

Criticality in Living Systems

Jairo M. Rojas

May 2021

Abstract

Various phenomena present in living systems, such as tissues, bacterial colonies, and neural networks, are the result of the interaction of a large number of components and, therefore, can be studied using statistical physics techniques. Thanks to new experimental technologies, it is now possible to study biological systems in detail and build statistical mechanics models directly from the data. Interestingly, the parameters for the models found are very close to a critical point. This essay describes experimental observations, simulations, and mathematical analyzes of biological systems where criticality has been found and discusses the presence of self-organizing criticality phenomena as a result of evolution.

1 Introduction

In biology the existence of different levels of organization is well known, ranging from cells, tissues, to ecosystems and the entire biosphere. At each level, we can observe different phenomena which are the result of the interaction of their lower-level components. For example, we have flocks of birds at the population level or extrusion of epithelial cells at the level of living tissues. These emerging phenomena have motivated scientists to use statistical physics techniques to explain systems from their active units, such as birds in flocks and cells in tissues. An active unit is an element that can obtain material and energy from its environment, and use them to move and interact with other units or the environment itself. This flux of energy and matter between the environment and the systems makes a living system state a state out of equilibrium. However, for living systems to be functional, these states must be located in special parameter regions, even under the changes in the environment, and therefore the biological system requires certain robustness in its non-equilibrium state.

Until a decade or so it was not possible to follow the behavior of each active unit present in biological systems, independently and simultaneously, due to their large habitual numbers and, on occasions, complex movements and interactions [1]. It is for this reason that recent experiments shed new light on the study of active matter. The detailed data allowed, without the need for a precise model, to calculate probabilistic distributions from raw data and build statistical mechanics models directly from them. From these studies, it was recognized that regardless of the level of organization, different statistical models for different biological phenomena shared something in common, which was that they were all relatively close to criticality [2] [3] [4]. The biological systems models give rise to a parameter space, which supports a phase diagram given by different qualitative behaviors. The set of parameters found in the experiments, however, were not established in one phase or another but were located very close to critical surfaces of the parameter space.

To explain the presence of this phenomena, an evolutionary discussion is required, “Nothing in biology makes sense except in the light of evolution” [5]. To be close to a critical point must represent an increase in fitness for the species, so these regions have been favored by evolution with the flow of time. For this reason using both, statistical mechanics and information theory, it is shown that adaptation to heterogeneous environments is more efficient when the system is close to criticality, since it provides a better balance between precision and flexibility.

In this essay, we begin by presenting how statistical models are built from raw data obtained in biological systems, and what phenomena are signs of criticality. Later, using these techniques, examples of criticality are presented at different levels of organization: bacterial clusters, ant colonies, flocks of birds, and networks of neurons. Finally, we present a discussion on the emergence of criticality the reason why it was favored by natural selection.

2 Thermodynamics in Biological Systems

To build a link between data obtained from biological systems and thermodynamics we need to build a model that reproduces key measurements, such as mean neural activity or mean velocity. For this reason, it is necessary to move to the probabilistic perspective of thermodynamics, which originated in statistical physics. Any thermodynamic observable in systems with a large number of degrees of freedom is captured by the Boltzmann distribution:

$$P_{\sigma} = \frac{1}{Z} \exp(-\beta \epsilon_{\sigma}) \quad (1)$$

where the probability to have a microstate σ is given by a normalized distribution that depends on the temperature and its energy ϵ_σ .

To be more specific, for a system with N degrees of freedom, where N is a large number, we identify the state of each i th element and place it in an array $\sigma = (\sigma_1, \sigma_2, \dots, \sigma_N)$. To build a model in the most general sense, without the need for a prior structure, from raw data with many degrees of freedom, we use the principle of maximum entropy [6]. This principle states that given an observed distribution $P_r(\sigma)$, the most appropriate probability distribution to model this data, is given by the distribution $P_m(\sigma)$ that maximizes the Shannon entropy:

$$S[P_m(\sigma)] = - \sum_{\sigma} P_m(\sigma) \log P_m(\sigma), \quad (2)$$

while at the same time, it satisfies our prior knowledge. This prior knowledge is usually given by moments of $P_r(\sigma)$ as the average of some observable:

$$\langle \mathcal{O}_a(\sigma) \rangle_m = \langle \mathcal{O}_a(\sigma) \rangle_r. \quad (3)$$

Finally, with the use of Lagrangian multipliers, we can write the explicit form of $P_m(\sigma)$ as:

$$P_m(\sigma) = \frac{1}{Z} \exp \left(\sum_a \beta_a \mathcal{O}_a(\sigma) \right), \quad (4)$$

with β_a the Lagrangian multipliers associated with the different modes \mathcal{O}_a .

Once the probability distribution is built, we are able to define the “energy” of the probability distribution as:

$$E(\sigma) = - \log P_m(\sigma). \quad (5)$$

Furthermore, it is common to identify different microstates that share energy in common, and for this, it is necessary to take into account the number of these states. For this reason, we define the microcanonical entropy $S(E)$

$$S(E) = \log \mathcal{N}(E) \quad (6)$$

where $\mathcal{N}(E)$ is the number of possible σ with energy less than E . For large N , the entropy becomes very peak at a value $E = E^*$, solution of:

$$\frac{dS(E)}{dE} = 0. \quad (7)$$

For this reason, for large N most of the microstates have the same energy E^* .

The special properties of the system, such as the interaction of the degrees of freedom, are encoded in $S(E)$ and can be studied by its form. For example, $S''(E) < 0$ is the footprint for first-order transitions. Also, $S''(E) = 0$ are footprints for second-order phase transitions where the variance of E diverge, phenomena associated with a long correlation length. We mention footprints because they are sufficient but not necessary conditions for the presence of criticality. In the study of biological systems, the knowledge of a critical behavior considerably reduces the space of microstates visited and can help in the understanding of the emergent phenomena.

It should be noted that the maximum entropy distribution is not necessarily the real model of biological systems, and it is also arbitrary in a sense since one chooses in an arbitrary way which statistical moments to use in the Lagrangian multipliers process. For this reason, some other statistical moments must be kept out of the model while it is being built. The reliability of the model will then be tested by predicting these moments.

3 Criticality in Biological Systems

3.1 Bacterial Clusters

Studies of colonies of *Bacillus subtilis* under controlled systems [7] have shown the emergence of dynamic clusters. Bacterial clusters are small organizations of bacteria, with a variable number of members, where the center of mass of each bacteria pair is separated, at most, by a fixed distance R and the direction of movement differs only up to a maximum value of α . The values of R and α are imposed, however, the results found were weakly dependent on them if one considers sound values.

In [7] the position, orientation and speed of each bacteria is measured at different times, and with this they analyze different clusters and their dynamics. Different clusters are identified as shown in Fig. 1, and the average velocity inside the I th cluster $\vec{V}_I = \langle \vec{v}_{i,I} \rangle_I$, speed $\vec{S}_I = \langle |\vec{v}_{i,I}| \rangle_I$, direction of movement $\vec{P}_I = \langle \frac{\vec{v}_{i,I}}{|\vec{v}_{i,I}|} \rangle_I$ and orientation $\vec{\Theta}_I = \langle \vec{\theta}_{i,I} \rangle_I$ along with their variations are calculated, where i labels different bacteria inside the cluster.

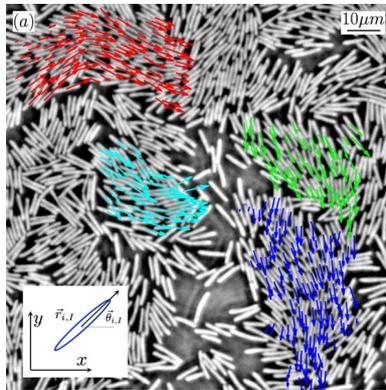


Figure 1: Identification of four different clusters overlaid on an experimental image. Here the white rods represent individual bacteria. Image obtained from [7].

Finally, a study of the spatial correlation of variations is performed. For example, correlation C^ϕ , of the average variation of Θ over clusters of the same size L , are shown in 2.

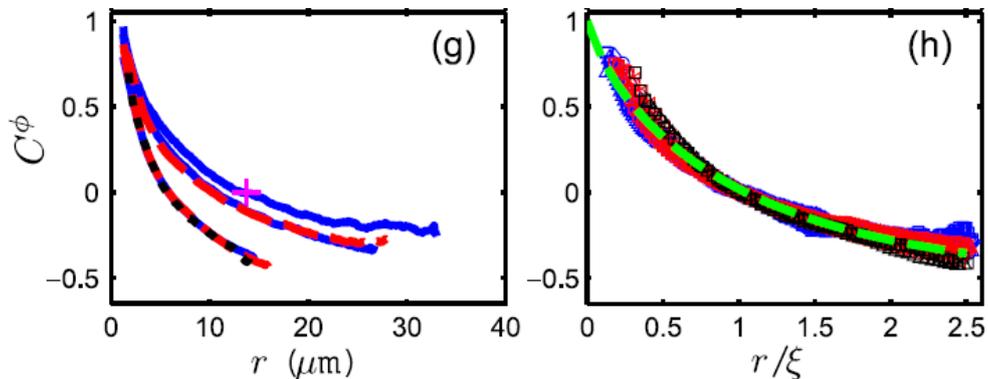


Figure 2: Correlation of the orientation variance as a function of the distance r , and the unitless parameter r/ξ . The image on the left presents three different curves that corresponds to three different cluster sizes, $L = 18.5\mu m, 36.5\mu m,$ and $54.5\mu m$. We observe that the correlations functions are practically identical once the distance r is divided by their respective ξ . Image obtained from [7].

A good measure of the correlation length ξ is given by the distance when C^ϕ touches zero. This distance changes as one deal with different cluster size L , however, as it is also shown in Fig. 2, up to ξ , the correlation behavior is similar. After computing the four average correlation functions, corresponding to the motion direction, velocity, speed, and orientation, it was found that all of them had a correlation length that follows $\xi(L) = 0.3L$. The fact that correlation in bacteria clusters are found to be scale-invariant, long-range order, and only dependent on the cluster size suggests the existence of criticality.

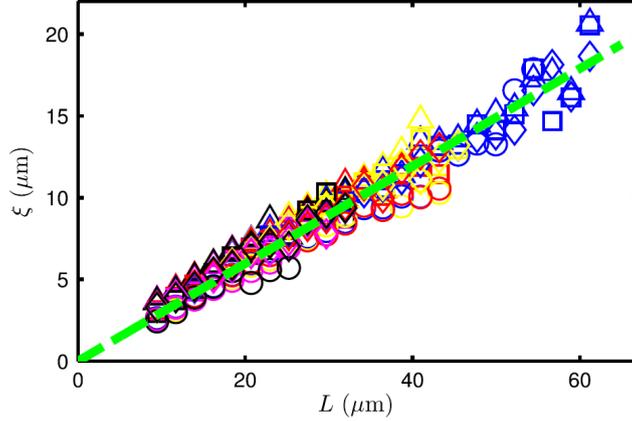


Figure 3: Correlation length ξ as a function of the cluster size L . Different colors represent different objects under study: direction, velocity, speed, and orientation variance, however, as can be observed, the correlation length is independent of the choice of source, and it only depends, linearly, on the cluster size L . Image obtained from [7].

3.2 Ant Colonies

In ecology studies, large-scale spatial patterns are important to understand species diversity, stability, etc. In [8], a study of ants *Azteca instabilis* in a completely homogeneous region of shady trees was performed. It was observed that these ants tend to form cluster colonies as observed in Fig. 4a. The separation of the colonies into clusters can be explained by the presence of natural enemies that generally have a density-dependent response. What was not as expected was a power relationship between the size and frequencies of these clusters, a signature of criticality, as we observe in Fig. 4b. What is more, by reproducing the population dynamics with cellular automatons, they found that there is a wide region around the measured parameters where this power law holds. The last observation indicated that, if there was criticality, it was a robust criticality.

3.3 Flocks of Birds

Flocks of birds are not as simple organizations as just thousands of birds that fly with the same average velocity. As expected for survival strategies, the flock should be a dynamic structure capable of responding to hazards that can only be observed from a certain region of the flock. In addition, the signal of this danger must spread over large distances and speed, producing a change in the average movement of individuals, far from the signal source.

This theory is corroborated by recent measurements of flocks of European starlings, *Sturnus vulgaris* in [9] [10]. The evolution in time of the 3D position and speed of each bird is recorded. The results showed that the flight is not only coordinated but even the fluctuations in the

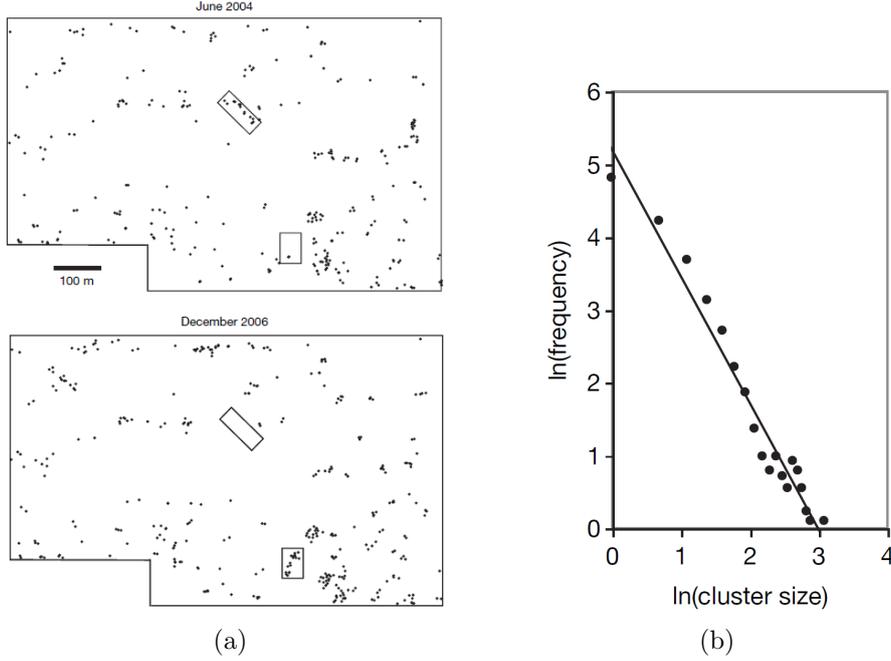


Figure 4: (a) Distribution of ant nests over 45 hectare at two different years. We can observe the total population form clusters. These clusters have dynamics, we can observe certain drift from 2004 to 2008, and also, the creation and annihilation of clusters as shown inside the little frames. (b) The appearance frequency of clusters and their size are related through a power function. It is less probable to find large clusters than smaller ones. Images obtained from [8].

average speed of each bird are strongly correlated. This correlation is present even in birds separated by very long distances with what appears to be a linear dependence on the flock size. As we expect birds to only interact locally, the obtainment of long-range correlations provides us with some clue for the presence of criticality, as a result of the desired maximization of the range of influence while minimizing each bird speed variation.

To elaborate our mathematical model, we first define the state of the flock by the flight speed of each bird $v_i = |\vec{v}_i|$ and its direction $\vec{s}_i = \vec{v}_i/v_i$. Then, the similarity between the motion of neighboring birds is given by the correlation:

$$Q_{\text{int}} = \frac{1}{2v_0^2 N} \sum_{i=1}^N \frac{1}{n_c} \sum_{j \in i \text{ NNs}} |\vec{v}_i - \vec{v}_j|^2 \quad (8)$$

where NNs means nearest neighbors, n_c is the number of nearest neighbors, and v_0 is just a normalization term for the correlation to be dimensionless. Another useful quantity to build the model is the average flock speed:

$$V = \frac{1}{N} \sum_{i=1}^N v_i, \quad (9)$$

and the speed variation:

$$\sigma^2 = \frac{1}{N} \sum_{i=1}^N (v_i - V)^2, \quad (10)$$

leading us to the following maximum entropy distribution:

$$P(\vec{v}_i) = \frac{1}{Z} \exp\left(-\frac{J}{4v_0^2} \sum_{i=1}^N \sum_{j \in i \text{ NNs}} |\vec{v}_i - \vec{v}_j|^2 + \frac{\mu}{v_0} \sum_{i=1}^N v_i - \frac{g}{2v_0^2} \sum_{i=1}^N v_i^2\right). \quad (11)$$

To verify the model, it was tested with correlations for arbitrary distances:

$$Q(r) = \frac{1}{V^2} \langle |\vec{v}_i - \vec{v}_j|^2 \rangle, \quad (12)$$

fluctuations over the mean direction:

$$C_{\text{dir}}(r) = \langle (\vec{s}_i - \vec{P}) \cdot (\vec{s}_j - \vec{P}) \rangle_{r_{ij}=r} \quad \text{where } \vec{P} = \frac{1}{N} \sum_{i=1}^N \vec{s}_i \quad (13)$$

and correlations between speed fluctuations

$$C_{\text{sp}}(r) = \langle (v_i - V) \cdot (v_j - V) \rangle_{r_{ij}=r}. \quad (14)$$

The results of this comparison are shown in Fig. 5.

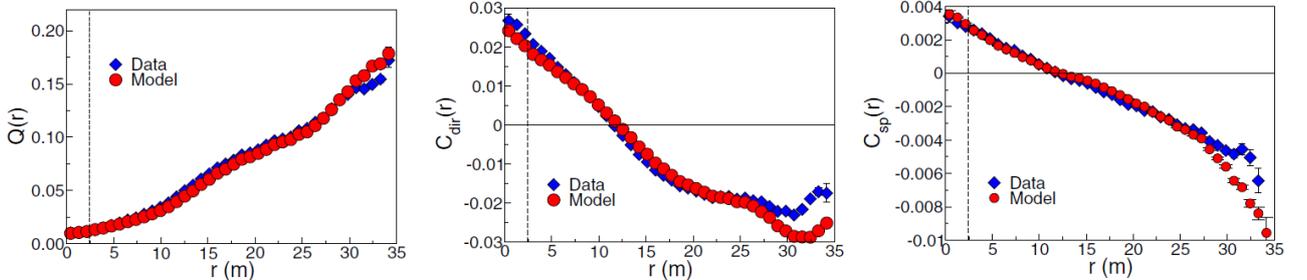


Figure 5: Measured correlation functions (blue) compared with the correlation functions predicted by the maximum entropy model (red). Images obtained from [3].

Criticality can be quantified by the value of g/Jn_c , and the value found in the model, which is $\approx 10^{-3}$, explains why we observe scale-free speed correlations. The fact that it is not exactly zero is because they work with finite sizes. In the model, we can see that the speed correlation is associated with the parameter g , and it suggests long-range correlations for small values of g , as we can see in Fig. 6. What is more, the model predicts that for large values of g , we find that the speed variance is small and that the correlation decreases rapidly with distance, on the other hand, for small g , both the speed variance and the correlation-length are maximized, as the last one tends to a linear function of distance. It is worth noting that both, the measured value of g , and the one predicted by the model, are in the last regime. Also, with an analysis similar to the study of bacteria in the previous subsection, where one relates the correlation length ξ to the position where the correlation becomes zero, they found that the correlation length is also linearly dependent on the flock size L . These two observations clues for the possible existence of criticality in the system.

It should be noted that the flock system is, for three main points, very different from the system of bacterial clusters [7]. The first point is the type of interactions they have, whereas birds have topological separation, bacteria interact through hydrodynamics, excluded volume, and intertwining flagella. Second, interactions between different flocks are rare, while bacteria clusters often interact. Lastly, flocks are 3D systems and bacterial clusters 2D. The similar results found are a clue that the emergence of criticality could be a general characteristic of collective motion.

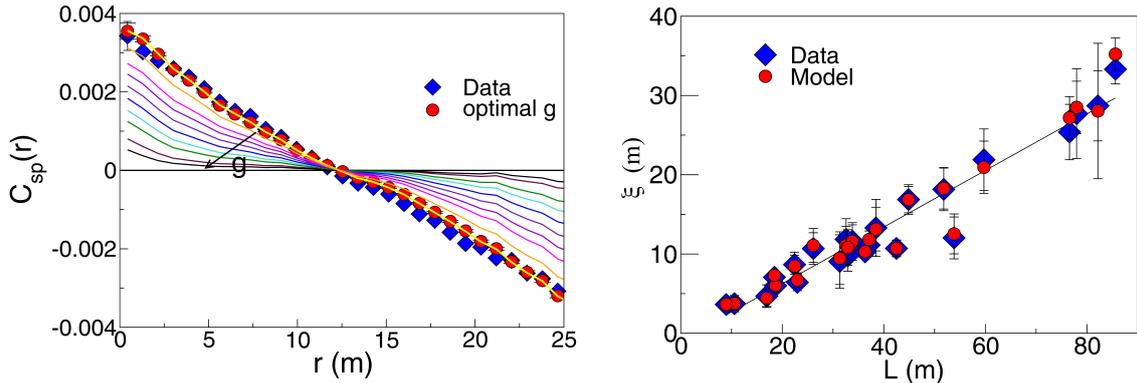


Figure 6: On the left, we observe the correlation function of the speed variance predicted by the maximum entropy model. Different colors represent different values of g , value that increases in the direction the arrow. We observe that for smaller values than the optimal g , which is the one that optimizes the model with the data, the correlation function collapses into the same yellow curve. On the right, we observe the linear dependence of the correlation length ξ on the flock size L . Images obtained from [3].

3.4 Network of Neurons

The activity in networks of neurons has been studied by measuring the on/off of states of each neuron as they are performing certain work [2]. From the data obtained, it has been possible to construct an entropy function for the activities, and when analyzing its energy dependence it was discovered that the model is located at a critical point.

To simultaneously monitor a large number of neurons, the experimental setup worked on the retina of a salamander while watching gray-scale movies of a swimming fish. In this way, the activity of 120 retinal ganglion cells was recorded in a span of 120 minutes. It is worth noting that the recorded cells belong to an area of the retina that covers a specific visual region, and therefore, their activity can be related to certain pixels of the video. The data obtained from this measure are the peak $\sigma_i = +1$ and the silence $\sigma_i = -1$ activity for each neuron i of the 120 neurons, as can be seen in Fig. 7.

With these data, they build a model using the maximum entropy method where the observables are the mean probability that each neuron generates a peak $\langle \sigma_i \rangle$, the correlation between spiking in pairs of neurons $\langle \sigma_i \sigma_j \rangle$, and the probability that K out of N neurons spike in a time interval $P(K)$:

$$P(\sigma) = \frac{1}{Z} e^{-E(\sigma)} \quad (15)$$

$$E(\sigma) = - \sum_{i=1}^N h_i \sigma_i - \frac{1}{2} \sum_{i,j=1}^N J_{ij} \sigma_i \sigma_j - V \left(\sum_{i=1}^N \sigma_i \right). \quad (16)$$

This model was tested with correlations between a triplet of neurons, and the probability of spiking of individual neurons given the global activity, the last one presented in Fig. 8.

Finally, it was found that the relationship of entropy and energy. This relation tends to a linear map as the value of N increases in the model, as one can observe in Fig. 9. For large N this relation implies $\frac{d^n S}{dE^n} = 0$ for all $n \geq 2$, signature of being located at a very unusual critical point.

In a system in equilibrium, $S''(E) = 0$ does represent the divergence of some specific heat, this is not exactly our case since we work in a system that is not in equilibrium. However,

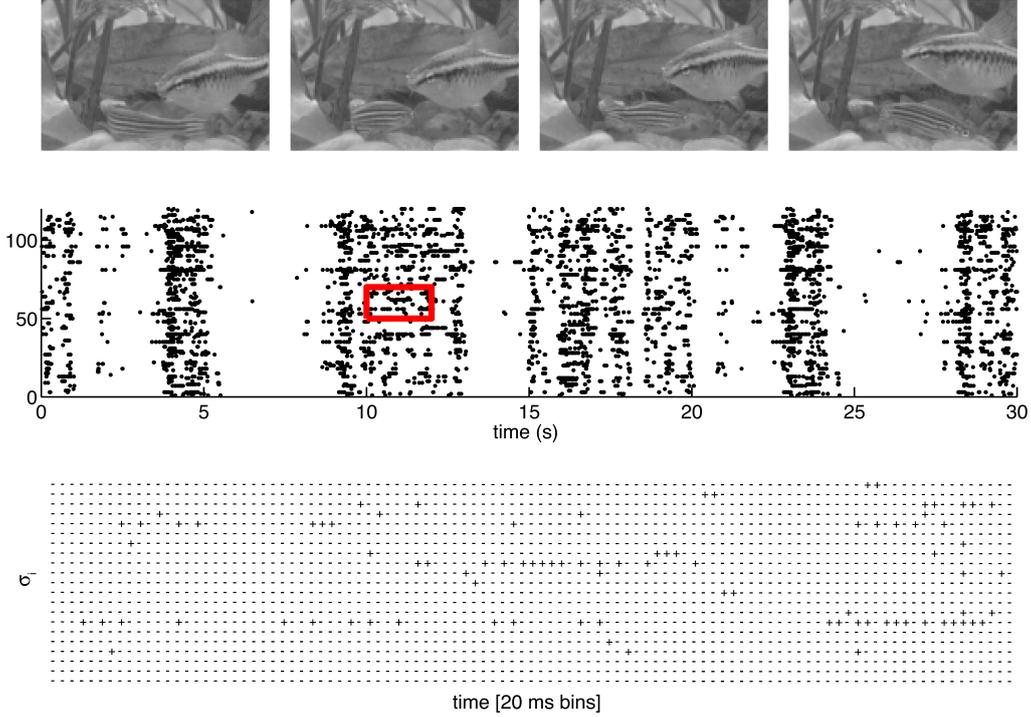


Figure 7: From top to bottom. Four frames of the movie presented to the salamander. The response of neurons to the the video, black points represent peak activity. Discretized neuronal activity using $\Delta\tau = 20\text{ms}$ bins, these is the data that will be used to compute probabilities. Image obtained from [11].

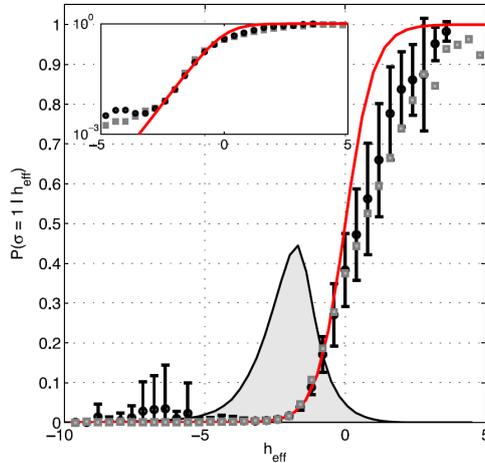


Figure 8: Spiking probability of individual neurons as a function of the effective activity that surrounds it. Measured activity are represented with black dots, while the model prediction is given by the red curve. Image obtained from [11].

since we work with thermodynamics, we can still calculate the specific heat in the usual way, defining an effective temperature T as a model parameter in:

$$P(\sigma, T) = \frac{1}{Z(T)} e^{-\frac{E(\sigma)}{T}} \quad (17)$$

Do note that the original maximum entropy model, that reflects nature, is given by $P(\sigma, 1)$.

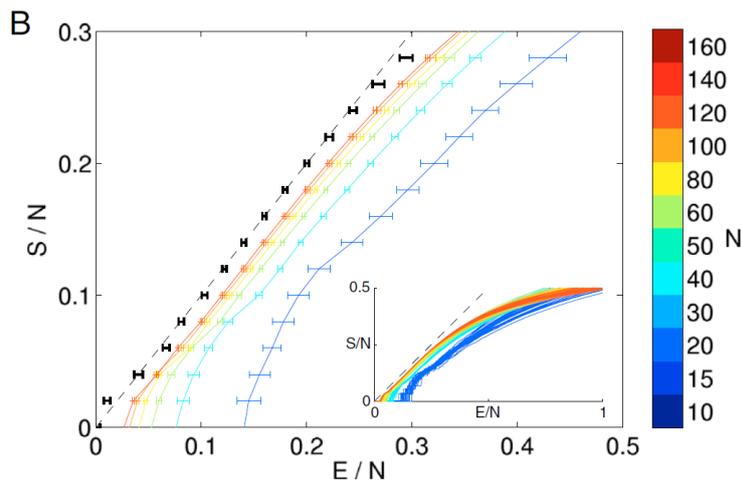


Figure 9: Entropy vs Energy computed from the maximal entropy model. Different colors represents results for different number of neurons in the model. Image obtained from [2].

The results of this process are shown in Fig. 10 and the presence of a peak at $T = 1$ is notorious, what is more, this peak increase its value as N goes to the thermodynamic limit.

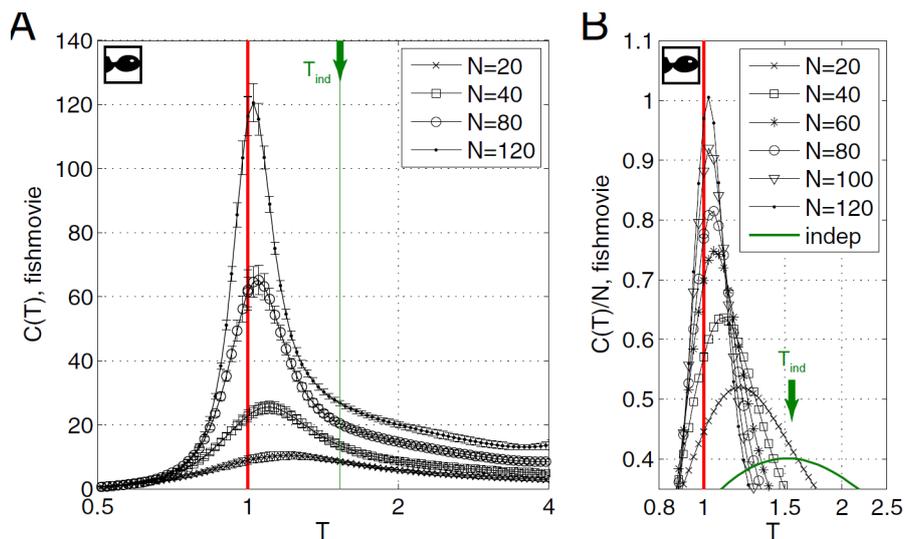


Figure 10: Heat capacity in maximum entropy models with one parameter T for different number of neurons N . The presence of a peak at $T = 1$, where the original model is located, indicates the presence of criticality in the system. Image obtained from [2].

4 Emergence of Criticality

To understand the emergence of criticality in biological systems, we must explore the evolutionary reason for its appearance or, in other words, answer the question of whether there is any advantage in fitness in the presence of critical phenomena. In [12] this evolutionary explanation is explored in the field of information theory. Living beings are in constant interaction with others and their environment, so natural selection optimizes the ways of perceiving and responding to these interactions. Obtaining and analyzing information is vital for the survival

of living beings. However, there is a problem if the information to analyze is too detailed, as it makes it difficult to interpret. Only essential features of the environment should produce internal changes of state, like tuning the active/non-active genes in a genetic regulatory network, and be the basis for future responses.

4.1 Model

In a large and unpredictable external environment, living beings can only internalize the world through probability distributions. In this way, a certain set of parameters $\alpha = (\alpha_1, \alpha_2, \dots)$ present in the real world, like the temperature, amount of nutrients around, or pH, can only be probabilistically represented in the internal state of the active unit. This state, without loss of generality, can be written as an array of binary values s_i : $s = (s_1, s_2, \dots, s_N)$, and can be interpreted, for example, as tuning the on/off states of different N genes in a genetic regulatory network.

In this way, defining $P_{\text{src}}(s|\alpha)$ as the probability that given an external environment α , the most convenient internal state to obtain is s , living things, as they cannot obtain or process all the information α , handle a reduced set of parameters β , producing a change of internal state with probability $P_{\text{int}}(s|\beta)$, as we can see in Fig. 11. Finally, to translate the environment to internal states as efficiently as possible, $P_{\text{int}}(s|\beta)$ should be as close as possible as $P_{\text{src}}(s|\alpha)$.

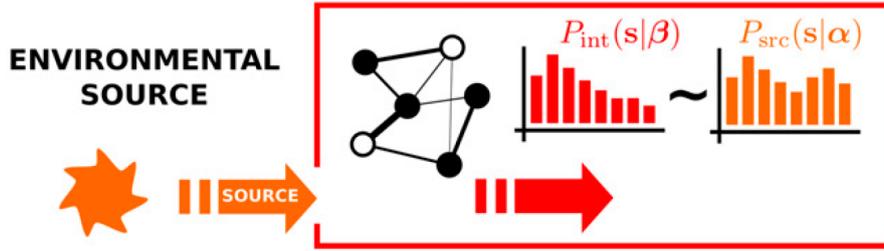


Figure 11: Schematic representation of a living being responding to the environment labeled by a set of parameters α . This set α can only be probabilistically gauged by the living being [6]. The most accurate change of internal state s given by the probability distribution $P_{\text{src}}(s|\alpha)$, can not be accessed by the living system, so they use a reduced set β that captures the most important features and work with an imperfect proxy $P_{\text{int}}(s|\beta)$. Image obtained from [6].

The closeness between probabilities distributions can be measured by the Kullback-Leibler (KL) divergence $D(\alpha|\beta)$:

$$D(\alpha|\beta) = \sum_s P_{\text{src}}(s|\alpha) \log \frac{P_{\text{src}}(s|\alpha)}{P_{\text{int}}(s|\beta)}. \quad (18)$$

which has its minimum value of zero when the two probability distributions are identical, and quantifies the loss of information when one works with $P_{\text{int}}(s|\beta)$ instead of $P_{\text{src}}(s|\alpha)$. So, if obtaining a better good internal representations of the world increases fitness, the goal of evolution should be to minimize the KL divergence, setting the optimal parameters β for it.

To find the most optimal set β we map the probability distribution to one that resembles statistical physics:

$$P(s|\gamma) = \frac{1}{Z(\gamma)} e^{-H(s|\gamma)}, \quad (19)$$

where H can be generally written as:

$$H(s|\gamma) = \gamma_\mu \phi^\mu(s) \quad (20)$$

for $\phi^\mu(s)$ observables of the variable s , similarly to the construction of maximum entropy models. Now, the minimization of the KL divergence is given by the set β that best reproduces the lowest moments of $P_{\text{src}}(s|\alpha)$:

$$\langle \phi_{\text{src}}^\mu \rangle_\alpha = \langle \phi_{\text{int}}^\mu \rangle_\beta. \quad (21)$$

Furthermore, to add different possible environments, a probability $\rho_{\text{src}}(\alpha)$ is also added, leading to a more general condition:

$$\langle \phi_{\text{int}}^\mu \rangle_\beta = \int d\alpha \rho_{\text{src}}(\alpha) \langle \phi_{\text{src}}^\mu \rangle_\alpha. \quad (22)$$

Now let's take a simple case when there is only one parameter α , $\langle \phi \rangle_\alpha$ has sigmoid shape with transition at $\alpha = \alpha_c$, and $\rho(\alpha)$ covers both phases. An optimal β will match $\langle \phi_{\text{src}}^\mu \rangle$ which is between the two asymptotic values of the sigmoid, so β , for heterogeneous environments, will end up close to α_c . In general, minimizing the KL divergence is analogous to maximizing the susceptibility $\chi = -\frac{d\langle \beta \rangle}{d\beta}$, and it results that generally, χ has a peak close to a critical region. The demonstration of these statements are out of the scope of the essay but a discussion of it can be found in [12] [13] [14]. This result can be interpreted as the following: it is advantageous to favor the region where a small parameter change provides the maximum variability for different complex sources, i.e. a region close to criticality, because then the most distinguishable outputs can be produced by the model. It offers the best possible trade-off between accuracy and flexibility, to accommodate both regular and noisy signals.

4.2 Simulation Results

To test this hypothesis, a computational evolutionary simulation is designed. Here, a population of M active members with one-dimensional parameters β is exposed to a variety of complex environments, that is, different values of α , with probability $\rho_{\text{src}}(\alpha)$, and is left to evolve using a genetic algorithm. In this algorithm, from time to time a pair of individuals is chosen and one of them is eliminated with a probability according to its fitness, given by who has the least divergence KL. The living unit that survives, reproduces, creating a pair with parameters β very close to the original up to some random mutations. This algorithm simulates natural selection under different external conditions. The presented evolutionary scheme converges to a stable state, which is presented in Fig. 12 for different forms of $\rho_{\text{src}}(\alpha)$. We observe that for heterogeneous media, i.e. well distributed $\rho_{\text{src}}(\alpha)$, the optimal internal state is close to the critical point, while, in homogeneous models, the β parameter depends largely on specific sources and is not necessarily close to the critical point.

5 Summary and Future Steps

This essay reviews many biological systems close to criticality. We show that, for complex systems such as networks of neurons, where a mathematical model is still incomplete, the principle of maximum entropy provides a first toy model that allows us to observe and study some inherent features of the phenomena, characteristics that the complete model must also present. This approach was only possible recently due to advances in technology, as a simultaneous recording of the different degrees of freedom is required. The resulting models are successfully tested with other statistical moments and explored through simulations, to obtain a model that is as reliable as possible. From these ‘‘experiments’’ a common characteristic was observed in many biological systems, which is that their models are positioned very close to critical points.

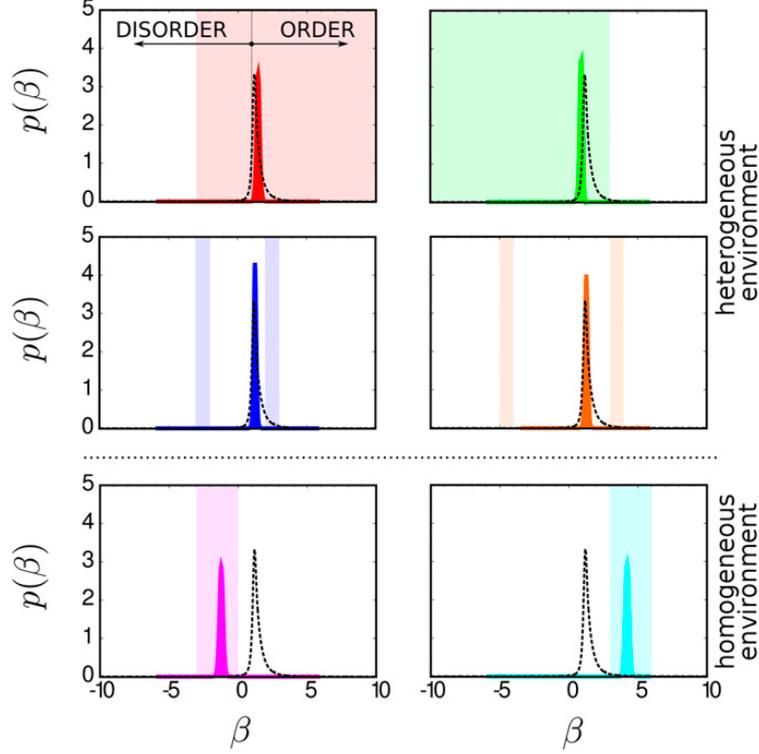


Figure 12: Probability of β having a specific value in a population after this populations has evolved with a genetic algorithm and achieve an steady state. Heterogeneous and homogeneous external conditions are imposed to the population of N elements, and it can be see that, for the heterogeneous cases, the β parameter converges close to criticality. Dashed lines represent the susceptibility χ of the internal probability distribution, which has its peak close to the critical point. Image obtained from [6].

It seems that it is a common feature of these types of systems, and it opens the option that there could be some deeper theoretical system behind their behaviors [1]. It makes it a valuable reason to study different cases when criticality arises, test the type of criticality, and in the future explain the reason why this might happen. Could there be an inherent reason related to being using the maximum entropy principle? We have observed in the first two examples the presence of criticality signs that do not use the mentioned method, however, there may still be some statistic problem that is still eluding us. On the other hand, there is much speculation about why criticality should be observed in biological systems [3], specifically based on the effective propagation of information over long distances, or obtain the most efficient information possible from the real world [12], so far no conclusive evidence has been found. Exploration of more critical phenomena in biology, and understanding first, if it is intrinsically related to living things, and then why evolutions lead to it and if there is any relationship behind its appearance in some different processes or if it is just a coincidence, they are future direction of the area.

References

- [1] Thierry Mora and William Bialek. “Are Biological Systems Poised at Criticality?” In: *Journal of Statistical Physics* 144.2 (June 2011), pp. 268–302. ISSN: 1572-9613. DOI: [10.1007/s10955-011-0229-4](https://doi.org/10.1007/s10955-011-0229-4). URL: <http://dx.doi.org/10.1007/s10955-011-0229-4>.
- [2] Gašper Tkačik et al. “Thermodynamics and signatures of criticality in a network of neurons”. In: *Proceedings of the National Academy of Sciences* 112.37 (2015), pp. 11508–11513. ISSN: 0027-8424. DOI: [10.1073/pnas.1514188112](https://doi.org/10.1073/pnas.1514188112). eprint: <https://www.pnas.org/content/112/37/11508.full.pdf>. URL: <https://www.pnas.org/content/112/37/11508>.
- [3] William Bialek et al. “Social interactions dominate speed control in poisoning natural flocks near criticality”. In: *Proceedings of the National Academy of Sciences* 111.20 (2014), pp. 7212–7217. ISSN: 0027-8424. DOI: [10.1073/pnas.1324045111](https://doi.org/10.1073/pnas.1324045111). eprint: <https://www.pnas.org/content/111/20/7212.full.pdf>. URL: <https://www.pnas.org/content/111/20/7212>.
- [4] Dmitry Krotov et al. “Morphogenesis at criticality”. In: *Proceedings of the National Academy of Sciences* 111.10 (2014), pp. 3683–3688. ISSN: 0027-8424. DOI: [10.1073/pnas.1324186111](https://doi.org/10.1073/pnas.1324186111). eprint: <https://www.pnas.org/content/111/10/3683.full.pdf>. URL: <https://www.pnas.org/content/111/10/3683>.
- [5] Theodosius Dobzhansky. “Nothing in Biology Makes Sense except in the Light of Evolution”. In: *The American Biology Teacher* 35.3 (Mar. 1973), pp. 125–129. ISSN: 0002-7685. DOI: [10.2307/4444260](https://doi.org/10.2307/4444260). eprint: <https://online.ucpress.edu/abt/article-pdf/35/3/125/30618/4444260.pdf>. URL: <https://doi.org/10.2307/4444260>.
- [6] E. T. Jaynes. “Information Theory and Statistical Mechanics”. In: *Phys. Rev.* 106 (4 May 1957), pp. 620–630. DOI: [10.1103/PhysRev.106.620](https://doi.org/10.1103/PhysRev.106.620). URL: <https://link.aps.org/doi/10.1103/PhysRev.106.620>.
- [7] Xiao Chen et al. “Scale-Invariant Correlations in Dynamic Bacterial Clusters”. In: *Phys. Rev. Lett.* 108 (14 Apr. 2012), p. 148101. DOI: [10.1103/PhysRevLett.108.148101](https://doi.org/10.1103/PhysRevLett.108.148101). URL: <https://link.aps.org/doi/10.1103/PhysRevLett.108.148101>.
- [8] J. Vandermeer, I. Perfecto, and S. Philpott. “Clusters of ant colonies and robust criticality in a tropical agroecosystem”. In: *Nature* 451 (2008), pp. 457–459.
- [9] Andrea Cavagna et al. “The STARFLAG handbook on collective animal behaviour: 1. Empirical methods”. In: *Animal Behaviour* 76.1 (2008), pp. 217–236. ISSN: 0003-3472. DOI: <https://doi.org/10.1016/j.anbehav.2008.02.002>. URL: <https://www.sciencedirect.com/science/article/pii/S0003347208001152>.
- [10] A. Cavagna et al. “The STARFLAG handbook on collective animal behaviour: Part II, three-dimensional analysis”. In: *arXiv: Quantitative Methods* (2008).
- [11] G. Tkačik et al. “Searching for Collective Behavior in a Large Network of Sensory Neurons”. In: *PLoS Computational Biology* 10 (2014).
- [12] Jorge Hidalgo et al. “Information-based fitness and the emergence of criticality in living systems”. In: *Proceedings of the National Academy of Sciences* 111.28 (2014), pp. 10095–10100. ISSN: 0027-8424. DOI: [10.1073/pnas.1319166111](https://doi.org/10.1073/pnas.1319166111). eprint: <https://www.pnas.org/content/111/28/10095.full.pdf>. URL: <https://www.pnas.org/content/111/28/10095>.

- [13] J. J. Binney et al. *The Theory of Critical Phenomena: An Introduction to the Renormalization Group*. USA: Oxford University Press, Inc., 1992. ISBN: 0198513933.
- [14] H. Eugene Stanley. *Introduction to phase transitions and critical phenomena, by H. Eugene Stanley*. English. Clarendon Press Oxford, 1971, xx, 308 p., 3 plates. ISBN: 0198512570.