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PERSPECTIVE



A devil's advocate view on 'self-organized' brain criticality

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Abstract

Stationarity of the constituents of the body and of its functionalities is a basic requirement for life, being equivalent to survival in first place. Assuming that the resting state activity of the brain serves essential functionalities, stationarity entails that the dynamics of the brain needs to be regulated on a time-averaged basis. The combination of recurrent and driving external inputs must therefore lead to a non-trivial stationary neural activity, a condition which is fulfilled for afferent signals of varying strengths only close to criticality. In this view, the benefits of working in the vicinity of a second-order phase transition, such as signal enhancements, are not the underlying evolutionary drivers, but side effects of the requirement to keep the brain functional in first place. It is hence more appropriate to use the term 'self-regulated' in this context, instead of 'self-organized'.

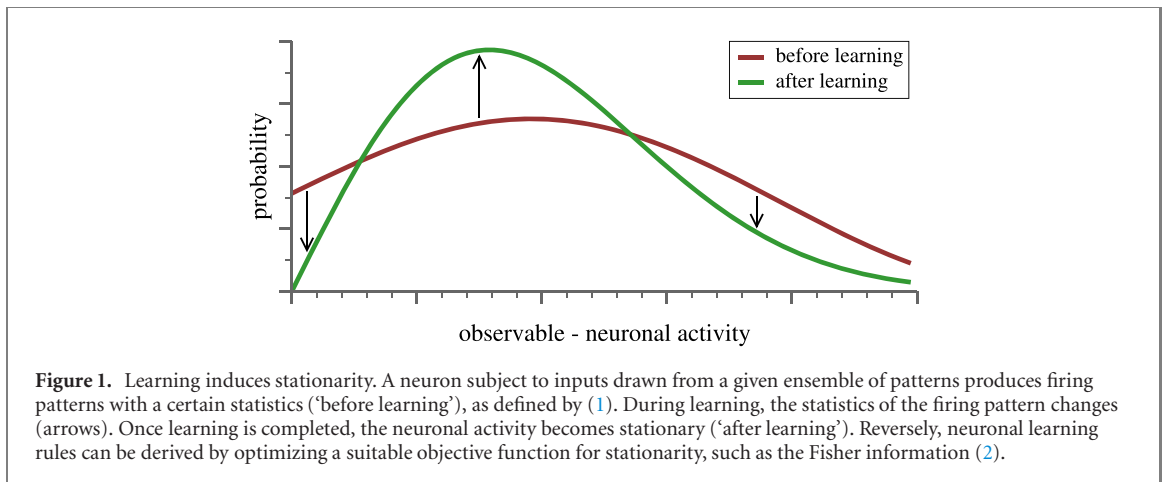
1. Life as a stationary flow equilibrium

A plethora of definitions may be used to characterize what it means to 'live' [1]. Putting aside philosophical niceties, it is clear that survival is guaranteed on a day-to-day basis only when a certain constancy of the body and its core functionalities is achieved. Here we will lay out a compact line of arguments on how this type of 'constancy' can be quantified in terms of a stationary flow equilibrium. In particular we will argue that statistical stationarity is a condition sine qua non for the brain and that it necessarily implies a modus operandi close to criticality. Critical, or near-critical brain dynamics is in this perspective nothing more than a particular aspect of the demand to retain stationary functionalities, here the resting state activity. This does not rule out secondary advantages of operating close to second-order phase transition, like improved information processing [2, 3].

Our considerations are embedded in the ongoing discussion of experimental evidences regarding critical [4], quasi-critical [5], or sub-critical [6] neuronal brain dynamics, which include also alternative explanations for the observed non-universal power laws [7]. Overall, the interaction between theory and experiments is in a state of fluid progress [8]. We will start with a general definition of stationary processes, which is then applied and illustrated in a first step to two problems from the neurosciences, Hebbian learning and spectral radius regulation. The latter will lead in a subsequent step to the control of overall brain activity, and with it to brain criticality.

1.1. Stationarity of essential functionalities

Everything is in motion, 'Panta Rhei' as the Greek philosopher Heraclitus expressed it [9]. This in particular true for higher lifeforms, which are characterized by high metabolic turnover rates. Consider, f.i., the continued recycling of proteins occurring on a daily rhythm in our cells. Once synthesized, protein have a finite lifetime, which ranges from hours to weeks [10], with typical half lifes of about twenty hours [11]. Half of us is gone when we look into the mirror the next day. But we do not notice, generically speaking, because our cells work in a stationary flow equilibrium, continuously regenerating degenerated proteins. Constancy of biological features is obtained hence in large part by self-regulated flow equilibria. A specific example are the spines of neuronal cells, which can persist for 2–3 weeks in the adult CA1 of the hippocampus [12], and even longer in the neocortex [13]. This notwithstanding that the constituent proteins, including synapse-forming membrane complexes [14], have substantially shorter life times.



1.2. Statistical stationarity

So far, we did discuss stationarity in general terms. The statistical aspect can be captured to first order by simple probability distributions, like

$$p_t(s) = \frac{1}{T} \int_{t-T}^t dt' \delta(s - S(t')), \quad (1)$$

which measures the probability that the observable $S = S(t)$ takes the value s in the interval $[t - T, t]$, with T being the observation period. The observable could be, f.i., the interspike interval, or the neural activity, the later when dealing with rate encoding neurons. A system is stationary, in a strict sense, when $p_t(s)$ is invariant with respect to time t . In practice, time invariance will be satisfied only approximately. Another caveat concerns the diverging time scales that appear when closing in to a second order phase transition. At this point the observation period should also be taken to diverge, $T \rightarrow \infty$, strictly speaking. The same caveat holds when attempting to tune a system slowly to a critical point [15].

Of course, instead of the distribution of a single scalar variable, one could consider the cross-correlation between neural activities, or other non-trivial or higher-order statistical ensembles. For the purpose of the present article, $p_t(s)$ is sufficient. Next we illustrate how the concept of statistical stationarity can be put to work.

2. Hebbian learning as a 'side effect' of stationary activity

The stationarity principle is not just an abstract, high-level concept. Instead, it is relevant on a definitively practical level. As an example we show that the stationary principle can be used to derive concrete expressions for a fundamental process, Hebbian-type learning.

The framework is deceptively simple. Consider a rate encoding neuron, for which the distribution of outputs s is given by $p_t(s)$, as defined by (1). The neuron learns, forming a receptive field by adapting its synaptic weights w_i in response to the ensemble of input patterns received [16]. As usual one assumes that the statistics on the afferent activity patterns is stationary [17].

During learning, the afferent synaptic weights $w_i = w_i(t)$ change, and with it the distribution $p_t(s)$ of the output activity. Synaptic weights will cease to change once the receptive field has formed, viz when learning is complete. At this point also $p_t(s)$ stops to change, becoming stationary, as illustrated in figure 1. Stationarity is hence a consequence of Hebbian learning.

Reversely, given that stationarity results from Hebbian learning, one can derive Hebbian learning rules by optimizing suitable information-theoretical objective functions for stationarity [18]. A key candidate is the Fisher information [19], which takes the general form

$$F_{\Theta} = \int ds p_t(s) [\Theta \ln(p_t(s))]^2, \quad (2)$$

where Θ is a differential operator with respect to a quantity of interest. As an example consider with

$$\Theta \rightarrow \frac{\partial}{\partial w_i} \quad (3)$$

the derivative relative to a specific afferent synaptic weight w_i . The Fisher information (2) then measures how $p_t(s)$ changes when w_i is modified, which is exactly what happens during Hebbian learning.

Using (2) in conjunction with (3) as an objective function for Hebbian learning is not suitable, with the reason being that inter-synaptic competition, the driver for receptive field formation, would be absent. An alternative is the scalar differential operator

$$\Theta \rightarrow \sum_i w_i \frac{\partial}{\partial w_i}, \quad (4)$$

for which the respective Fisher information (2) incorporates the sensitivity of $p_t(s)$ with respect to all synaptic weights on an equal footing. Indeed, it can be shown that non-linear Hebbian learning rules are obtained by minimizing F_Θ , when Θ is given by (4). The obtained learning rules do what all Hebbian learning rules do, a principal component analysis, being at the same time self-limiting [18, 20].

The previous considerations show that activity regulation is more than just another homeostatic process. Given that one can derive core synaptic plasticity rules, it is evident that the stationarity of neural activity can be considered to play the role of a first principle. This does not rule out the significance to optimize alternative objective functions, f.i. entropy for intrinsic plasticity [21], mutual information within linear networks [22], and for spike-time dependent plasticity [23]. It has been argued in this context, that self-organizing systems may be ‘guided’ with the help of a range of competing generating functionals [24], one for every degree of freedom.

3. Stationary activity flows

As a first step towards understanding the role of the stationary condition for brain criticality we pointed in the previous section to the interplay between stationary activity and learning. Now we turn to the interrelation between the flow of activity through individual neurons and the spectral radius of the recurrent synaptic weight matrix. The latter determines in turn the closeness to the critical point.

The eigenvalues λ_α of a real, but non-symmetric matrix \hat{W} are in general complex. The spectral radius R_w of \hat{W}

$$R_w = \max_\alpha |\lambda_\alpha|, \quad \hat{W} \mathbf{e}_\alpha = \lambda_\alpha \mathbf{e}_\alpha, \quad (5)$$

is given by the largest eigenvalue in absolute terms. The matrix in question is here the synaptic weight matrix, $(\hat{W})_{ij} = w_{ij}$. For small activities, in the linear regime, the type of recurrent dynamics generated by \hat{W} is uniquely determined by the spectral radius:

$$R_w : \begin{cases} < 1: & \text{subcritical} \\ = 1: & \text{critical} \\ > 1: & \text{chaotic} \end{cases} \quad (6)$$

Activity dies out in the subcritical regime when the network is isolated, viz when there is no driving external input. Neural activity starts a runaway growth in contrast when $R_w > 1$, which is however limited by the non-linearity of the transfer function. The resulting state is then chaotic, given that R_w determines whether the flow contracts or expands, when time is discrete [19, 25], as assumed here. For continuous time the system is instead critical when the maximal Lyapunov is zero [19].

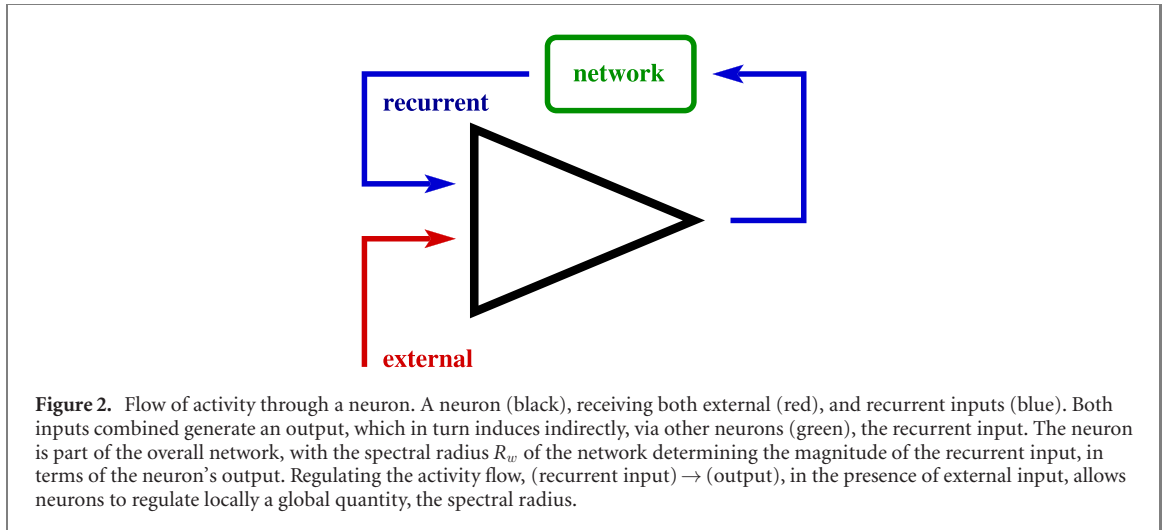
Our considerations are based, as stated above, on models with discrete time, but this is not a restriction. The reason is that the overall flow of activity through a neuron is governed by a propagator, $P_{\Delta t}$, which maps the input the neuron receives at a given time t to the input received later, at time $t + \Delta t$. The exact sampling frequency $1/\Delta t$ is not relevant, as long as it reflects the time scales of the involved biological processes, which may include refractory periods [26]. In general the spectral radius of $P_{\Delta t}$ is to be considered, and not of the bare synaptic weight matrix \hat{W} , as done above for simplicity. Both are however identical in the linear regime, the situation discussed here, for which eventual neuronal gains act functionally as synaptic scaling factors.

3.1. Spectral radius regulation

In practice, neurons receive both recurrent and external inputs, as illustrated in figure 2. The output of a given neuron flows through the embedding network, becoming in the end the recurrent input. On the average, the activity generated by the neuron considered is rescaled on its way through the surrounding neurons by the spectral R_w . This is because all other components of the activity are subleading in an eigenspace decomposition of the synaptic weight matrix, since $|\lambda_\alpha| \leq R_w$. Stationarity is achieved when

$$(\text{recurrent input})^2 \equiv R_w^2 (\text{output})^2 \quad (7)$$

holds as a suitable time averages. Given a target spectral radius R_w , neurons can satisfy the flow condition (7) by regulating their gain [3], which corresponds to a rescaling of the afferent synaptic weights. This is quite



remarkable, as it implies that a global quantity, the spectral radius, can be regulated by relying solely on local information.

The adaption rule resulting from (7), which has been termed ‘flow control’ [3], is effectively based on the circular law of random matrix theory, which states that the spectral radius of a matrix with uncorrelated entries is given by the variance of its elements [27]. The circular law states also that the eigenvalues of a real but non-symmetric matrix \hat{W} are uniformly distributed in the complex plain on a disk with radius R_w . This implies that most eigenvalues are smaller in magnitude. Note that flow control is an online rule, functioning while the system is operative, viz while processing a continuous stream of external inputs [3].

3.2. Input induced activity

A network of rate-encoding neurons subject to external inputs will settle into a continuously active dynamical state. The input is characterized typically by the variance σ_{ext}^2 , which is taken here to subsume both presynaptic activities and the weights of the afferent synapses. The steady-state variance σ_y^2 of the neural activity is then determined by the self-consistency condition [3]

$$2R_w^2(1 - \sigma_y^2)^2\sigma_y^2 = 1 - (1 - \sigma_y^2)^2(1 + 2\sigma_{\text{ext}}^2), \quad (8)$$

where R_w is the spectral radius of the synaptic weight matrix. Compare figure 2. The derivation of (8) is based on the assumption that inter-site correlations can be neglected, together with the Gaussian approximation $\tanh^2(x) \approx 1 - \exp(-x^2)$ for the squared neuronal transfer function, taken here to be $\tanh(\cdot)$. This approximation to the transfer function is similar in spirit to the use of the error function as the neural transfer function [20]. Expanding in small variances σ_y^2 and σ_{ext}^2 , one finds

$$\sigma_y \sim \begin{cases} \sigma_{\text{ext}} & \text{for } R_w < 1 \\ \sqrt{\sigma_{\text{ext}}} & \text{for } R_w = 1 \\ \sqrt{R_w - 1} & \text{for } R_w > 1 \text{ and } \sigma_{\text{ext}} = 0 \end{cases}. \quad (9)$$

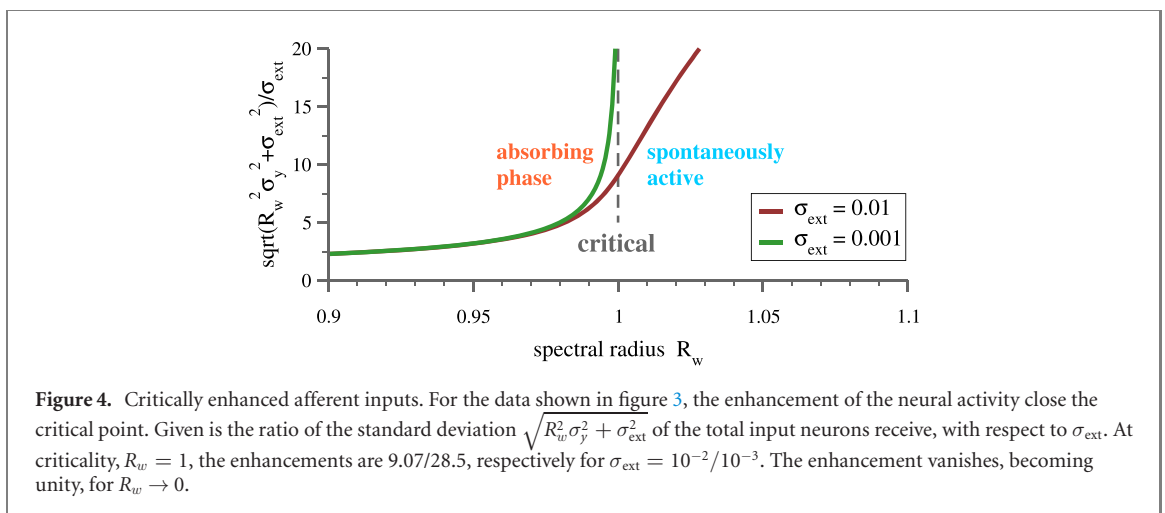
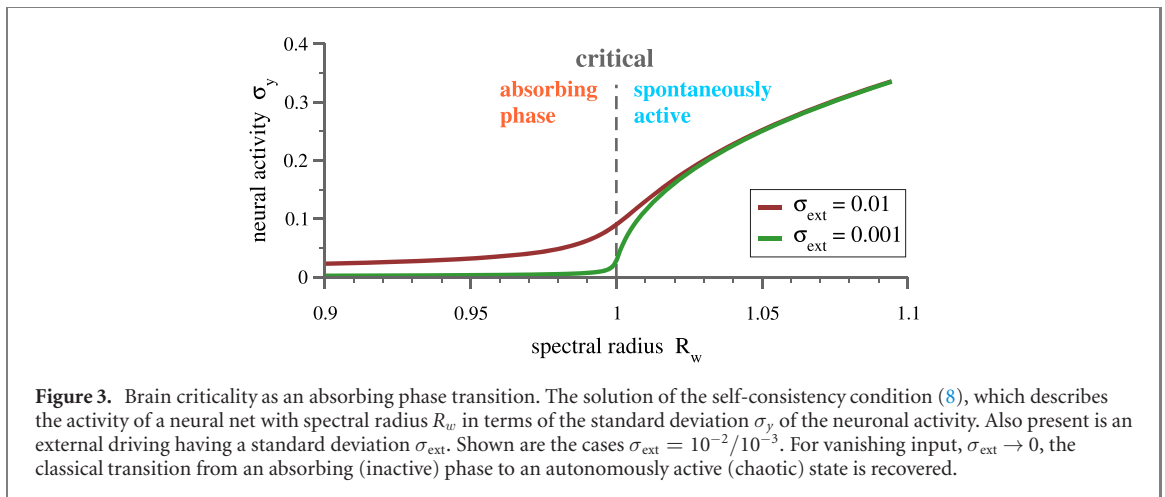
In the subcritical region one has linear response, as expected, with the limiting relation $\lim_{R_w \rightarrow 0} \sigma_y = \sigma_{\text{ext}}$. The system is in contrast highly susceptible to perturbations at criticality.

The activity resulting from the stationarity condition (8) is illustrated in figure 3. One observes the classical phenomenology of an absorbing phase transition [19], with the driving input σ_{ext} taking the role of an external field. For the isolated system, when $\sigma_{\text{ext}} \rightarrow 0$, a transition from an inactive absorbing phase to an autonomously active state takes place at $R_w = 1$. Finite fields σ_{ext} smooth the transition.

Regarding the brain, of interest is the enhancement of the induced activity by the recurrent contribution. A precise quantification of the activity enhancement is provided by the ratio

$$E_\sigma = \sqrt{\frac{R_w^2\sigma_y^2 + \sigma_{\text{ext}}^2}{\sigma_{\text{ext}}^2}}, \quad (10)$$

where $\sqrt{R_w^2\sigma_y^2 + \sigma_{\text{ext}}^2}$ is the standard deviation of the total input a typical neuron receives, and σ_{ext} the standard deviation of the driving afferent activity. Note that there is no enhancement in the absence of recurrent



connections, viz that $E_\sigma \rightarrow 1$ when $R_w \rightarrow 0$. At criticality, when $R_w = 1$, it follows from (9) that E_σ diverges like $1/\sqrt{\sigma_{\text{ext}}}$, the telltale sign of computation at the edge of chaos [28, 29]. The functional dependence is illustrated in figure 4.

Instead of E_σ one could equally well consider the difference between neural activities with and without external driving, which is done by subtracting for $R_w > 1$ the autonomous contribution $\sigma_y \sim \sqrt{R_w - 1}$, as listed in (9). The resulting susceptibility has a characteristic peak at the transition [19].

3.3. Spiking vs rate encoding neurons

The stationarity condition (8) provides, modulo residual inter-site correlations, a universal and faithful description of driven networks of rate encoding neurons. The result is that an absorbing phase transition is observed, and not any other kind, ruling out that the brain operates, f.i., at the edge of synchronization or percolation [8, 30]. The operative reason is, intuitively, that adapting mechanisms need to be able to make excursions to both sides of the transition line. Both the sub- and the over-critical state must hence be biologically viable. One may ask whether this insight is particular to networks of rate encoding neurons. This seems not to be the case.

It has been shown recently, that generalized, non-conserving sandpile models undergo absorbing phase transitions [31]. A close correspondence between toppling and spiking events is present in these models, which strongly suggest that transitions from inactive to autonomously ongoing neural dynamics follows the phenomenology of absorbing phase transitions also for spiking networks.

3.4. Absorbing phase transitions vs branching processes

Transitions from inactive to active neural dynamics are separated by an absorbing phase transition. This holds, as argued above, generically, in particular both for networks of spiking and rate-encoding neurons. Alternatively, it has been argued, that close-to critical brain activity shares features with branching processes [32]. This would be somewhat surprising, if true, given that the activity of a super-critical branching process strictly

diverges. For the sake of terminology it may hence be worth pointing out that what has been denoted in [32] a branching model, corresponds in reality to a discretized stochastic neural network which undergoes, as expected, an absorbing phase transition. There is nevertheless a close analogy between subcritical branching processes and the dynamics leading to an absorbing state [33]. Both processes die out exponentially, with the respective decay times diverging when approaching the critical point. Regarding the associated universality classes, it has been established that absorbing phase transitions belong in many cases to the universality class of directed percolation [31, 34]. For the brain, the large degree of inter-connectivity corresponds to high-dimensional lattice models, which follow mean-field scaling.

4. Self-sustained and resting state brain activity

Our brains use a non-negligible amount of energy, about 20% of what the body consumes [35], for ‘doing nothing’, to say, namely for the upkeep of its resting state. Engaging in tasks needs comparatively little additional energy, of the order of 5% of the resting state consumption [36]. This would be a trivial observation if the energy demand of the brain would be dominated by basic metabolism, just to keep our wetware alive, which is however not the case. The larger part of the energy consumed by the brain involves information processing [37]. Energy balance considerations suggest then that human brains are concerned mostly with themselves, a view that is reinforced by the observation that only a comparatively small number of synapses is devoted to stimuli processing [38].

4.1. Is the brain driven or modulated?

Various views regarding the role of the resting state activity are viable [39, 40]. A first one would be to assume that the primary task of the ongoing autonomous neural dynamics is to prepare the brain for the processing of external stimuli. This view is often implicitly assumed when positing that the brain operates close to criticality [41], given that working regimes in the vicinity to a phase transition come with favorable statistical properties for the processing of external inputs [2].

As a second possibility one may take the existence of a substantial resting state activity as an indication that the brain is not a driven system, in terms of stimulus-response functionalities, but a modulated organ [42, 43]. The ongoing and to most parts self-sustained activity involves in this view non-trivial information processing, which is in general redirected, viz modulated by incoming sensory stimuli [44, 45], but not driven. Only stimuli of exceptionally large intensities would force subsequent brain areas to specific responses. Sensory inputs interact in this view with the ongoing transitions between internal cognitive states [46, 47], which means that perception induces transitions among neuronal attractor states [48].

A candidate framework for the modulated interaction between brain and outside world is semantic learning, for which pre-existing internal states acquire semantic meaning while interacting with the environment [49]. This process is ongoing, viz while the brain is autonomously sampling available internal states. Learning occurs when sensory stimuli redirect the sequence of neuronal states. Experimentally, there are indeed indications that the brain acts as a nonlinear dynamical system, with trajectories that are tightened when performing a task [50].

The distinction between modulated and driven systems is, strictly speaking, not rigorous. In both cases sensory stimuli leave in the end an imprint on the brain. It is however a question of starting points. In physics, to give an example, one can develop the theory of a non-ideal gas starting either from zero temperature, or from the high-temperature limit. Depending which regime one wants to describe, either can be the better starting point. The same holds in our view for the role of the resting state activity. We posit here that the appropriate starting point for the brain is the hypothesis that the autonomous activity involves non-trivial internal computations which are essential to the functioning of the brain, and not just an side effect.

As an interesting twist one could speculate which ingredients are necessary for an hypothetical, silicon-based artificial brain. Assuming that such an AI would be based on biological correspondence principles, the question would be whether an operational regime close to criticality is just performance enhancing, or a *conditio sine qua non*, with the first option corresponding to the viewpoint that the brain is in essence a reflexive organ.

4.2. Stationary resting state activity

There are good reasons to assume, as pointed out above, that the resting state activity of the brain has intrinsic functionality [51], viz that it is doing more than to help the brain to process incoming stimuli somewhat more efficiently. See, e.g., [52] for a review. Following the stationarity principle, this implies that the overall amplitude of the autonomous activity needs to be regulated. This can be achieved for an arbitrary spectral radius $0 < R_w$ when tuning up the afferent synaptic weights correspondingly, namely by selecting an appropriate

σ_{ext} . Compare figure 3. The desired internal activity level could be generated in this way, at least as a matter of principle. There are however two caveats.

The first point regards the balance between invoked and internally generated activity, given that an R_w substantially lower than unity is characteristic for driven systems. There would be no room for a non-trivial resting-state dynamics. The second caveat is that the intensity of the input, quantified in (8) by the average standard deviation σ_{ext} , is not constant. Consider as an example the task dependency of the activity levels of specific brain areas, which can be in part substantial [53]. These are typically local enhancements with only limited impact on the overall energy consumption of the brain in its entirety [36]. Brain areas project however further on, which implies that the respective downstream areas have to deal with varying levels of input intensities, which is arguably a generic feature of neural circuits. In the end, the only venue to attain neural activity that is generated internally, at least in good part, is a spectral radius close to unity. This view is consistent with an analysis of *in vivo* spike avalanches that indicates that the brain is slightly subcritical [6].

4.3. Regulated or self-organized criticality?

It has always been controversial, what the term ‘self organization’ exactly means [54]. Roughly speaking, it implies that novel, somewhat non-trivial properties emerge from basic rules [19]. In particular one would like to see that the emerging properties do not result from a straightforward ‘get out what you put in’ mechanism. These considerations definitively hold for the original concept of self-organized criticality by Bak *et al* [55], for which power-law scaling results from two ingredients: infinite time scale separation and energy conservation [7]. The situation is less clear when it comes to the explicit regulation of a system close to the point of a phase transition. The resulting system will be critical, but clearly not in a ‘self-organized’ critical state [56]. An example for a basic rule allowing a neural network to adapt towards criticality is flow control, as defined by (7). A state close to criticality may be achieved also indirectly by tuning in first place the EI (excitation/inhibition) balance [57, 58].

5. Routes towards criticality

When it comes to evolve neural networks towards criticality, all proposed methods regulate in the end the flow of activity through the network. Whether the flow contracts or expands is determined by the spectral radius (5) of the propagator in question, which is typically composed of the synaptic weight matrix modulo neuronal rescaling factors, such as the gain. The various conceivable routes for achieving stationarity, either directly or indirectly, can be classified along several criteria:

- Direct vs indirect.
- Online vs offline.
- Adapting synaptic weights vs other parameters.

Direct methods control the flow explicitly, indirect approaches do not. Online routes towards criticality can be implemented while the system is operative, ideally while processing afferent signals. Offline algorithms consider on the other side isolated systems. The prime target for adaption is often the synaptic weight matrix, a procedure which could interfere however with internal Hebbian-type learning. Other parameters to be adapted are either global, e.g. in the context of neuromodulation, or local. Examples for the latter case are individual neuronal gains and thresholds. Of importance is also how long it takes to close in towards criticality, at least in order of magnitude. Note in this regard that the time scales for compensatory mechanisms in the brain are often faster in models, than experimentally reported [59]. On the backdrop of these general considerations, we discuss now some representative examples, albeit without aiming for completeness. For an overview regarding the role of distinct types of synaptic plasticities see [60].

A direct and potentially online method is anti-Hebbian tuning [61], which acts expressively on the synaptic weight matrix. Time is continuous, which implies that the real part of the eigenvalues of the synaptic weight matrix matter, as laid out in section 3. Interestingly, not just the real part of the largest, but of all eigenvalues are forced to adapt to zero, which is not the case for standard echo-state frameworks. For anti-Hebbian tuning non-local information is necessary, namely the cross correlation of arbitrary pairs of neurons.

An example for an indirect algorithm is a proposal by Bornholdt and Rohlf [62], which makes use of the properties of the attracting states emerging in fully isolated systems. The update rules of the connection matrix are dependent in this scheme on the properties of the observed attractors [63]. The method is hence offline, with an diverging timescale for the adaption process, which may be in conflict with the experimentally observed lack of neuronal time-scale separation [6, 64].

A recently investigated abstract mechanism makes use of the fact that order-parameter fluctuations, in essence the susceptibility, peak at the locus of a second order phase transition [65]. Adapted is a global

parameter, the temperature. For the estimates of the order-parameter fluctuations non-local information is necessary. A generalization to systems with external fields, viz inputs, should be possible.

Adaption mechanisms for fully operative systems, viz for networks continuously processing incoming signals, are a rare species. An example is flow control, which regulates the flow of activity through individual neurons, using an adaption scheme that is based on locally available information. Regulating intrinsic neuronal parameter, typically the gain [3], an online method is obtained. Here the spectral radius R_w enters expressively the stationarity condition for the neuronal activity, as given by (7).

6. Discussion

It is tempting to assume that enhanced information processing [66, 67] is the prime evolutionary driver for cortical networks to evolve close to a critical point [68]. We have pointed here to an alternative, namely the need to maintain a non-trivial level of autonomously generated neural activity. To this regard several adaption mechanisms encoding the evolution of an operative system towards the onset of a second order phase transition have been proposed, by monitoring either the intrinsic activity, as for flow control [3], or higher-order correlation functions [65]. A common precondition is the existence of a non-vanishing ongoing activity that is not induced in its entirety by external inputs. The rationale is straightforward. Internally generated activity is directly impacted by a nearby critical point, evoked activity in contrast only indirectly—which loops back to the starting point, the assumption that the resting state activity has key functionalities. To which extend this assumption holds needs in our view further efforts regarding the study of the interplay between the autonomous brain dynamics and cognitive information processing. Present data seem to support the notion that ongoing neural activity does not just encode statistically structured noise, but multidimensional behavioural information [69].

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Data availability statement

Any data that support the findings of this study are included within the article.

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