiguously occupied or
connected lattice sites) are small. Above $P_c$, the probability of a spanning cluster is always greater than zero (Figure 5a,c). Importantly, if the probability of site occupation is exactly $P_c$, then the sizes of clusters that emerge on the lattice distribute according to a power law (Figure 5b). Thus, $P_c$ represents a ‘critical’ point where the possibility of a spanning cluster coexists with a high diversity of pattern sizes. Although this simple percolation model does not involve interactions between its elements, as in the cortex, it nevertheless demonstrates an important phenomenon: the occurrence of a ‘phase transition’ at a finely tuned critical probability that produces a large diversity of pattern sizes, as reflected by the power law, indicating the ability of distant regions to be contiguously linked. In the cortex, the emergence of the power law distribution of pattern sizes with slope $-1.5$ depends on an optimal concentration of dopamine [16] and on the balance of excitation and inhibition [15,16], suggesting that particular parameters must be appropriately ‘tuned’. One could therefore hypothesize that the cortex operates in a similar critical regime characterized by an effective probability of local excitability (i.e. $0 < P_c < 1$).

A class of models with greater parallels to the propagation seen in an avalanche is that of the branching process [33,34], which similarly produces a high diversity of spatio-temporal patterns, along with the ability to link distant sites. The principle of a branching process is illustrated in the schematic in Figure 6a. Each active site (blue) has the probability of successfully activating $n$ new sites with probability $P_c$, and a corresponding probability of failure of $1-P_c$. A realization of this process results in a chain of active sites over time. A key descriptor of any branching process with nonoverlapping generations is the branching parameter $s$, signifying the average ratio of descendents to ancestors that emerges in the system. The branching parameter can be most intuitively understood in the case of the population growth of a species [35]. Although some ancestors might produce numerous offspring and others none, for the population to remain in a steady state, on average there should be the same number of descendents as ancestors, giving rise to a $s = 1$. By contrast, a $s < 1$ will result in population decay, and a $s > 1$ in population growth. Importantly, many branching processes [33,34] will generate chain sizes that distribute according to a power law with an exponent $\alpha = -1.5$ at the critical value of $s = 1$ (Figure 6b).
group of active electrodes (the ancestors) in one time bin ‘gives rise’ to a group of descendents in the next generation or successive time bin. Because there might be more than one ancestor in a time bin, it is not possible to ascertain which descendent arose from which ancestor. Thus, the branching parameter for each individual avalanche $s_i$ was approximated as the ratio of the total descendents in time bin $t+1$ to the total ancestors in time bin $t$. $s_i$ was obtained in this manner for the first generation for every avalanche (Figure 6c) [15]. By this method, the branching parameter for the system was found to be close to 1 (0.90 ± 0.19 for all avalanches; 1.04 ± 0.19 for avalanches initiated by a single ancestor; Figure 6d), indicating that a local synchronous group on average triggers one other local synchronous group.

Several aspects of propagation in the cortex extend beyond the simplicity of these models. First, in their most simple form, branching processes assume that each successive generation is independent of previous generations. This is not likely to be the case in neuronal networks, where the activation of one site might alter its future participation in avalanche formation owing to refactoriness or short-term plasticity. Second, uniform branching probabilities across all sites do not favor the recurrence of particular chains [36] (Figure 6e). Thus, for preferred spatiotemporal patterns to emerge from a branching process, the probabilities must differ between branches or paths (Figure 6f). Such selectivity in the sequential engagement of sites could reflect the wide range of synaptic weights encountered at the single-neuron level.

Nonetheless, even if a branching process were to give rise to preferred spatial paths, a stochastic process might not be appropriate for the degree of predictability required for cortical function. A third class of models that can be fully deterministic in nature and provides an alternative solution is that of self-organized criticality (SOC) [20]. These models demonstrate a critical regime characterized by a power law distribution of event sizes that evolves out of the system dynamics rather than fine-tuning of a global critical parameter, such as the value of $P_o$ as discussed earlier. In SOC models, a feedback loop between a slow process that increases energy at lattice sites through external inputs, and a fast, threshold-dependent process that dissipates energy in the form of cascades or avalanches, pushes the system to a critical density of active sites, where a power law of avalanche sizes emerges [37]. These models can yield power law exponents of $−1.5$ in accordance with the findings on neuronal avalanches [38]. When applied to the cortex, one can think of the ‘density’ as the fraction of neurons that are active, the threshold of the fast process as the firing threshold, and the interactions between sites as the rules governing transmission [38–41]. In addition, several specific mechanisms have been identified that enable neuronal networks to reach and maintain the critical state. Changes in synaptic connectivity regulated by Hebbian covariance plasticity can stabilize a network of excitatory and inhibitory neurons in the critical regime [42]. Short-term plasticity can expand the critical regime in networks of nonleaky integrate-and-fire neurons [43]. Importantly, specific wiring rules, implemented either directly in the network design [44], by removing or depressing activated synapses that produce undesirable outputs (‘learning from mistakes’) [45], or arising from local homeostatic regulation of neuronal interactions [46], can achieve critical neuronal dynamics. Finally, electrically coupled neuronal networks can also show critical behavior [47]. Although these various models suggest how, in principle, criticality could be achieved in the brain, their relationship with respect to neuronal avalanches has yet to be determined.

### Other theoretical models of power law formation

Although we focus here on ‘critical state’ models, we point out the existence of other classes of models that also give rise to power law distributions of event sizes across a wide range of parameters. In these examples, the power laws arise in different contexts that are not analogous to the dynamical process of avalanche formation but might nonetheless have some conceptual underpinnings that are related.

One example is the Yule process [48], a class of models that has been used to explain various power law distributions of event sizes such as in the population sizes of cities and number of species in a genus [26]. Central to these processes is a growth rule of ‘rich get richer’ [49], where the probability of growth of an entity or object in the system is proportional to its size. Such a process is not readily applicable to dynamics because it is designed specifically for the growth of persistent entities (such as a city) and relies on an interdependence of these entities in each growth cycle. For example, in networks growing through a ‘preferential attachment’ rule [50], existing nodes compete with each other for newly formed links with incoming nodes. Importantly, Yule processes result in power laws for event size distributions with exponents steeper than $−2$, which is different from the exponent of $a = −1.5$ observed for neuronal avalanches. For a more detailed discussion of power laws as they might relate to cortical anatomy, see [51–53].

Another example is a class of models called highly optimized tolerance (HOT), which approaches the emergence of power law distributions uniquely from the perspective of system design [54,55]. HOT models are predominantly focused on the optimization of system outcome (such as the growth of an entity) and robustness to damage, arising, for example, from environmental challenges. At the optimum, the entity is often distributed according to a heavy tail function, such as a power law. These models require heterogeneous external initiations to create internal diversity, and result in systems that are not self-similar – that is, have design components that differ at different spatial scales. This is different from avalanche dynamics in the cortex, where similar power law behavior emerges from each site of initiation. However, conceptually, one could imagine that such design optimization might be at play in the cortex, influencing unexplored aspects of avalanche formation, such as the spatial selectivity of propagation.

### Summary and conclusions

We have described several features of the organizing principles of neuronal avalanches in the cortex that suggest...
that they reflect the dynamics underlying cells assembly formation. First, neuronal avalanches represent a rich diversity of spatiotemporal patterns with long-range spatial correlations, as implied by their power law organization. Second, these patterns are stable beyond chance and recur with millisecond precision over many hours. Third, they arise in the superficial layers of multiple functional regions and form across multiple cortical columns with a scale-invariant organization, suggesting that they represent a dynamical process that can be scaled to link distant regions. Finally, neuronal avalanches arise from the dynamics underlying the propagation of local synchrony. Thus, we suggest that neuronal avalanche activity in the cortex is a strong candidate for the representation of cell assemblies in the cortex, and warrants further investigation in this context. Questions of immediate interest include the significance of avalanches in information processing and their relevance in vivo, particularly with respect to cognitive outcome.

The various models described here provide insight into the origins of these dynamics. Several models have been proposed as explanations for the power laws that emerge in nature, of which critical state models are the most relevant to avalanche dynamics. For instance, the finding of a branching parameter of 1 hints at the possibility of a critically balanced branching process that has been shown to optimize at least some aspects of information transmission in feedforward networks [15,56]. Alternatively, SOC and related models provide examples of how the dynamics of a system could enable it to ‘evolve’ into a critical state, possibly positioning the system for maximal computational ability [57]. However, to get deeper insight into the process and its relevance to cell assembly formation, new models must account for additional features of neuronal avalanches that are not captured in these models, such as the stable recurrence of particular spatiotemporal patterns and the conditions under which these patterns can be retrieved.

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