Unifying criticality and the neutral theory of neural avalanches

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Abstract

The distribution of collective firing of neurons, known as a neural avalanche, obeys a power law. Three proposed explanations of this emergent scale-free behavior are criticality, neutral theory, and self-organized criticality. We show that the neutral theory of neural avalanches can be unified with criticality, which requires fine tuning of control parameters, and rule out self-organized criticality. We study a model of the brain for which the dynamics are governed by neutral theory. We identify the tuning parameters, which are consistent with experiments, and show that scale-free neural avalanches occur only at the critical point. The scaling hypothesis provides a unified explanation of the power laws which characterize the critical point. The critical exponents characterizing the avalanche distributions and divergence of the response functions are shown to be consistent with the predictions of the scaling hypothesis. We use an universal scaling function for the avalanche profile to find that the firing rate for avalanches of different sizes shows data collapse after appropriate rescaling. Critical slowing-down and algebraic relaxation of avalanches demonstrate that the dynamics are also consistent with the system being at a critical point. We discuss how our results can motivate future empirical studies of criticality in the brain.

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I. INTRODUCTION

Systems with many interacting units can lead to phenomena at macroscopic scales which cannot be elucidated from microscopic behavior [1, 2]. For a system tuned to its critical point, emergent phenomena occurs at all length scales and can be partially understood using concepts like scaling and universality [1, 3]. There is a growing interest in the question whether certain biological systems operate near a critical point [4-6]. One case that has received a great deal of attention is the question of whether the brain operates near a critical point [4] and is commonly referred to as the criticality hypothesis [4]. Experiments have shown that neural avalanches in vivo and in vitro exhibit scale-free behavior similar to thermal systems near the critical point [7-11]. The interest in the criticality hypothesis has been amplified by arguments that criticality in the brain may benefit memory storage and information processing [4, 12, 13].

Although scale-free avalanches have been observed in real neural systems [7], the existence of a tuning parameter is disputed [14, 15]. This has lead to an alternate explanation that neural systems self-organized criticality [16, 17] where systems generically exhibits power law distributions without the need for any tuning [18]. However, self-organized criticality has strict requirements such as time-scale separation and local conservation laws that may not apply to neural systems [19, 20].

The temporal-proximity binning method of defining neural avalanches [7-11] can show discrepancies from the true behavior of avalanches especially when multiple avalanches are propagating through the system [19, 21]. Reference [19] partly addressed this issue by introducing the neutral theory model where avalanches are defined by tracking causal-connections between firing neurons. Authors of the neutral theory model [19] have suggested that the scale-free neural avalanches may be explained without criticality.

Three competing explanations of scale free neural avalanches are criticality, neutral theory and self-organized criticality. Our main result is that neutral theory of neural avalanches can be reconciled with criticality but not self-organized criticality. We show that the causally-connected avalanches in the neutral theory model [19] follow a power law distribution only at the critical point. As we tune the system away from the critical point, large avalanches are suppressed. Additionally, the response functions diverge as power laws as the critical point is approached, analogous to thermal systems [11]. Our results indicate that the neutral theory
model is consistent with the predictions of the scaling hypothesis, which is a mathematical framework used to study systems near a critical point. We show that the scaling field in the system unifies the different tuning parameters in experiments [7, 8, 22, 23]. Additionally, we find that universal scaling functions describe the avalanche profile and relaxation dynamics. In addition to showing neutral theory of neural avalanches is consistent with criticality, we discuss why it cannot be reconciled with self-organized criticality.

The paper is structured as follows. In Sec. [II] we outline the neutral theory model and discuss the connections to experimental studies of criticality in neural systems. Our main results are summarized in Sec. [III] In Sec. [IIIA] we measure the critical exponents $\tau$, $\sigma$ and $\gamma$ which characterize the scale-free behavior in the neutral theory model. We show that our measured critical exponents are consistent with the scaling hypothesis in Sec. [IIIB] In Sec. [IIIC] we use scaling arguments to derive the universal avalanche profile and show data collapse for the firing rates for avalanches of different sizes. Critical slowing down in the neutral theory model is analyzed in subsection [IID] In Sec. [IIIE] we use tools from non-equilibrium statistical mechanics to analyze the universal relaxation dynamics in the neutral theory model near the critical point. Lastly, in Sec. [IV] we discuss how our analysis supports the idea that scale-free neural avalanches in the neutral theory model is due to the critical point. We also discuss how our results may inform future empirical studies of neural systems.
II. MODEL

The brain is a complex system consisting of many interacting neurons. In the resting state, neurons have intrinsic voltages which fluctuate around some residual value. A neuron, triggered by some stimuli (endogenous or external), sends voltages or spikes to its connected neighbors. A recipient neuron may also fire and send its voltage to the connected neighbors thereby resulting in an avalanche. The firing neurons in this avalanche are causally-connected. The neutral theory model [19] introduced the idea of defining neural avalanches using causal-connection and showed that this definition of neural avalanches does not suffer the ambiguities commonly found in the temporal-proximity binning method [21]. In the neutral theory model, multiple neural avalanches can propagate concurrently because of the causally-connected definition. The avalanches are neutral [19, 24] or symmetric because the rates that describe the dynamics of the avalanches are the same for all labels.

![Diagram of neural avalanches](image)

**FIG. 1. Neutral theory describes the dynamics of causally-connected neural avalanches.** Different colors correspond to different causally-connected avalanche. The rates for the dynamics are identical for all avalanches. A new avalanche is triggered at the driving rate, $\epsilon$. An active neurons can trigger an inactive neuron at the propagation rate $\lambda$. Both neurons share the same label as they are causally-connected. An active neuron becomes inactive at the decay rate, $\mu$. For neural avalanche labeled by black, the size $S = 2$ is the total number of activated neurons and the duration $D = 2$ is the time elapsed between the first activation until all the black neurons with becoming inactive.
The neutral theory model consists of $N$ neurons which are fully connected. Every neuron interacts with every other neuron. Each neuron can be either inactive, $I$, or active $A_k$, where the index $k$ denotes the avalanche label. In Fig. 1, different colors correspond to different causally-connected avalanches. The stochastic dynamics of the avalanches are described by rate equations. A new avalanche with a new label is triggered at the driving rate, $\epsilon$. An avalanche increases in size at the propagation rate, $\lambda$, as inactive neurons are triggered by active neurons. Active neurons become inactive at the decay rate, $\mu$. The rate equations describing the neutral theory model \cite{19} are

\begin{align}
I & \xrightarrow{\epsilon} A_{\text{max}[k]+1} \\
I + A_k & \xrightarrow{\lambda} A_k + A_k \\
A_k & \xrightarrow{\mu} I
\end{align}

An avalanche ends when all neurons with a given label $k$ become inactive. The avalanche size $S$ is the number of activations and the avalanche duration $D$ is the time between the activation of the first neuron with label $k$ to when all neurons with index $k$ become inactive, as shown in Fig. 1.

The neutral theory model captures many of the salient biological mechanisms relevant to neural avalanches. The ratio of inhibitory to excitatory neurons \cite{7, 22, 23} and the spontaneous triggering rate \cite{8} affect the statistics of neural avalanches. In the neutral theory model, we can tune the propagation rate, $\lambda$, and the decay rate, $\mu$, to achieve a similar result to varying the ratio of inhibitory and excitatory neurons in experiments. The driving rate, $\epsilon$, in the neutral theory model is analogous to the spontaneous triggering of neurons \cite{8}. We can explore the criticality of neural avalanches in the neutral theory model in a way that is comparable to experiments.
III. RESULTS

One of the main results is that behavior of the neutral theory model is consistent with a critical point, which requires fine tuning of the control parameter to observe scale-free behavior. Although the dynamics of the neural avalanches in the model are neutral, we show that the proximity to the critical point controls the characteristic scale of the neural avalanches, in contrast to the claims in Ref. [19]. The neural avalanches satisfy power law distributions characterized by critical exponents only at the critical point. We determine how the response function diverges as the critical point is approached. We use the scaling hypothesis [1, 25] to find criteria for criticality. Our measured critical exponents are consistent with the predictions of the scaling hypothesis. We also find universal scaling functions for the causally connected neural avalanches. The neutral theory model exhibits critical slowing down as the system approaches the critical point. By using tools from directed percolation, we find that the relaxation dynamics shows algebraic decay at the critical point.
A. Approaching Criticality

When a system is tuned to its critical point, emergent phenomena occurs at all length scales and the system is said to be scale free [1]. We show that the distribution of avalanche sizes and durations follows power laws only when the neutral theory model is tuned to its critical point. As the system is tuned away from the critical point the large avalanches are suppressed. Although the distribution of size and duration of smaller avalanche still yield the same power law exponents, there is an exponential cutoff for large events [26, 27]. The mean avalanche size also diverges as a power law as the system approaches critical point.

One of the challenges of the criticality hypothesis is that the tuning parameters in real neural systems are not known. Different experiments have suggested different tuning parameters [8, 22, 23]. In Ref. [8], the experiments in vitro and in vivo show that the spontaneous triggering rate of neurons may be interpreted as a tuning parameter. This parameter corresponds to $\epsilon$ in the neutral theory model. The experiments reported in Ref. [7, 22, 23] use pharmacological means to alter the excitation-inhibition ratio to alter proximity to the critical point. We can achieve similar results by varying the rates $\lambda$ and $\mu$. Our analysis shows that the scaling field for the neutral theory model is a function of the driving rate $\epsilon$ and propensity $\Delta = \mu - \lambda$, which unifies the different experimental results [7, 8, 22, 23]. We find that the critical point for the neutral theory model is $\Delta = \mu - \lambda = 0$ and $\epsilon = \epsilon_c$. The critical value of the driving rate, $\epsilon_c$, corresponds to infinitesimal driving such that there is at most one causally connected neural avalanche.

In Fig. 2, we see that the distribution of the avalanche sizes, $n_S$, and duration, $n_D$, satisfy power law at the critical point with the exponents $\tau$ and $\tau_D$. As we tune the system away from the critical point by increasing the driving rate, $\epsilon$, or by decreasing the propensity, $\Delta$, we find exponential suppression of the large avalanches characterized by the exponents $\sigma$ and $\sigma_D$ for the size and duration respectively. The distribution functions for the avalanche size and duration are

$$n_S \sim S^{-\tau} \exp[-(\epsilon + \Delta)S^\sigma]$$

(4)

$$n_D \sim D^{-\tau_D} \exp[-(\epsilon + \Delta)D^{\sigma_D}]$$

(5)

Our measured value of $\tau$ and $\tau_D$ in Fig. 2 are consistent with the theoretical mean field values, $\tau^{\text{MF}} = 1.5$ and $\tau_D^{\text{MF}} = 2$ [4].
In many systems, the response functions diverge as the critical point is approached \cite{1}. A commonly used response function is the mean avalanche size, $\chi$, as defined in percolation theory \cite{27,28}, is given by

$$\chi = \frac{\sum S^2 n_S}{\sum S n_S}. \quad (6)$$

The mean avalanche size, $\chi$, is analogous to the susceptibility in thermal systems. $\chi$ diverges with the critical exponent $\gamma$ as the critical point is approached \cite{1,27}. In Fig. 3, the exponent, $\gamma$, is found to be the same whether the critical point is approached by decreasing $\Delta$ at $\epsilon_c$ or by decreasing $\epsilon$ at critical value of propensity $\Delta = 0$. When we vary $\Delta$ we measured $\gamma = 2.00 \pm 0.02$ and when we vary $\epsilon$ the exponent is $\gamma = 1.97 \pm 0.04$.

Our data indicates that the neutral theory model exhibits scale-invariant avalanches at the critical point. The mean avalanche size diverges as the critical point is approached. These measured power laws are the first evidence that the neutral theory is consistent with criticality. Furthermore, the requirement of tuning to the critical point implies that the neutral theory model is inconsistent with self-organized criticality, where scale-free phenomena are independent of any tuning parameter.
FIG. 2. The distribution of avalanche sizes and durations follows a power law at the critical point, $\Delta = 0$ and $\epsilon = \epsilon_c$. As the system is tuned away from the critical point, there is an exponential suppression of large avalanches. The various exponents are the same for both tuning parameters. In the top row, $\Delta = 0$ and $\epsilon$ is varied. (A) The exponents for the avalanche size distribution $\tau = 1.53 \pm 0.05$ and $\sigma = 0.55 \pm 0.08$. (B) The avalanche duration distribution is characterized by exponents $\tau_D = 1.92 \pm 0.11$ and $\sigma_D = 0.93 \pm 0.16$. In the bottom row, $\Delta$ is varied for $\epsilon = \epsilon_c$. (C) For the avalanche size distribution, the exponents are $\tau = 1.51 \pm 0.05$, $\sigma = 0.54 \pm 0.12$. (D) $\tau_D = 1.93 \pm 0.11$, $\sigma_D = 1.02 \pm 0.15$ are the critical exponents for the avalanche duration distribution.
FIG. 3. The mean avalanche size, $\chi$, diverges as the system approaches the critical point. The exponent $\gamma$ characterizes the divergence and is the same for when the critical point is approached at constant driving $\epsilon_c$ or constant propensity $\Delta = 0$. (A) For constant driving $\epsilon_c$, varying the propensity $\Delta$ the exponent is $\gamma = 2.00 \pm 0.02$ (B) Varying the driving rate, for constant propensity $\Delta = 0$, the exponent is $\gamma = 1.97 \pm 0.04$. 
B. Scaling Hypothesis

The scale free behavior at critical points can be attributed to underlying singularities [1, 26]. The scaling hypothesis assumes that near the critical point, the response functions can be described by generalized homogeneous functions [1]. The predictions of the scaling hypothesis have been verified in both experiments and numerical models [1]. According to the scaling hypothesis, the different power laws, characterized by critical exponents, are interconnected as they are caused by the same underlying mechanism.

Near the critical point, we can write the avalanche size distribution as \( n_S(S) \approx S^{-\tau} G(S/S_\xi) \), where, \( G(S/S_\xi) \) is a scaling function that depends on proximity to the critical point. The characteristic avalanche size scales as \( S_\xi \approx \epsilon^{-1/\sigma} \) for \( \Delta = 0 \) near the critical point. We can write the response function in Eq. 6 as

\[
\chi = \frac{\sum_S S^2 n_S}{\sum_S S n_S} = \frac{\int_1^\infty S^{2-\tau} G(S/S_\xi) \, dS}{\int_1^\infty S^{1-\tau} G(S/S_\xi) \, dS},
\]

We make change of variables \( u = S/S_\xi \) to find

\[
\chi = \frac{S_\xi^{3-\tau} \int_{1/S_\xi}^{\infty} u^{2-\tau} G(u) \, du}{S_\xi^{2-\tau} \int_{1/S_\xi}^{\infty} u^{1-\tau} G(u) \, du},
\]

and set \( G(u) = \exp(u) \) [26] to express \( \chi \) as

\[
\chi = S_\xi \frac{\Gamma(3-\tau)}{\Gamma(2-\tau)},
\]

where \( \Gamma \) is the gamma function. Near the critical point, the response function scales

\[
\chi \sim S_\xi \sim \epsilon^{-1/\sigma} \sim \epsilon^{-\gamma}.
\]

Our measured exponents in Figs. 2 and 3 is consistent with the predictions with Eq. 11 which shows that \( \gamma = 1/\sigma \). The results are the same when we vary \( \Delta \) at \( \epsilon_c \). Our derivation is very similar to scaling arguments commonly used in percolation theory [27], except that the denominator of the response function also contributes to the divergence.

We can also relate the size of the neural avalanche to the duration using similar scaling arguments. As the critical point is approached by varying \( \epsilon \) for \( \Delta = 0 \), the average avalanche size scales as \( \langle S \rangle \sim \epsilon^{-1/\sigma} \), correlation length scales as \( \xi \sim \epsilon^{-\nu} \) and the decorrelation time
FIG. 4. The scaling of the average avalanche size as a function of the duration at the critical point is consistent with the scaling laws. For $\epsilon_c$ and $\Delta = 0$, the $\langle S \rangle \sim D^{1/\sigma \nu z}$, the numerical estimate of $\frac{1}{\sigma \nu z} = 1.93 \pm 0.03$ is consistent with Eq. 13.

scales as $t \sim \xi^z$, where $z$ is the dynamic critical exponent. At the critical point, the scaling of the avalanche size and durations are given by $n_S \sim S^{-\tau}$ and $n_D \sim D^{-\tau_D}$. From the scaling it follows that

$$\langle S \rangle \sim D^{1/\sigma \nu z}. \quad (12)$$

The same scaling arguments can be used when $\Delta$ is varied for $\epsilon_c$. Relating this to our earlier scaling relation between the avalanche size and duration, we find the identity

$$\frac{\tau_D - 1}{\tau - 1} = \frac{1}{\sigma \nu z}. \quad (13)$$

We measure the exponents on the left and right side of Eq. 13 independently. The measured value of $1/(\sigma \nu z) = 1.93 \pm 0.03$ is consistent with $(\tau_D - 1)/(\tau - 1)$ in Fig. 2. The scaling arguments presented here are similar to the analysis of Barkhausen noise in magnetic systems[25].

The predictions of the scaling hypothesis provide stricter criteria for criticality than just the existence of a power law distribution. We have used scaling arguments to show that the different measured critical exponents are connected. Additionally, we used simple
scaling arguments to deduce the relation between the average size and duration, which was then numerically verified. Our results show that the neutral theory is consistent with the prediction of the scaling hypothesis.
C. Universality

Another remarkable consequence of the scaling hypothesis is the existence of universal scaling functions which are usually obtained via data collapse [1, 3, 25], where results for different values of the control parameters collapse on to a single curve after appropriate rescaling.

We show that the avalanche profile, which describes the firing rate as a function of time, can be described by a universal scaling function. The firing rate corresponds to the number of activations per unit time. From the scaling hypothesis, we assume the average firing rate is described by a generalized homogeneous function which can be written as

\[ f_R(t, D) = D^b f_R(t/D) \]

The exponent \( b \) can be obtained by using

\[ \langle S \rangle(D) = \int f_R(t, D) dt = \int f_R(t/D) dt \approx D^{b+1}. \]  

By using the scaling identity \( \langle S \rangle(D) \sim D^{1/(\sigma \nu z)} \), we find \( b = 1/(\sigma \nu z) - 1 \). Figure 5 shows the data collapse for avalanches of different durations, when we scale the firing rate by \( D^{1-1/(\sigma \nu z)} \) and plot it as a function of the scaled time \( t/D \).
FIG. 5. Neural avalanches have an universal avalanche profile at the critical point. The firing rate scaled by \( D^{1-1/(\sigma \nu z)} \) as a function of the scaled time \( t/D \) shows data collapse for avalanches of different durations.

Data collapse is an impressive example of universality in neural avalanches. Universal scaling functions can be used as strict criteria for criticality as the data collapse is only observed sufficiently close to the critical point. Data collapse for the avalanche profile holds for \textit{in vitro} experiments under certain circumstances \cite{9} and may be used as a test for criticality in future experiments.
D. Critical Slowing down

A well-known consequence of criticality is a divergent timescale \[29\], which is known as critical slowing down. Here, we analyze how the time to reach a stationary state diverges as the system is tuned to the critical point.

We study the equilibration time for neutral theory model after initializing with a single active neuron. We determine that the system has reached a stationary state when the number of unique causally-connected avalanches, \( U(t) \), reaches a constant rolling time average. In Fig. 6 we plot the time for \( U(t) \) to reach a steady-state, \( t_E \), as a function of the driving rate \( \epsilon \) at \( \Delta = 0 \). We can use scaling arguments to relate the dynamic exponent \( z \) to the other critical exponents. The correlation length and time scale as \( \xi \sim \epsilon^{-\nu} \) and \( t_E \sim \xi^z \) respectively. As the system approaches the critical point, \( t_E \) diverges as \( t_E \sim \xi^z \sim \epsilon^{\nu z} \). Our measured dynamic critical exponent \( \nu z = 0.95 \pm 0.04 \), is consistent with Eq. 13 and \( 1/(\sigma \nu z) \), where \( \sigma \) is measured independently. The results remain the same when we repeat the analysis using the total activity, \( \rho \), instead of \( U \).

![Equilibration time, \( t_E \) diverges as the system approaches the critical point \( \epsilon \to 0 \) with \( \Delta = 0 \). \( t_E \) is the the time for \( U \) to reach a steady-state value when the neutral theory model is initiated with single active neuron. We find \( t_E \sim \epsilon^{-\nu z} \), where the measured value, \( \nu z = 0.95 \pm 0.04 \), is consistent with scaling arguments.](image)

We have shown that the neutral theory exhibits a divergent timescale characteristic of
critical systems. Additionally, the measured dynamic exponent is consistent with our predictions using scaling arguments. This further highlights the universality of the neural avalanches.
E. Relaxation Dynamics

Neuronal systems may not be in equilibrium because of their dissipative dynamics and the constant bombardment of stimuli [8, 30]. The neutral theory model is related to directed percolation [19], which exhibits a non-equilibrium phase transition [31, 32]. Directed percolation type models have been used to describe a variety of dynamical systems such as liquid spreading through a porous material [33, 34] and the spreading of forest fires [35, 36].

![Graph A: Constant Propensity (Δ = 0)](image1)
![Graph B: Constant Driving (ε = εc)](image2)

**FIG. 7.** The number of unique causally-connected avalanches, \( U(t) \) decays as a power law, \( U \sim t^{-\alpha} \), at the critical point. The measured critical exponent \( \alpha = 0.99 \pm 0.04 \) matches mean field directed percolation prediction, \( \alpha_{\text{MF}} = 1 \). (A) For subcritical driving, \( U \) reaches a steady state. (B) For subcritical propensity, \( U \) decays exponentially to the absorbing state. Inset plots show data collapse for rescaled axis, \( Ut^\alpha \) as a function \( t(\epsilon + \Delta)^{-\nu z} \).

A common technique in directed percolation is to initialize the system in a fully active state and analyze the relaxation to either a fluctuating state or an absorbing(inactive) state [31, 32]. We initialized the neutral theory model with every neuron active and belonging to a unique causal avalanche. In Fig. 7A, the system decays to an absorbing state as we have set the driving rate \( \epsilon = 0 \). We find that the number of unique avalanches, \( U(t) \), decays as a power law for the critical value of the propensity, \( \Delta = 0 \), and exponentially for subcritical values. In Fig. 7B, we set \( \Delta = 0 \) and vary the driving rate \( \epsilon \) and analyze how
the system decays to an absorbing state. The critical exponent $\alpha$ characterizes the power law relaxation. Our measured value is $\alpha = 0.99 \pm 0.04$ in Fig. 7 and is consistent with the mean-field value of $\alpha_{MF} = 1$ \[32\]. Inset plots in Fig. 7 shows data collapse for the relaxation of $U(t)$ by plotting the rescale variables $U \rightarrow Ut^\alpha$ and $t \rightarrow (t|\epsilon + \Delta|)^{\nu z}$.

Our analysis other dynamical properties in the neutral theory also support criticality. For finite values of the driving rate $\epsilon$, the system evolves to a stationary state. The time-averaged value of the number of unique clusters scales as $\langle U \rangle \sim \epsilon^\lambda$ where $\lambda = 0.80 \pm 0.02$. The time scale to reach the stationary state diverged with a similar exponent in Sec \[III\]D.

By analyzing the neutral theory model using tools of non-equilibrium statistical mechanics, previously used in the study of directed percolation, we have found characteristic power laws at the critical point. Furthermore, the data collapse for the decay of $U(t)$ highlights the universal dynamics in the neutral theory model near the critical point.
IV. DISCUSSION

Scale-free neural avalanches \textit{in vivo} and \textit{in vitro} are a remarkable emergent phenomena which have intrigued physicists \cite{1} and neuroscientists \cite{15}. The theory of critical phenomena is a promising explanation of the scale-free behavior \cite{9, 10, 37}, and is further motivated by the arguments that criticality in the brain may have functional advantages \cite{38}.

Neutral theory \cite{19} and self-organized criticality \cite{16, 17} have been proposed as alternative descriptions of scale-free neural avalanches. One of our main results is that the neutral theory of neural avalanches is consistent with the criticality hypothesis but not with self-organized criticality. As we vary the different parameters in the neutral theory model to its critical point, the response function exhibit a power law divergence, similar to thermal systems \cite{1}. Additionally, the causally-connected neural avalanches show scale-free distributions only at the critical point. Large neural avalanches are exponentially suppressed as we tune the system away from the critical point. This is in contrast to systems which exhibit self-organized criticality, where power law distributions are a generic feature. Reference \cite{19} report the $\tau$ and $\tau_D$ exponent, which is consistent with our measured values. Our analysis supports the interpretation that an underlying critical point is responsible for the scale-free neural avalanches in the neutral theory model.

Using the scaling hypothesis, we construct a strict criteria for criticality in the neutral theory model. Our measured exponents are consistent with the predictions of the scaling hypothesis. We also use simple scaling arguments to relate the average avalanche size to the duration and numerically verify the result. A striking prediction of the scaling hypothesis is the existence of universal scaling functions. In the neutral theory model, the avalanche profile shows data collapse after appropriate rescaling. Our results highlight the universality of neural avalanches.

We show that the dynamical properties of the neutral theory model are also consistent with criticality. When we initialize the system with a single active neuron, the system reaches a steady state over some characteristic time. As the critical point is approached, we find there is a divergent timescale. The dynamic critical exponent characterizes the critical slowing down and our measured value is consistent with scaling arguments. Using methods from directed percolation, we analyze how the system relaxes from a maximally diverse state. We find deviations from power law decay to both the absorbing or fluctuating state.
that depend on the distance from the critical point. By using simple scaling arguments, we find data collapse for the relaxation dynamics.

Our analysis of the neutral theory model is in agreement with experiments \cite{8, 22}. We can vary the driving rate, $\epsilon$, and the propensity, $\Delta$, to control the proximity to the critical point. The experiments in Ref. \cite{8} imply that the control parameter may be the spontaneous triggering rate, which corresponds to the driving rate $\epsilon$ in the neutral theory model. In separate experiments \cite{7, 22, 23}, the excitation-inhibition ratio was varied to tune the system towards criticality, which we achieved by varying the propensity, $\Delta$ in the neutral theory model. Our results unify the two seemingly disparate methods of tuning the system towards criticality.

Our results may motivate future experimental studies of neural avalanches. The divergence of the response function can be used to locate the critical point in real neural systems. Additionally, we find data collapse of the avalanche profile at the critical point. Experiments in Ref. \cite{9} reported similar data collapse for certain samples. An important question is whether the parameters in the neutral theory model correspond to the same values in the experiments. Our results emphasize the need to incorporate causal connections in future experiments studying neural avalanches as pointed out by Ref. \cite{19}.

Numerous studies \cite{4, 12, 13} have discussed the possible functional benefits of criticality in the brain. Our results raise the important question of whether these benefits also apply to biological learning mechanisms such as spike-timing-dependent plasticity STDP which uses causal information about firing neurons \cite{19}.

In summary, we have presented a case for unifying criticality with the neutral theory of neural avalanches. Our results can explain past experimental data \cite{7, 8}, motivate questions for future studies and provide a promising first step for a unified theory of neural avalanches.

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