The brain: What is critical about it?

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Abstract. We review the recent proposal that the most fascinating brain properties are related to the fact that it always stays close to a second order phase transition. In such conditions, the collective of neuronal groups can reliably generate robust and flexible behavior, because it is known that at the critical point there is the largest abundance of metastable states to choose from. Here we review the motivation, arguments and recent results, as well as further implications of this view of the functioning brain.

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INTRODUCTION

The brain is a complex adaptive nonlinear system that can be studied along with other problems in nonlinear physics from a dynamical standpoint. With this perspective here we discuss a proposal [5, 15, 16, 17, 18, 19] claiming that the brain is spontaneously posed at the border of a second order phase transition. The claim is that the most fascinating properties of the brain are -simply- generic properties found at this dynamical state, suggesting a different angle to study how the brain works. From this viewpoint, all human behaviors, including thoughts, undirected or goal oriented actions, or simply any state of mind, are the outcome of a dynamical system -the brain- at or near a critical state.

The starting point for this conjecture is that it is only at the critical point that the largest behavioral repertoire can be attained with the smallest number of degrees of freedom. *Behavioral repertoire* refers to the set of actions useful for the survival of the brain and *degrees of freedom* are the number of (loosely defined) specialized brain areas engaged in generating such actions. A number of ideas from statistical physics can be used to understand how the brain works by looking at the problem from this angle.

This article is dedicated to discussing the basis and specifics of this proposition along with its implications. The paper is organized as follows: The second section begins by reviewing the problem. Basic features of the physics of critical phenomena are introduced and used to support the Darwinian notion that brains are needed to survive

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in a critical world. The third section addresses predictable observations, and the fourth section reviews recent results that support the idea of a critical state in brain function. The paper closes with a short discussion of its implications.

WHAT IS THE PROBLEM?

New fascinating discoveries about brain physiology are reported every week , each one uncovering a relatively isolated aspect of brain dynamics. Yet the reverse process - how these isolated pieces can be integrated to explain how the brain works- is rarely discussed. Large-scale knowledge of the nervous system is generally only casted in psychological terms, with little discussion of underlying mechanisms. The goal should be, as it is in physics, to explain all macroscopic phenomena -regardless of their nature- on the basis of their underlying microscopic dynamics.

The problem discussed here concerns which underlying properties allow the brain to work as a collective of neuronal groups. How chief brain abilities work in concert, how perception and action are engaged, and how the conscious mind emerges out of electrical impulses and neurochemistry is what we wish to understand, to name a few. This is essentially equivalent, for instance, to understanding how culture (or any other community emergent property) emerges from each individual's intellectual capital. It is clear that the solution of these questions, as for other complex systems, requires more than the mere enumeration of all the knowledge about the individual components.

The task of understanding how a collective works together is challenging, but even more is in the case of the brain. As a whole the brain has some notoriously conflictive demands. In some cases it needs to stay "integrated" and in others must be able to work "segregated", as discussed extensively by Tononi and colleagues [48, 49].[1] This is a non trivial constraint, nevertheless mastered by the brain as it is illustrated with plenty of neurobiological phenomenology. Any conscious experience always comprises a single undecomposable scene [48], i.e., an integrated state. This integration is such that once a cognitive event is committed, there is a refractory period in which nothing else can be thought of. At the same time segregation properties allow for a large number of conscious states to be accessed over a short time interval. As an analogy, the integration property we are referring to could be understood as the capacity to act (and react) on an all-or-nothing basis, similar to an action potential or a travelling wave in a excitable system. The segregation property could be then visualized as the capacity to evoke equal or different all-or-nothing events using different elements of the system. In fact, this metaphor may be more than applicable.

It will be discussed below that the segregation-integration conflict shares many similarities with the dynamics seen in nonlinear systems near a order disorder phase transition.

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[1] Perhaps the same conflict can be identified also in other complex systems.

What is special about being critical

Work in the last two decades has shown that complexity in nature often originates from the tendency of non-equilibrium extended nonlinear systems to drift towards a critical point. There are many examples in which this connection was made more or less rigourously including problems in physics, economy, biology, macroeconomics, cosmology and so on [32, 41, 50, 5, 10]. It had been argued already [5, 15, 16, 18, 19] that the same approach should be used to understand large scale brain dynamics.

To review such a proposal we will briefly discuss which features of the critical state are pertinent to the conjecture that the brain is critical. As an example we will use the well known Ising model of the magnetization in ferromagnetic materials, but it should be noted that the important point are the universal features of the phase transition and not the model itself.

We can describe the Ising model by considering a relatively small square lattice containing $N = LxL$ sites, with each i site associated with a variable s_i, where $s_i = +1$ represents an "up" spin and $s_i = -1$ a "down" spin. Then any particular configuration of the lattice is specified by the set of variables $s_1, s_2, ..., s_N$. The energy in absence of external magnetic field is given by

$$E = -J \sum_{i,j=nn(i)}^{N} s_i s_j \qquad (1)$$

where J is the coupling constant and the sum of j runs over the nearest neighbors of a given site i ($nn(i)$). The simulation is usually implemented with the Metropolis Monte Carlo algorithm [30, 46] solving for a given heat bath temperature T.

Collectively, spins will show different degrees of order and magnetization values depending on the temperature, as seen in the ferromagnetic-paramagnetic phase transition illustrated in Figure 1. A material is ferromagnetic if it displays a spontaneous magnetization in absence of any external magnetic field. If we increase the temperature the magnetization gets smaller and finally reaches zero. At low temperature the system is very ordered with only very large domains of equally oriented spins, a state almost invariant in time. At very high temperatures, spin orientation changes constantly and become correlated only at very short distances resulting in vanishing magnetization. Only in between these two homogeneous states, at the critical temperature, does the system exhibit peculiar fluctuations both in time and space. The temporal fluctuations of the magnetization is scale invariant. Similarly, the spatial distribution of spins clusters show long range (power law) correlations and scale invariance reflected in a fractal structure of clusters of aligned spins. It is important to realize two points: 1) these large structures only emerge at the critical point, and 2) they extend up to the system size despite the fact that the interactions between the systems elements are only *short-range* (i.e., between the nearest neighbors). Thus, at the critical temperature, the system is able to maintain correlation between far away sites (up to the size of the system) staying long periods of time in a given meta-stable state but also exploring a large diversity of such states. This behavior is reflected in the maximization of the fluctuations of magnetization, a typical signature of a second order phase transition.
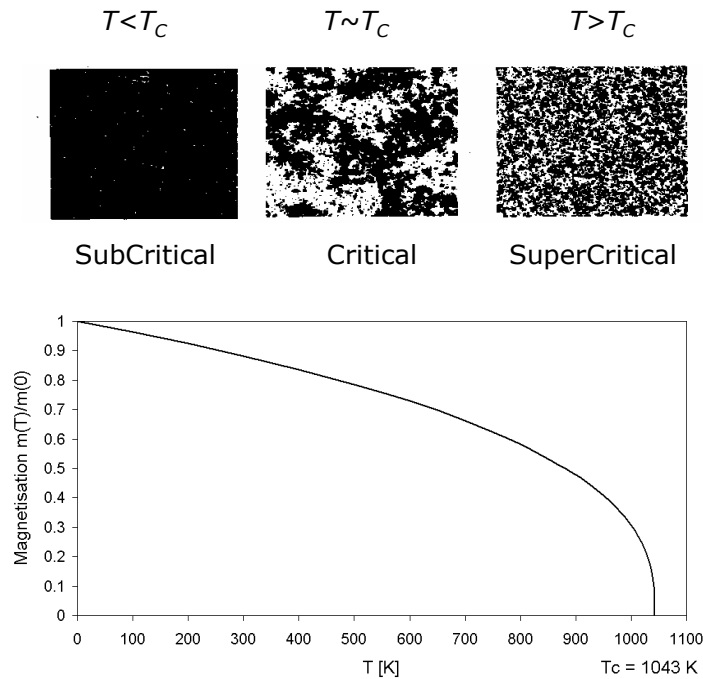
FIGURE 1.   Ferromagnetic-paramagnetic phase transition. Bottom: Temperature dependence of magnetization m(T) for Fe. Top three panels are snapshots of the spins configuration at one moment in time for three temperatures: subcritical, critical, and supercritical.

We propose that this dynamical scenario -generic for any second order phase transition- is strikingly similar to the integrated-segregated dilemma discussed above, and is necessary for the brain to operate as a conscious device. It is important to note that there are no other conceivable dynamical scenarios or robust attractors known to exhibit these two properties simultaneously. Of course, any system could trivially achieve integration and long range correlations in space by increasing links' strength among faraway sites, but these strong bonds prevent any segregated state.

Why do we need a brain?

This question may sound frivolous but it is not at all, because in Darwinian terms it is necessary to consider the brain embedded in the rest of nature, and co-evolving according with the constraints of natural selection. Although some views could advocate for computational properties in specific neural circuits and find mathematical justification for it existence, we simply think that the brains we see today are the ones that -for whatever means- got an edge and survived. How consistent is our view of the brain near a critical point will be answered by considering these Darwinian constraints. We propose that the brains we see today are critical because the world in which they have to

survive is up to some degree critical as well. Let us look at the other possibilities. If the world were sub-critical then everything around will be simple and uniform (as in the left top panel of Figure 1); there would be nothing to learn, a brain will be superfluous. In a supercritical world, everything would be changing all the time (as in the right top panel of Figure 1); in these conditions it would be impossible to learn. Thus in neither extreme could a brain have provided an edge to survive- in the very uniform world there is nothing to learn and in the wildly fluctuating one there is no use for learning. The brain, therefore, must only be necessary to navigation in a complex, critical world.[2] In a critical world, things are most often the same, but there is always room for surprises. To us, this is -intuitively speaking- how the dynamics with power law correlations look like, there is always a very unlikely event that always surprises us, i.e., some novelty on a background of well known usual things. We "need" a brain *because* the world is critical [5, 6, 7, 15, 32].

Furthermore, a brain not only needs to learn and remember, but also has to be able to forget and adapt. If the brain were sub-critical then all brain states would be strongly correlated with the consequence that brain memories would be frozen. On the other extreme, a supercritical brain would have patterns changing all the time, resulting in the inability to hold any long term memory. One must conclude therefore that in order to be highly susceptible the brain itself has to be near the critical state.

Of course these ideas are not entirely new, indeed almost the same intuition prompted Turing half a century ago to speculate about learning machines using similar terms [51].

WHAT SHOULD BE SEEN?

In previous writings we have advanced a tentative list of features of the critical point that should be observed in brain experiments. These included:

1. At large scale:
   Cortical long range correlations in space and time. Large scale anti-correlated cortical states.
2. At small scale:
   "Neuronal avalanches", as the normal homeostatic state for most neocortical circuits. "Cortical-quakes" continuously shaping the large scale synaptic landscape providing "stability" to the cortex.
3. At behavioral level:
   All adaptive behavior should be "bursty" and apparently unstable, always at the "edge of failing". Life-long learning should be critical due to the effect of continuously "rising the bar".

In addition one should be able to demonstrate that a brain behaving in a critical world performs optimally at some critical point, thus confirming the intuition that the problem can be better understood by considering the environment from which brains evolved.

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[2] It has been already argued elsewhere [5, 32] that the world at large is critical.

In the list above, the first item concerns the most elemental facts about critical phenomena: despite the well known short range connectivity of the cortical columns, long range structures appear and disappear continuously. The presence of inhibition as well as excitation together with elementary stability constraints determine that cortical dynamics should exhibit large scale anti-correlated structures as well [22]. The features at smaller scales could have been anticipated from theoretical considerations, but avalanches were first observed empirically in cortical cultures and slices by Plenz and colleagues [11]. An important point that is left to understand is how these quakes of activity shape the neuronal synaptic profile during development. At the next level this proposal suggests that human (and animal [13, 37]) behavior itself should show evidence of criticality and learning also should be included. For example, in teaching any skill one chooses increasing challenging levels that are easy enough to engage the pupils but difficult enough not to bore them. This "raising the bar" effect continues through life, pushing the learner continuously to the edge of failure! It would be interesting to measure some order parameter for sport performance to see if shows some of these features for the most efficient teaching strategies.

RECENT RESULTS

Neuronal avalanches in cortical networks

The first demonstration that neuronal populations can exhibit critical dynamics were the experiments reported by Plenz' lab [11]. What they uncovered was a novel type of electrical activity for the brain cortex. This type of population activity, which they termed "neuronal avalanches", sits half way in between two well known patterns: the oscillatory or wave-like highly coherent activity on one side and the asynchronic and incoherent spiking on the other. In each neuronal avalanche it is typical of a large probability to engage only few neurons and a very low probability to spread and activate the whole cortical tissue. In very elegant experiments Plenz and colleagues estimated a number of properties indicative of critical behavior including a power law with an exponent $\sim 3/2$ for the density of avalanche sizes (see Figure 2). This agrees exactly with the theoretical expectation for a critical branching process [57]. Further experiments in other settings, including monkey and rat in vivo recordings, have already confirmed and expanded upon these initial estimations [12, 34, 45, 33].

An unsolved problem here is to elucidate the precise neuronal mechanisms leading to this behavior. Avalanches of activity such as the one observed by Plenz could be the reflection of completely different scenarios. It could be that the power law distribution of avalanches sizes reflect several non- homogeneous Poisson processes that when added together look like a scale free process. This is unlikely, and scaling analysis should show that this is not the case. It could also reflect a structural (i.e., anatomical) substrate over which travelling waves in the peculiar form of avalanches occur. This would imply that the long range correlations detected are trivially due to long range connections. If that is the case, as was discussed above, this would have nothing to do with criticality, and furthermore would imply that segregation is impossible. Based of what is known about the connectivity, it is reasonable to think of a dynamical mechanism responsible for this
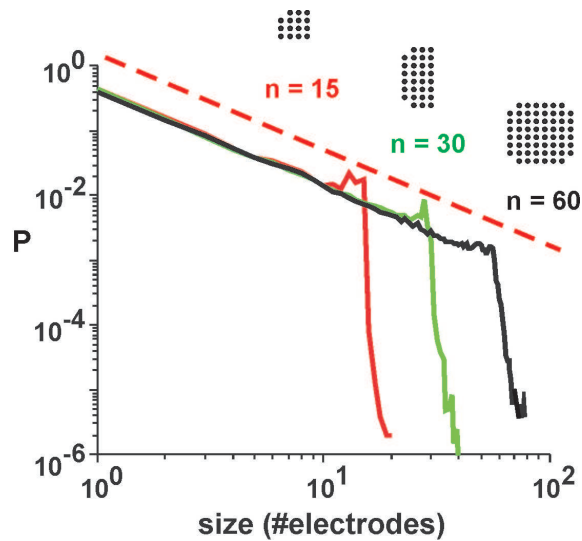
FIGURE 2. Scaling in neuronal avalanches of mature cortical cultured networks. The distribution of sizes follows a power law with an exponent $\sim 3/2$ (dashed line) up to a cutoff which depends on the grid size. The data, re-plotted from Figure 4 of [11], shows the probability of observing an avalanche covering a given number of electrodes for three sets of grid sizes shown in the insets with n=15, 30 or 60 sensing electrodes (equally spaced at $200\mu m$). The statistics is taken from data collected from 7 cultures in recordings lasting a total of 70 hours and accumulating 58000 ($+-$ 55000) avalanches per hour (mean $+-$ SD).

type of activity. One can assume that the neuronal avalanches occur over a population of locally connected neurons. Their ongoing collective history will permanently keep them near the border of avalanching and each collective event will only excite enough neurons to dissipate the excess of activity. This is the most likely scenario, following the ideas put forward by Bak and colleagues [5, 6, 7, 32]; however, there is no theoretical formalization of these results as of yet.

The most significant theoretical effort to elucidate the mechanisms underlying neuronal avalanches was reported recently by Levina and colleagues [28]. They considered a network model of excitable elements with random connectivity in which the coupling is activity dependent, such that, as in reality, too much activity exhausts the synaptic resources. This induces a decreasing in coupling strength which in turn decreases the propagation of activity. The interaction between activity and coupling results in a self-organized drifting of the dynamic towards a critical avalanching activity with the statistics reported in Plenz' experiments. Further work is needed to see other spatiotemporal properties of neuronal avalanches to check if they follows the mechanism suggested by Levina et al. [28].

Functional brain networks are complex

Functional magnetic resonance imaging (fMRI) allows us to non-invasively monitor spatio-temporal brain activity under various cognitive conditions. Recent work using this
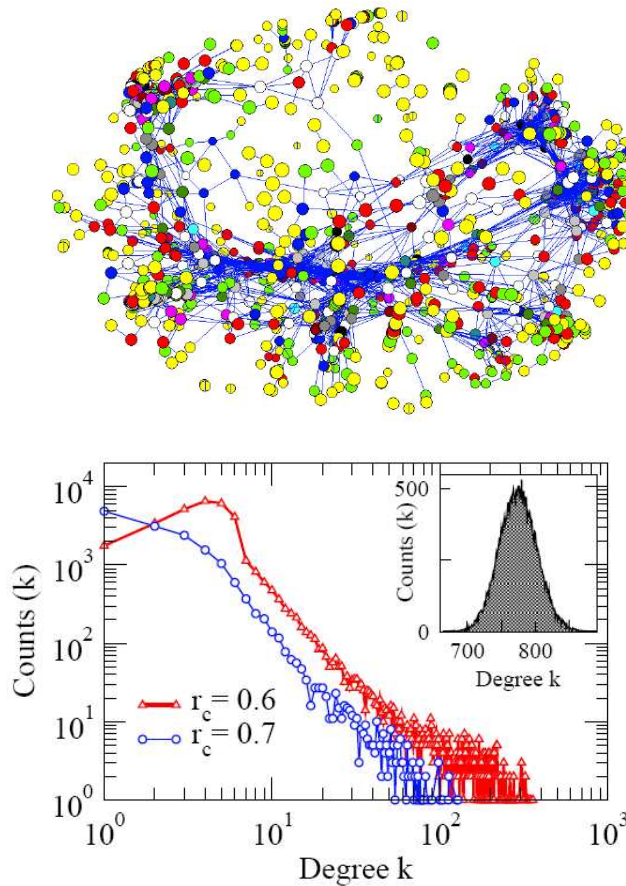
FIGURE 3. A typical brain network extracted from the correlations of functional magnetic resonance images. Top panel shows a pictorial representation of the network. The bottom panel shows the degree distribution for two correlation thresholds r_c. The inset depicts the degree distribution for an equivalent randomly connected network. Data re-plotted from [21].

imaging technique demonstrated complex functional networks of correlated dynamics responding to the traffic between regions, during behavior or even at rest (see methods in [21]. The data was analyzed in the context of complex networks (for a review see [42]). During any given task the networks were constructed first by calculating linear correlations between the time series of the blood oxygenated level dependent (BOLD) signal in each of $36 \times 64 \times 64$ brain sites called voxels. After that, links were defined between those brain sites whose BOLD temporal evolutions were correlated beyond a pre-established value r_c.

Figure 3, show a typical brain functional network extracted with this technique. The top panel illustrates the interconnected networks' nodes and the bottom panel shows the statistics of the number of links (i.e., the degree) per node. There are a few very well connected nodes in one extreme and a great number of nodes with a single connection. The typical degree distribution approaches a power law distribution with an exponent around 2. Other measures revealed that the number of links as a function of -physical-

distance between brain sites also decays as a power law, something already confirmed by others [39] using different techniques. Two statistical properties of these networks, path length and clustering, were computed as well. The path length (*L*) between two voxels is the minimum number of links necessary to connect both voxels. Clustering (*C*) is the fraction of connections between the topological neighbors of a voxel with respect to the maximum possible. Measurements of *L* and *C* were also made in a randomized version of the brain network. *L* remained relatively constant in both cases while *C* in the random case were much smaller, implying that brain networks are "small world" nets, a property with several implications in terms of cortical connectivity, as discussed further in [43, 42, 4, 38]. In summary, the work in [21] shows that functional brain networks exhibit highly heterogeneous scale free functional connectivity with small world properties. Although these results admit a few other interpretations, the long range correlations demonstrated in these experiments are consistent with the picture of the brain operating near a critical point, as will be further discussed below. Of course, further experiments are needed to specifically define and measure some order parameter to clarify the precise nature of these correlations. Furthermore, as more detailed knowledge of the properties of these networks is achieved, the need to integrate this data in a cohesive picture grows [44].

To gain insight into the possible dynamical origins of Eguiluz [21] findings we simulated the Ising model on a relatively small square lattice at the critical temperature. Then, as was done with the brain fMRI data, the linear correlations between the time series of each one the lattice points ($s_i = \pm 1$) were calculated:

$$r(i, j) = \frac{\langle s_i(t)s_j(t)\rangle - \langle s_i(t)\rangle\langle s_j(t)\rangle}{\sigma(s_i(t)\sigma(s_j(t)))}, \qquad (2)$$

where $\sigma^2(s(t) = \langle s^2(t)\rangle - \langle s(t)\rangle^2)$.

Figure 4 illustrates typical results for the critical temperature. The distribution of correlations is approximately Gaussian, encompassing both positive as well as negative correlations (see the left panel of Figure 4). This is related to the large domains of equally oriented spins found at the critical temperature, which are positively correlated amongst themselves and negatively correlated to domains with opposite spin orientation. These counterbalanced correlations are only present at the critical temperature, since for supercritical temperatures all correlations vanish and for subcritical values only a large domain of a given orientation survive.

In analogy with Eguiluz et al. methods, a correlation network was constructed by defining links between those lattice points whose fluctuations correlated beyond a a given r_c value. The degree distribution for $r_c = 0.4$ is depicted in Figure 4 and 5, where it can be seen that there is a mode centered around four (i.e., the number of neighbors in the simulation) and then a long tail which resembles very much the experimental results shown previously. Further details can be appreciated more clearly in Figure 5. The top right panel shows the degree for each lattice point, and the top left a correlation map. Notice that the tail of the degree distribution in the previous figure corresponds here to the points in the two clusters with highest degree (colored yellow-red). In the left panel, the origin of these clusters is clarified by selecting one of them as a seed (labelled S) and plotting its correlation values with the rest of the lattice points. Typical time series
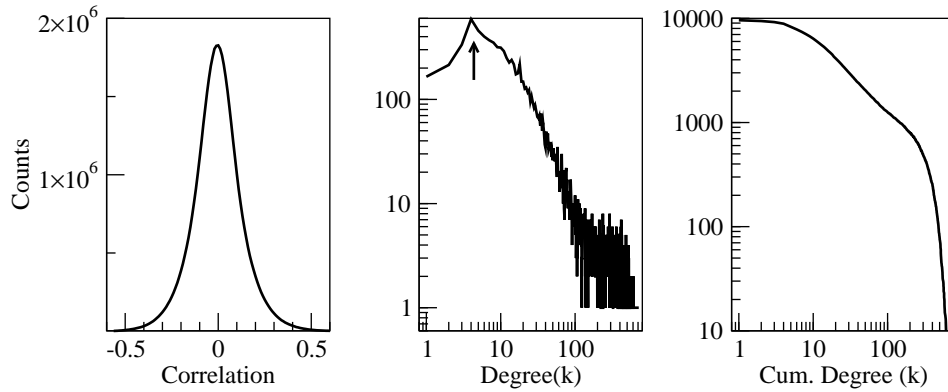
FIGURE 4. Ising model at the critical temperature: Left plot shows the distribution of correlation values. Middle and right plots depict the degree distribution of the network extracted. Arrow point at degree=nn=4. Correlation network constructed as in [21] using a threshold $r_c > 0.4$. Simulation of Eq. 1 with $k = 1$ and $J = 1$, discarding a transient $N_{equil} = 10^8$ steps, we chose $N_{time} = 1000$ configurations every $N_{sample} = LxL = 10^4$ steps. Each time step corresponds to a single spin flip. In all cases the system is at the critical temperature ($T_c \simeq 2.3J/k_B$)

of two nodes placed far away from the seed: one positively correlated (P) and the other negatively correlated (N) are also plotted in Fig. 5. Note that the two large anti-correlated domains correspond to the two hubs in the degree map.

Of course, these numerical experiments are very far from representing anything close to the details of brain physiology. Nevertheless, they serve the purpose of showing that key features of the correlations seen in the fMRI experiments are also observed in a paradigmatic critical system. The main point of these results is to demonstrate that a correlation network with scale free degree distribution as reported by Eguiluz et al. [21] can be extracted from a dynamical system, providing is at a critical point, regardless of the underlying connectivity. The example shown here uses the worst case scenario of a lattice with only *local* connectivity, but we expect the main conclusions to remain the same using other less ordered topologies.

It is important to remark that the dynamics described arises in the Ising model with ferromagnetic interactions, i.e., there is only positive correlations between neighbor sites (analogous to have only "excitatory synapsis"). Despite its absence in Eq. 1, negative correlations emerge as a collective property of the critical dynamics. Accordingly, these negative correlations manifest at relatively long time scales (reflecting the collective movements of spins) and not at short time scales. This agrees well both with observations made from fMRI experiments and with those extracted from a detailed model of the cortex [26]. Finally another aspect to note is that the ratio between the area covered by positive and negative correlations equal to one (see Fig. 5), just as it observed in the brain of healthy people [8] as discussed in the next section.
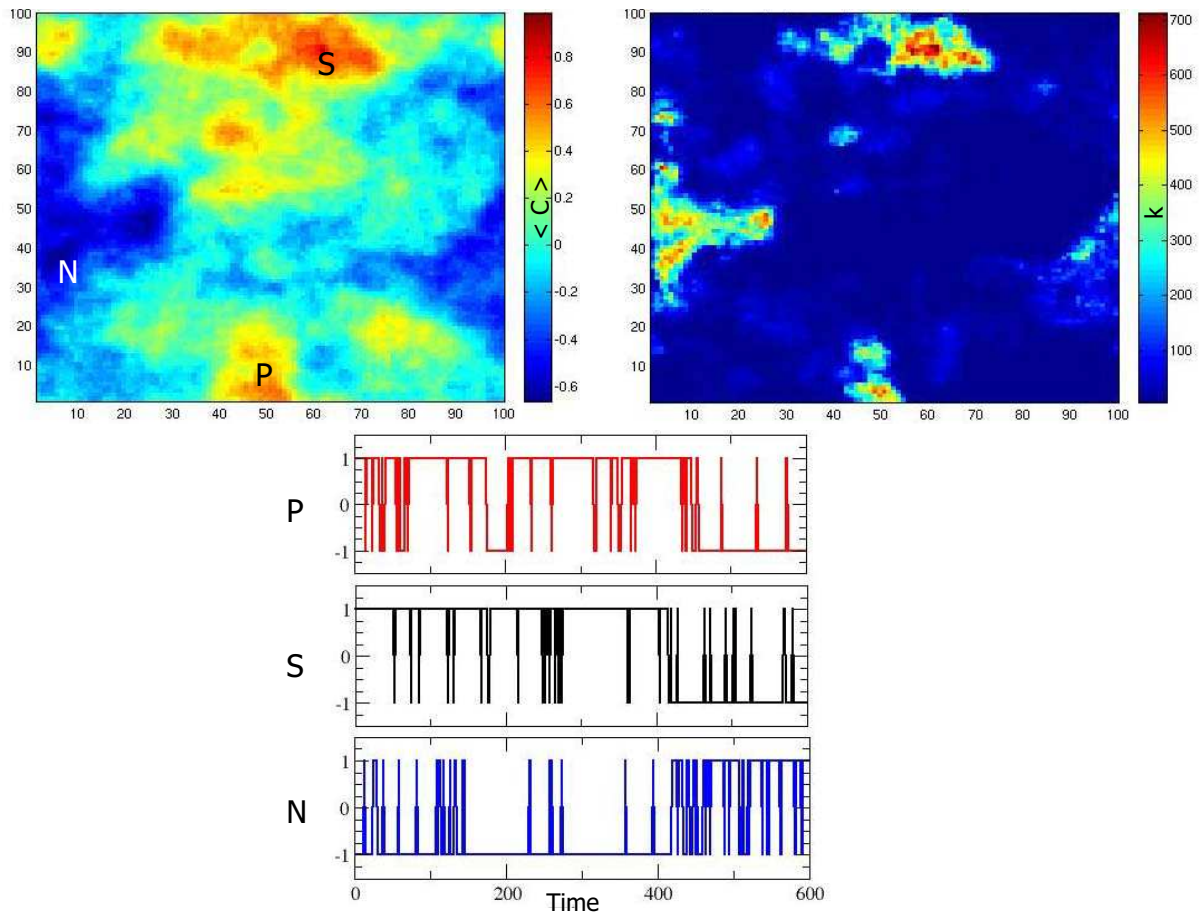
FIGURE 5. Ising model at the critical temperature: Top left: Correlations between the seed (S) and the rest of the lattice. Top right: Degree (k) of each lattice point. Bottom: Time series of three selected places, one for the seed (S) and one for a negatively (N) or positively (P) correlated point. Each time step here corresponds to 10^4 single flip spins.

What state is the brain "resting state"?

Over a decade ago [9] BOLD low-frequency fluctuations were shown to be correlated across widely spatially separated but functionally related brain regions (between left and right sensorimotor cortices) in subjects at rest. Brain "rest" can be defined - more or less unsuccessfully- as the state in which there is no explicit brain input or output.[3]

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[3] Readers familiar with Italian traditions advantageously can specify brain rest as the brain state resulting from *"dolce fare niente"*. Translated literally it reads "sweet do nothing" or also the "sweet act of doing nothing".

Various groups have suggested that these fluctuations are of neuronal origin and correspond to the neuronal baseline or idle activity of the brain. These fluctuations exhibit long-range correlations with the power of the spectrum decaying as $1/f^\beta$, with $\beta \sim 1$. Up until recently these observations were considered a nuisance in the majority of neuroimaging studies and disregarded as unwanted noise, despite the fact that they are the baseline against which other task-related conditions are usually compared.

The notion of a specific network of brain regions active in rest states was reinforced by the observation of a consistent pattern of deactivations seen across many goal-oriented tasks [40]. This observation coupled, with studies of cerebral blood flow led Raichle and colleagues [35] to propose a theory for the so called brain "default mode networks". This view sees BOLD signal decreases during cognitive tasks as one way to identify how the brain is active during rest. In other words, what part of the brain was more active during rest is inferred by identifying what is being deactivated during a given task.

One simple way used to study this network is to look at the linear correlations between the time series of BOLD activity of different regions of the brain [22]. Figure 6 shows a typical result from experiments in with the subjects were ask to track the height of a moving bar varying in time during fMRI data collection [8]. The depicted correlation maps were constructed by first extracting time series for the seeds (small green circles in Fig. 6, obtaining averaging a cube of 3x3x3 voxels) and then computing its correlation coefficient with the time series of all the other brain voxels. This is equivalent to the correlation map shown previously for the Ising model (Fig. 5 top left panel).

Figure 6 shows correlation maps associated with six predefined seed regions. Based on previous results, these seeds are known to be sensitive to the task being conducted. Three regions, referred to as task-positive regions, exhibit activity increases during the task, and three regions, referred to as task-negative regions, exhibit activity decreases (de-activation) during the attention task [22, 14]. Task-positive regions were centered in the intraparietal sulcus (IPS), the frontal eye field region (FEF), and the middle temporal region (MT). Task-negative regions were centered in the medial prefrontal (mPFC), posterior cingulate/precuneus (PCC), and lateral parietal cortex (LP).

The correlation maps of Figure 6 summarize the functional co-activation between a given seed region and the rest of the cortex. These maps replicate very closely the ones described at rest [22, 29, 35, 36], since it is known that in minimally demanding tasks brain functional connectivity approximates the functional connectivity seen during rest [22, 24, 25]. It displays brain regions that are positively correlated (red-yellow colors) and regions that are negatively correlated (blue-green colors) with any of the chosen seeds. An important experimental finding was that the ratio between the area covered by positive correlations and those with negative correlations was always very close to one [8] (see Fig. 5 and Fig. 6). This was consistently found in all healthy volunteers analyzed up to now. However, the same analysis carried out in patients that have suffered chronic pain for many years, revealed a ratio up to forty times larger [8]. This suggests a healthy dynamic balance of the resting state network, which deserves to be explored further.

The brain is clearly not a lattice and the connectivity is not homogeneous. Moreover the "small world" features revealed by fMRI described earlier are also found in the anatomical connectivity [43]. Thus, finding in any given complex spatiotemporal pat-
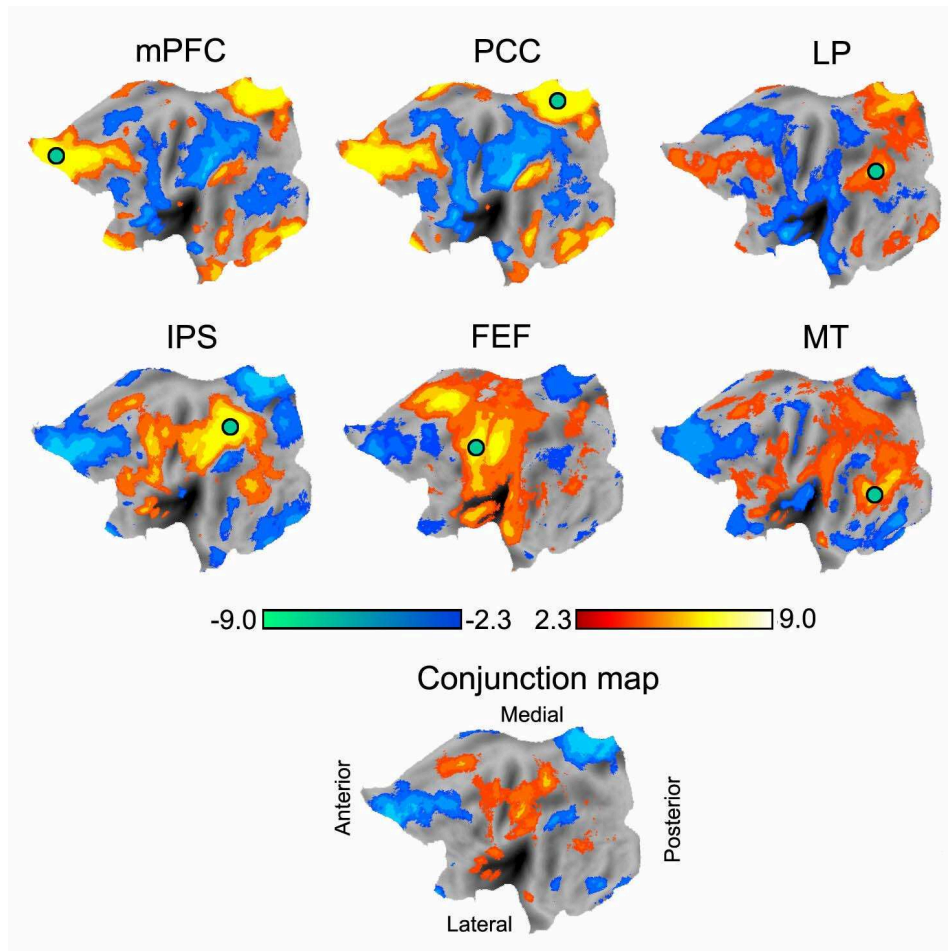
FIGURE 6. Typical balanced correlated-anticorrelated spatial domains of brain fMRI recorded from human volunteers during a simple attention task (replotted from Baliki et al. [8]. These patterns are typical of healthy individuals, where the total area covered by positive correlations is approximately the same as that covered by negatively correlations. The data shows averaged z-score maps (for a group of 15 volunteers) showing regions with significant correlations with the six seed regions (small circles). The results shown correspond to three task-negative seed regions: mPFC, PCC, and LP, as well as to three task-positive seed regions: IPS, FEF, and MT. Colors indicate regions with positive correlations (red-yellow) and negative correlations (blue-green); both have z-scores > 2.3 ($p<0.01$). The group z-score conjunction map below shows voxels significantly correlated or anti-correlated with at least five of the six seed regions.

terns what is due to the dynamics and what is induced by the underlying structure is still a difficult problem.

In an attempt to gain insight into the brain resting state fluctuations, Honey et al. [26], simulated the cerebral cortex using neuronal dynamics under the real structural connections given by known large scale connectivity. According with their results, coupled excitable elements embedded in this type of anatomical architecture, favors the emergence of spatio-temporal patterns such as those observed in the brain at resting condition. For instance, they found that the functional connectivity seen in the BOLD signal are present at low frequency as a result of fluctuations in the aggregate number of transients cou-

plings and decoupling occurring at a more rapid scale ($\approx 10 Hz$). At the slow time scale they identify two major anti-correlated functional clusters which, in their interpretation, are coordinated via anatomical connection patterns. Nevertheless, the results shown in Fig. 5 suggest that these anticorrelated clusters can be originated solely by the critical dynamics.

The possibility which we favor is that the correlations seen during resting state are very similar to those described for the Ising model at the critical temperature. Of course, this similarity is not in the details, but in the fundamental aspects of the dynamics. In this view, spins are represented by entire regions of coherent neuronal groups, say for instance any of the seeds we choose in Figure 6. Thus, at each moment in time, each cortical region competes or cooperates according with the connectivity and the dynamics at that moment. The experimental observation that at any given time positive and negative correlations are equal is awaiting to be explained, and its implications for disease further explored. We claim that the brain is always near criticality such that the spatiotemporal patterns illustrated above should be scale-invariant, and some other temporal variables describing its evolution power law distributed. If that is the case, then the resting state dynamical equivalent is criticality as in other extended non-linear systems near the edge of a phase transition.

Epileptic seizures as brain quakes?

In a recent paper, Osorio et al. [31] shows an interesting analysis of the temporal organization of epileptic seizures. They studied very large catalogues of seismic activity and epileptic seizures with special attention to the statistical distribution of event sizes, and waiting time between these events. Their analysis reveals an striking analogy between the dynamics of seizures and well known power laws governing earthquakes such as the Gutemberg-Ritcher and Omori laws.

Some counterintuitive conclusions are worth to mention, already noted for earthquakes [5], such as the meaningless use of intensity and duration to characterize a given seizure. This is analogous to the scale invariance noticed already in the analysis of earthquakes. In earthquakes, (as now seems in seizures) it is known that to establish the probability of any event one must specify a time window, a spatial grid size, and a given intensity of that event.

Osorio et al.'s approach also elegantly answers the classical question of why a seizure stops. An earthquake stops spontaneously whenever it has released the excess energy accumulated. In geology terminology an earthquake "starts without knowing how big is going to be or how long it is going to last". Neuronal avalanches, according to Plenz' work described earlier, also obey the same laws. According to the findings of Osorio et al. the mechanism by which seizures stop is related with the same critical process that triggers them. The authors comment that "scale invariance in seizures may be conceptualized as the hallmark of certain complex systems (the brain in this case) in which, at or near the critical point, its component elements (neurons) are correlated over all existing spatial (minicolum, column, macrocolum, etc.) and temporal scales (microseconds, seconds, tens of seconds, etc.)"
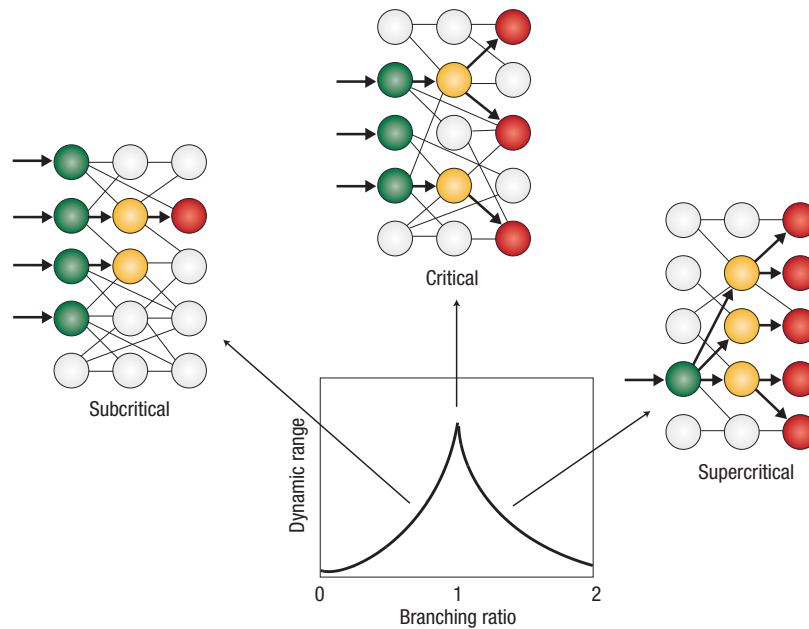
FIGURE 7. Sensory networks constructed with branching ratios close to one maintain, on the average, the input activity (green, followed by yellow and red), thus optimizing the dynamic range. In supercritical networks, however, activity explodes, while in subcritical ones are unable to sustain any input pattern. Redrawn from [17].

The similarities uncovered by Osorio et al. suggest that the researchers' intuition regarding the statistical laws governing epileptic seizures need to be adjusted accordingly.

Senses are critical

Of course brains are useful to escape from predators, move around, choose a mate or find food, and in these respects the sensory apparatus is critical for any animal survival. Recent results indicate that senses are also critical in the thermodynamic sense of the word. Consider first the fact that the density distribution of the various form of energy around us is clearly inhomogeneous, at any level of biological reality, from the sound loudness any animal have to adapt, to the amount of rain a vegetable have to take advantage. From the extreme darkness of a deep cave to the brightest flash of light there are several order of magnitude changes; nevertheless our sensory apparatus is able to inform the brain of such changes.

It is well known that isolated neurons are unable to do that because of their limited dynamic range, which spans only a single order of magnitude. This is the oldest unsolved problem in the field of psychophysics, tackled very recently by Kinouchi and Copelli [27] by showing that the dynamics emerging from the *interaction of coupled excitable elements*, is the key to solving the problem. Their results show that a network of

excitable elements set precisely at the edge of a phase transition - or, at criticality - can be both, extremely sensitive to small perturbations and still able to detect large inputs without saturation. This is generic for any network regardless of the neurons' individual sophistication. The key aspect in the model is a local parameter controlling the amplification of any initial firing activity. Whenever the average amplification is very small activity dies out, as it can be seen in the cartoon of Figure 7. In this case the system is subcritical and not sensitive to small inputs. On the other hand, choosing an amplification very large one sets up the conditions for a supercritical reaction in which for any - even very small - inputs the entire network fires. It is only in between these two extremes that the networks have the largest dynamic range. Thus, amplification around unity, i.e., at criticality, seems to be the optimum condition for detecting large energy changes as an animal encounters in the real world [17]. Of course, in a critical world energy is dissipated as a fractal in space and time with the characteristic highly inhomogeneous fluctuations. As long as the world around is critical, it seems that the evolving organisms embedded in it have no better choice than to be critical as well.

OUTLOOK

The study of collective phenomena is at the center of statistical physics. It is not surprising then, to see the recent outburst of physics and mathematics publications studying this type of phenomena in the context of computer science as well as social and economic settings. While in all these fields there is a clear transfer of methods and ideas from statistical physics, identical flow has yet to start in brain science.

This lack of communication is even more intriguing if one considers that most see brain science precisely as the study of collective patterns of neuronal activity. Nonetheless, this acknowledgment had not yet been translated into useful approaches. To the contrary, the literature contains numerous old and new promises to understand brain function by way of very large (and in some cases very detailed) numerical simulations of millions of neurons, completely orphan of considerations related with the statistical physics of collective phenomena in large systems.

To make the point above relevance of these ideas, let us recall once more the results presented in Figure 5 and the connectivity between the sites revealed in Figure 4. As it was discussed, on one side the connectivity says that the system is a lattice with only four nearest neighbors, but the correlations reveal a network with scale-free degree distribution. It seems to be a gross contradiction, but the apparent divorce between the patterns dictated by the coupling equations and those found by the analysis of the spatial correlations will not surprise those already familiar with emergent phenomena at the critical state. Again, lets remind ourselves that the divorce between "anatomy" (i.e., the coupling) and dynamics disappears both in the supercritical and subcritical state (as correlations vanish). Now, let suppose that the time series data in Figure 5 were to be from a typical brain experiment. Classical approaches of brain connectivity, based either in the analysis of correlations (i.e., so-called "functional" connectivity or in the anatomical (i.e., "effective") connections could never reach to the right conclusion and solve the puzzle. It is only by knowing about the features of critical phenomena that the apparent puzzle can be solved. As far as we know, there is no report in the literature

suggesting changes in the character of the functional connectivity due to the dynamics at the critical point as we suggest here.

In summary, according with the proposal reviewed here, several relevant aspects of brain dynamics *can* be only understood using the theoretical framework as for any nonequilibrium thermodynamic system near the critical point of a second order phase transition. That include the understanding of neuronal dynamics at small scale, the cooperative-competitive equilibrium seen at rest in the healthy cortex, the burst of brain quakes during seizures and the optimization of the dynamic range at the sensory periphery. We have mentioned but left out the discussion of behavior, which understanding we submit should also benefit from this approach.

Some of the ideas here are novel, but the motivation is not, since Ashby was probably the first to indicate how fundamental is to understand the way self-organization shapes brain function [1]. Nevertheless, these views are gaining momentum, and is refreshing to read recent reviews [53, 54, 55] advocating the further study of phase transitions, metastability and criticality in cognitive models and experiments. This enlightening perspective is even more meaningful coming from those that first introduced information theory to the study of sensation in neuroscience,... forty three years ago [56].

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