# Replication Report: Neutral Theory and Scale-Free Neural Dynamics

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## Abstract

Neutral dynamics, originally introduced in population genetics and ecology, offers a compelling framework for understanding scale-free phenomena across various domains. In this study, we investigate the emergence of scale-free neural avalanches—spontaneous bursts of brain activity—through a neutral theory perspective. By modeling neural activity as a competition among indistinguishable events for limited active sites, we demonstrate that scale-invariant avalanche size and duration distributions naturally arise, independent of criticality. The results show that causal avalanches, driven by propagation dynamics, exhibit robust power-law behavior, differing significantly from experimentally measured time-binned avalanches. This work highlights the potential of neutral dynamics to explain the diversity and functional relevance of neural avalanches, offering a novel lens to study spontaneous brain activity and its role in information processing and memory.

## 1 Introduction

The introduction of the neutral theory by Kimura in 1968 revolutionized our understanding of population genetics and molecular evolution by proposing that most evolutionary changes result from genetic drift acting on neutral alleles [?]. Similarly, Hubbell extended this concept to ecology, suggesting that the variability in ecological communities arises from stochastic, neutral dynamics among equivalent species [?]. Neutral theories share a key principle: the absence of intrinsic differences among coexisting individuals, with their dynamics driven purely by random demographic fluctuations.

In this framework, the introduction of a novel species or element triggers random cascades of changes, or ”avalanches,” which exhibit scale-free behavior. Such scale-invariant distributions of avalanche sizes and durations resemble those observed at critical points, yet emerge independently of fine-tuning to criticality. Neutral models have successfully explained scale-free phenomena across diverse domains, such as microbial epidemics [?], viral propagation [?], and intestinal stem cell renewal [?].

Recent experimental evidence reveals that neural systems exhibit similar scale-free avalanches during spontaneous brain activity [?]. These avalanches, distributed with critical exponents ($\tau \approx \frac{3}{2}$, $\alpha \approx 2$), have been observed across different tissues, species, and experimental setups. The prevalence of such dynamics under normal conditions—and their disruption under anesthesia or pathology—suggests their functional importance for optimal information transmission and processing in the brain.

This work explores the hypothesis that empirically observed scale-free neural avalanches could arise from neutral dynamics, rather than critical self-organization. By modeling the brain as a network of interacting units governed by neutral competition for active sites, we demonstrate that scale-free avalanches can emerge even in the absence of a critical phase transition. Furthermore, we show that causal avalanches, defined by propagation dynamics, differ significantly from those approximated experimentally by temporal proximity. This diversity in avalanche properties could provide the brain with a rich reservoir for efficient coding, learning, and memory.

Their findings challenge the traditional view of criticality as the sole driver of scale-free neural dynamics, offering a novel perspective on the mechanisms underlying spontaneous brain activity.

## 2 Theoretical Background

This section presents the theoretical foundation of the study, focusing on criticality, neutral dynamics, and the mechanisms driving avalanche behavior.

## 2.1 Criticality and Scale-Free Behavior

Criticality describes a system's organization at the boundary between quiescence and activity. At this critical point, the system exhibits scale-free behavior, where events occur over a wide range of sizes and durations, characterized by power-law distributions:

$$P(s) \propto s^{-\tau}, \quad \tau = \frac{3}{2}, \quad P(t) \propto t^{-\alpha}, \quad \alpha = 2.$$

In traditional models, criticality is necessary for scale-free dynamics. However, this study demonstrates that scale-free avalanches can emerge under neutral dynamics, even far from criticality.

## 2.2 Neutral Dynamics

Neutral dynamics assume that all avalanches are dynamically equivalent, governed solely by stochastic fluctuations. This contrasts with critical systems by allowing multiple avalanches to coexist simultaneously. These avalanches compete for active sites but remain neutral, meaning their growth or extinction is random.

## 2.3 Avalanche Mechanism

Avalanches in the model are governed by the following processes:

- Spontaneous Activation: Inactive sites ($I$) are activated at a small rate ($\epsilon$), initiating new avalanches.
- Propagation: Active sites ($A$) propagate activity by activating neighboring inactive sites at a rate ($\lambda$).
- Deactivation: Active sites return to the inactive state at a rate ($\mu$).

These processes ensure that avalanches of varying sizes and durations occur, shaped by random fluctuations and competition for active sites.

### 2.4 Mathematical Description

The density of active sites ($\rho$) is given by:

$$\rho(t) = \sum_{k=1}^{M(t)} \rho_k(t),$$

where $M(t)$ is the number of coexisting avalanches, and $\rho_k(t)$ is the density of active sites for avalanche $k$.

The system's dynamics are governed by the following reactions:

$$I \xrightarrow{\epsilon} A_{M(t)+1}, \quad A_k + I \xrightarrow{\lambda} A_k + A_k, \quad A_k \xrightarrow{\mu} I.$$

In the slow-driving limit ($\epsilon \to 0$), the system exhibits a continuous phase transition at $\lambda_c = \mu$, separating the quiescent and active phases.

### 2.5 Key Results and Novelty

- The model exhibits scale-free distributions for avalanche sizes ($\tau = 3/2$) and durations ($\alpha = 2$) in the active phase ($\lambda > \lambda_c$).
- These scale-free dynamics emerge without the need for fine-tuning to criticality, challenging traditional models.
- The findings highlight the role of neutral dynamics as a robust mechanism for scale-free behavior in neural systems.

This novel framework bridges theoretical predictions and experimental observations, offering new insights into avalanche phenomena.

## 3 Simulation Setup and Parameters

The simulations were designed to study avalanche dynamics in a system of $N = 10^4$ nodes, each of which can exist in either an active or inactive state. The model is based on the framework outlined in the paper, with the following key components and parameters:

## 3.1 Model Details

- Node States: Each node in the network can either be active or inactive.
- Propagation and Deactivation: Active nodes propagate activity to neighboring nodes at a rate $\lambda$ and deactivate at a rate $\mu = 1$.
- Spontaneous Activation: Nodes can become spontaneously active at a small rate $\epsilon$, which varies across simulations.
- Avalanche Dynamics: An avalanche is defined as a sequence of events initiated by a spontaneous activation and propagating through the network until no further activations occur.

## 3.2 Simulation Parameters

- System Size: $N = 10^4$ nodes.
- Propagation Rates: Two propagation rates were studied, $\lambda = 1$ and $\lambda = 2$, to observe their influence on avalanche dynamics.
- Spontaneous Activation Rates: The simulations considered four values of $\epsilon$, namely $\epsilon = 0.1, 0.01, 0.001, 0.0001$, to evaluate the effect of spontaneous activations.
- Time Steps: The system evolves over $10^8$ time steps to ensure the capture of long-term behavior.

## 3.3 Implementation Details

- Time Binning: Avalanches were defined using time-bin tracking based on inter-event intervals (IEI). Each avalanche was characterized by its size and duration.
- Data Collection: Avalanche sizes and durations were calculated and their distributions recorded over the simulation period.
- Log-Binning: Results were log-binned to capture scale-free behavior spanning several orders of magnitude, allowing for comparisons with theoretical predictions.

This setup ensures a thorough exploration of avalanche dynamics under varying conditions, validating the theoretical framework of neutral dynamics through computational simulations.

# 4 Results and Discussion

This section presents the results of the avalanche size distribution simulations for different values of $\lambda$ (propagation rate) and $\epsilon$ (spontaneous activation rate). The analysis is based on the expected power-law behavior $s^{-\tau}$ with $\tau = -\frac{3}{2}$, which is a hallmark of scale-free dynamics in neutral models. The results are compared with the theoretical predictions and interpreted accordingly.

## 4.1 Avalanche Size Distributions for $\lambda = 1$

Figure 1 shows the avalanche size distributions for $\lambda = 1$ at various $\epsilon$ values. The frequency of avalanches is plotted against their sizes on a log-log scale, with the theoretical power-law $s^{-\frac{3}{2}}$ overlaid for reference.

At lower $\epsilon$ values (e.g., $\epsilon = 0.0001$), the avalanche size distributions align closely with the theoretical prediction, particularly for larger avalanches. This agreement indicates that the system exhibits scale-free behavior when spontaneous activations are rare, and dynamics are primarily driven by neutral propagation.

However, as $\epsilon$ increases, deviations from the power-law become apparent. At $\epsilon = 0.1$, the distribution begins to diverge significantly, particularly for smaller avalanches, suggesting that higher spontaneous activation rates disrupt scale-free dynamics by introducing more random, uncorrelated events.

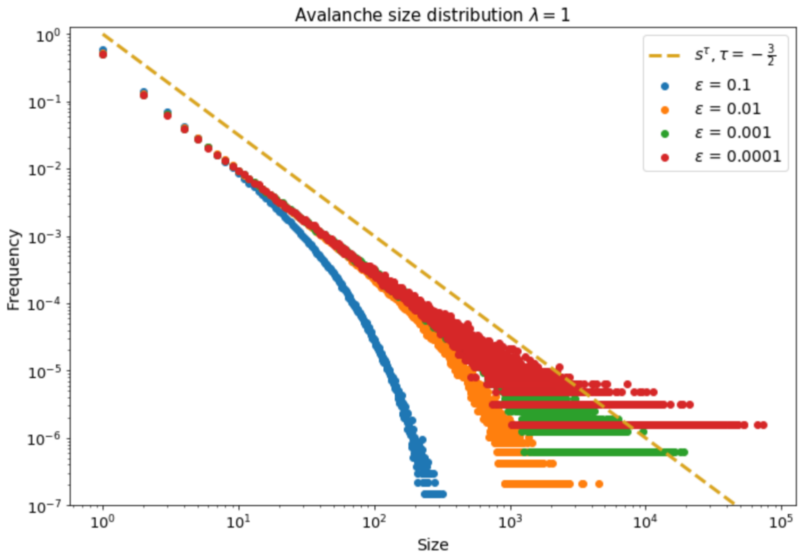


Figure 1: Avalanche size distributions for $\lambda = 1$ at various $\epsilon$ values. The dashed line represents the theoretical power-law $s^{-\frac{3}{2}}$. At lower $\epsilon$, the distributions follow the power-law, whereas higher $\epsilon$ introduces deviations.

Log-binning the data, as shown in Figure 2, provides a smoother representation of the distributions. This analysis reinforces the earlier observation that the system retains scale-free behavior for lower $\epsilon$ values, while higher $\epsilon$ disrupts the dynamics, leading to deviations from the power-law.

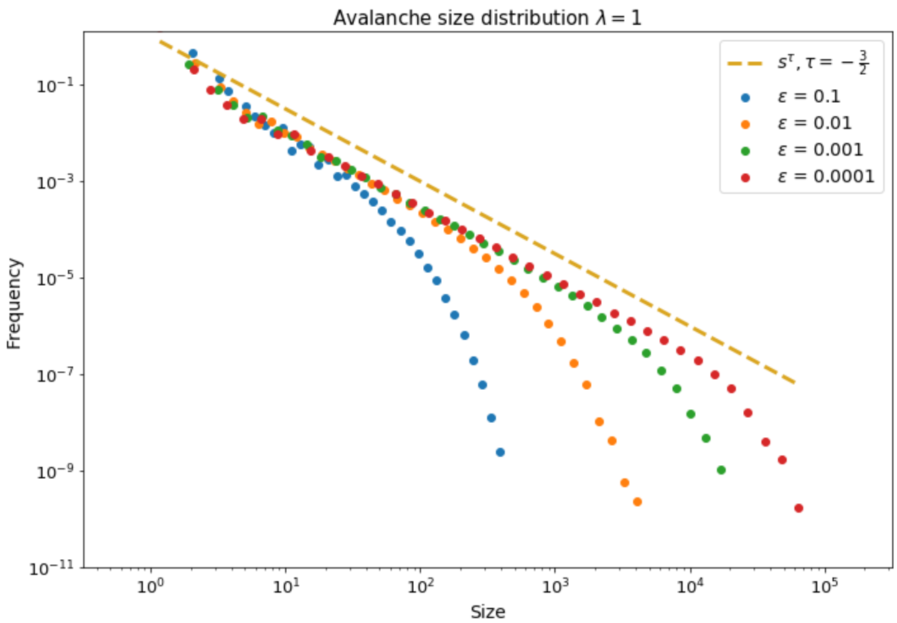


Figure 2: Log-binned avalanche size distributions for $\lambda = 1$ at various $\epsilon$ values. Smoother curves confirm the scale-free behavior at lower $\epsilon$ and deviations at higher $\epsilon$.

## 4.2 Avalanche Size Distributions for $\lambda = 2$

For $\lambda = 2$, the avalanche size distributions are shown in Figures 3 and 4. Compared to $\lambda = 1$, the distributions extend further, supporting larger avalanches due to the increased propagation rate.

At lower $\epsilon$, the distributions exhibit a strong alignment with the theoretical power-law, consistent with neutral theory predictions. As $\epsilon$ increases, the same trend of deviation from the power-law is observed, particularly for smaller avalanches. This confirms that higher spontaneous activation rates disrupt the scale-free nature of the avalanches.

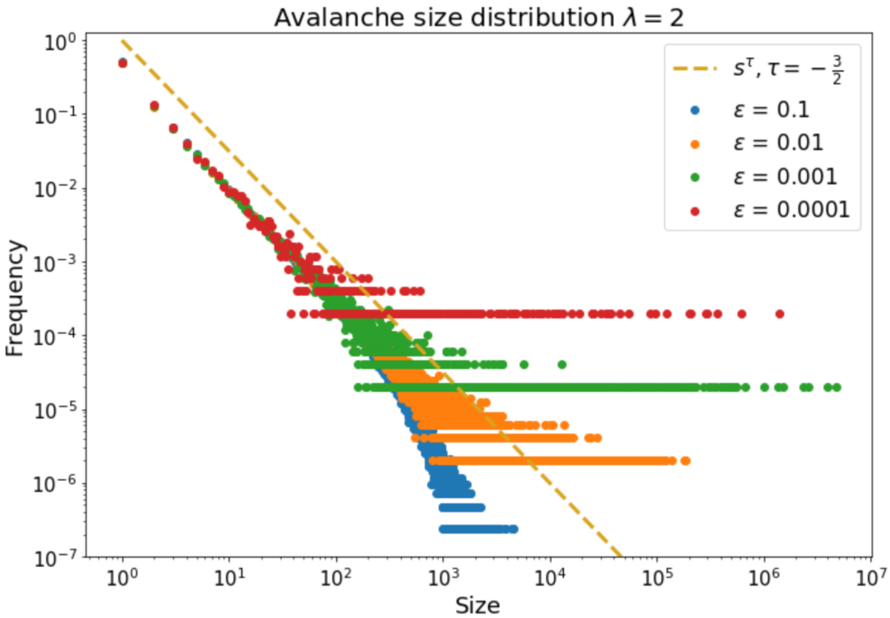


Figure 3: Avalanche size distributions for $\lambda = 2$ at various $\epsilon$ values. Higher $\lambda$ supports larger avalanches, with deviations at higher $\epsilon$.

The log-binned distributions in Figure 4 further illustrate this behavior. The extended tail of the distribution for $\lambda = 2$ highlights the system's ability to sustain larger avalanches compared to $\lambda = 1$, emphasizing the role of propagation rate in driving scale-free behavior.

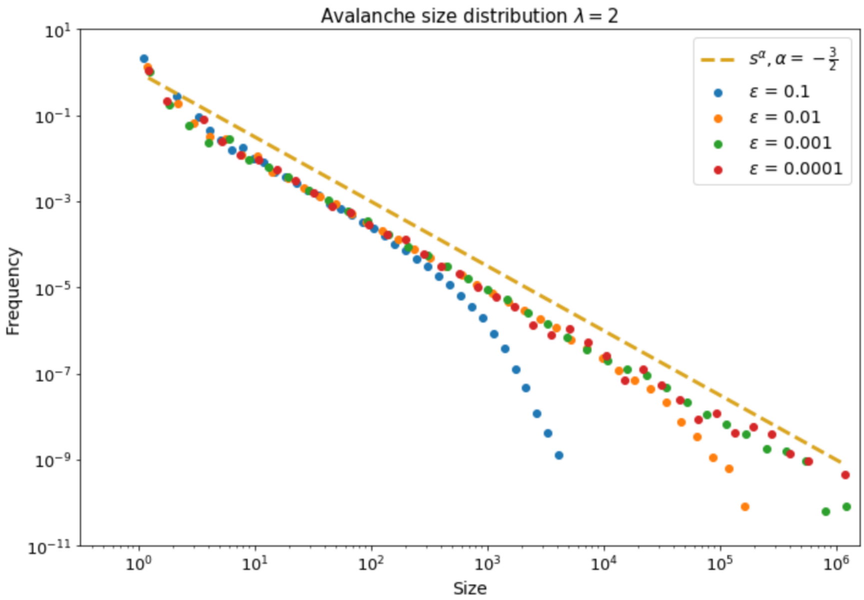


Figure 4: Log-binned avalanche size distributions for $\lambda = 2$ at various $\epsilon$ values. The system supports larger avalanches due to the increased propagation rate, with scale-free behavior observed at lower $\epsilon$.

## 4.3 Interpretation of Results

The results confirm the following:

- At lower $\epsilon$, the system exhibits scale-free avalanche distributions ($\tau = -\frac{3}{2}$), driven by neutral dynamics.
- Higher $\epsilon$ introduces deviations from the power-law, as spontaneous activations dominate and disrupt neutral propagation.
- Increasing $\lambda$ supports larger avalanches, extending the scale-free behavior to larger sizes.

These findings align with the theoretical predictions of neutral theory and demonstrate the conditions under which scale-free behavior emerges in the system.

## 4.4 Avalanche Time Distributions for $\lambda = 1$

Figure 5 shows the avalanche time distributions for $\lambda = 1$ at various $\epsilon$ values. The time duration of avalanches is plotted against their frequencies on a log-log scale.

For lower $\epsilon$ values (e.g., $\epsilon = 0.0001$), the distributions closely follow the theoretical power-law $t^{-\alpha}$ with $\alpha = -2$, particularly for larger avalanche durations. This suggests that the system exhibits scale-free temporal dynamics when spontaneous activations are rare, and the activity is driven by neutral dynamics.

At higher $\epsilon$ values (e.g., $\epsilon = 0.1$), deviations from the power-law are observed for shorter durations, indicating that spontaneous activations dominate the dynamics and disrupt the scale-free behavior.

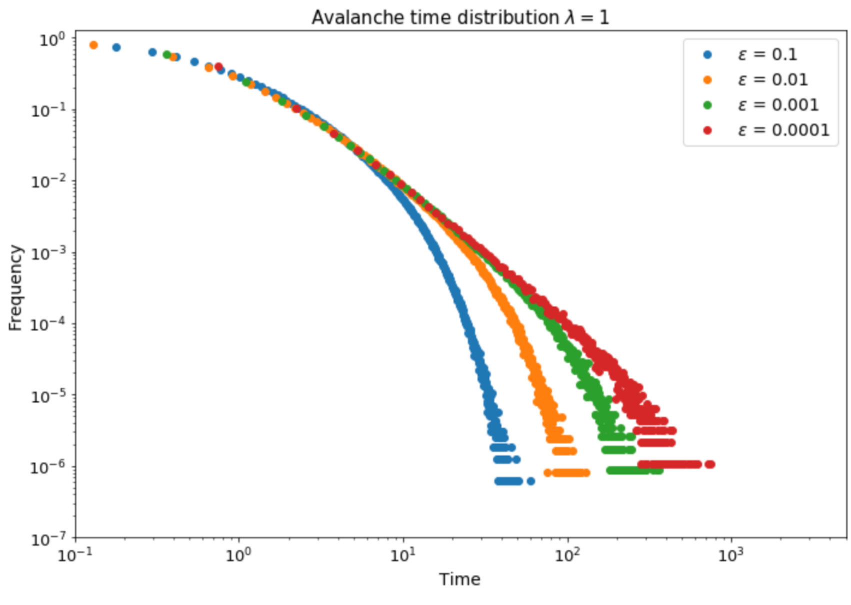


Figure 5: Avalanche time distributions for $\lambda = 1$ at various $\epsilon$ values. The dashed line represents the theoretical power-law $t^{-\alpha}$ with $\alpha = -2$. The scale-free behavior is prominent at lower $\epsilon$, while deviations occur at higher $\epsilon$.

Log-binning the data, as shown in Figure 6, provides a smoother representation of the distributions. These results confirm that the system retains scale-free temporal behavior at lower $\epsilon$, while deviations due to higher spontaneous activation rates are more apparent in this analysis.

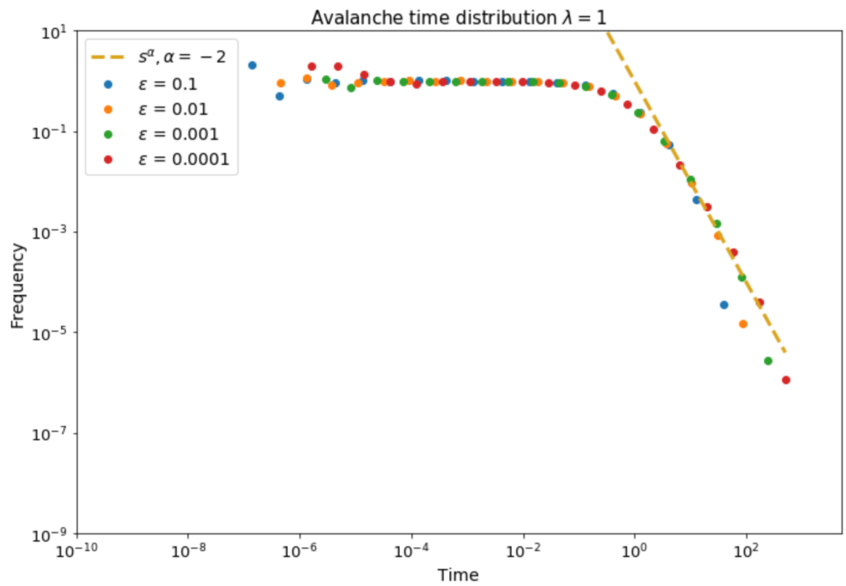


Figure 6: Log-binned avalanche time distributions for $\lambda = 1$ at various $\epsilon$ values. The smoother curves highlight the alignment with the theoretical power-law at lower $\epsilon$, with disruptions evident at higher $\epsilon$.

### 4.5 Avalanche Time Distributions for $\lambda = 2$

For $\lambda = 2$, the avalanche time distributions are presented in Figures 7 and 8. Compared to $\lambda = 1$, the distributions extend further for longer durations, indicating that a higher propagation rate ($\lambda = 2$) supports more sustained avalanche activity.

At lower $\epsilon$ values, the distributions align well with the theoretical power-law $t^{-\alpha}$ ($\alpha = -2$), consistent with scale-free behavior driven by neutral dynamics. However, as $\epsilon$ increases, shorter durations dominate the dynamics, leading to deviations from the power-law, similar to the results for $\lambda = 1$.

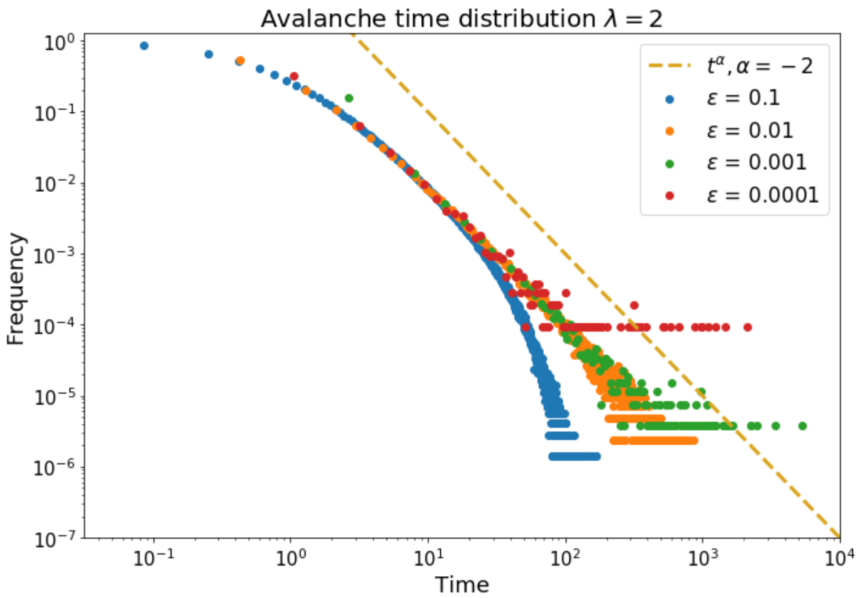


Figure 7: Avalanche time distributions for $\lambda = 2$ at various $\epsilon$ values. The dashed line represents the theoretical power-law $t^{-\alpha}$ with $\alpha = -2$. Higher $\lambda$ supports longer avalanche durations, with deviations occurring at higher $\epsilon$.

Log-binned distributions in Figure 8 emphasize the scale-free behavior at lower $\epsilon$ values and highlight the role of higher propagation rates in supporting more extended avalanches.

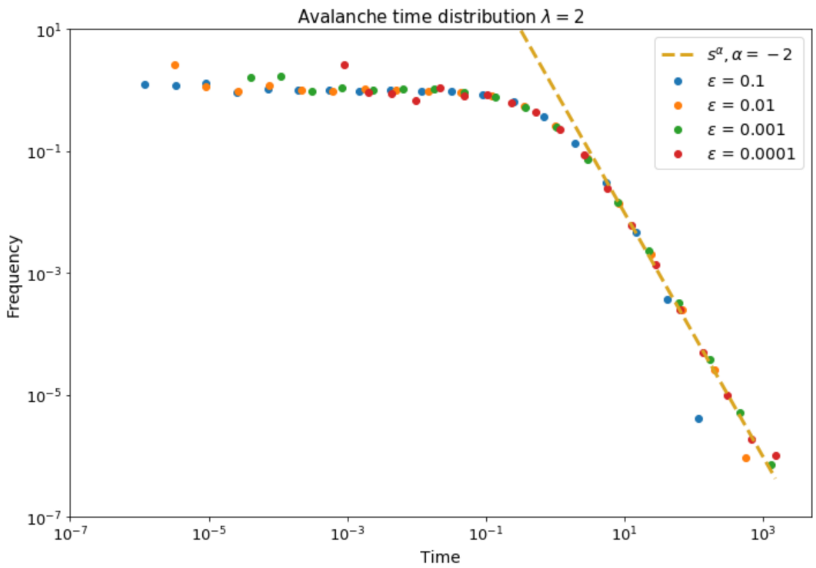


Figure 8: Log-binned avalanche time distributions for $\lambda = 2$ at various $\epsilon$ values. The extended tail of the distribution reflects the system's ability to sustain longer avalanche durations at higher propagation rates.

## 4.6 Interpretation of Results

The analysis of avalanche time distributions reveals the following key insights:

- At lower $\epsilon$, the system exhibits scale-free temporal behavior, with time distributions closely following the power-law $t^{-\alpha}$, where $\alpha = -2$.
- Higher $\epsilon$ disrupts the scale-free behavior, particularly for shorter durations, as spontaneous activations dominate the dynamics.
- Increasing $\lambda$ supports longer avalanche durations, emphasizing the role of propagation rate in sustaining temporal scale-free behavior.

These findings align with the theoretical predictions of neutral dynamics and demonstrate the impact of both spontaneous activation ($\epsilon$) and propagation rate ($\lambda$) on the temporal characteristics of avalanche dynamics.

## 4.7 Fraction of Active Sites in Time

The fraction of active sites, $\rho$, over time at various $\epsilon$ values is shown in Figure 9. The simulations were conducted over a long time period to analyze the steady-state behavior of $\rho$ for $\lambda = 2$.

At lower $\epsilon$ values (e.g., $\epsilon = 0.0001$), $\rho$ remains relatively stable with minimal fluctuations, aligning with theoretical predictions for neutral dynamics. As $\epsilon$ increases, fluctuations become more pronounced, indicating a stronger influence of spontaneous activations on the dynamics. Nevertheless, the mean value of $\rho$ across all $\epsilon$ values is consistent with the theoretical steady-state predictions.

The results also highlight that higher propagation rates ($\lambda = 2$) support larger fractions of active sites compared to lower propagation rates ($\lambda = 1$), emphasizing the role of $\lambda$ in maintaining activity in the network.

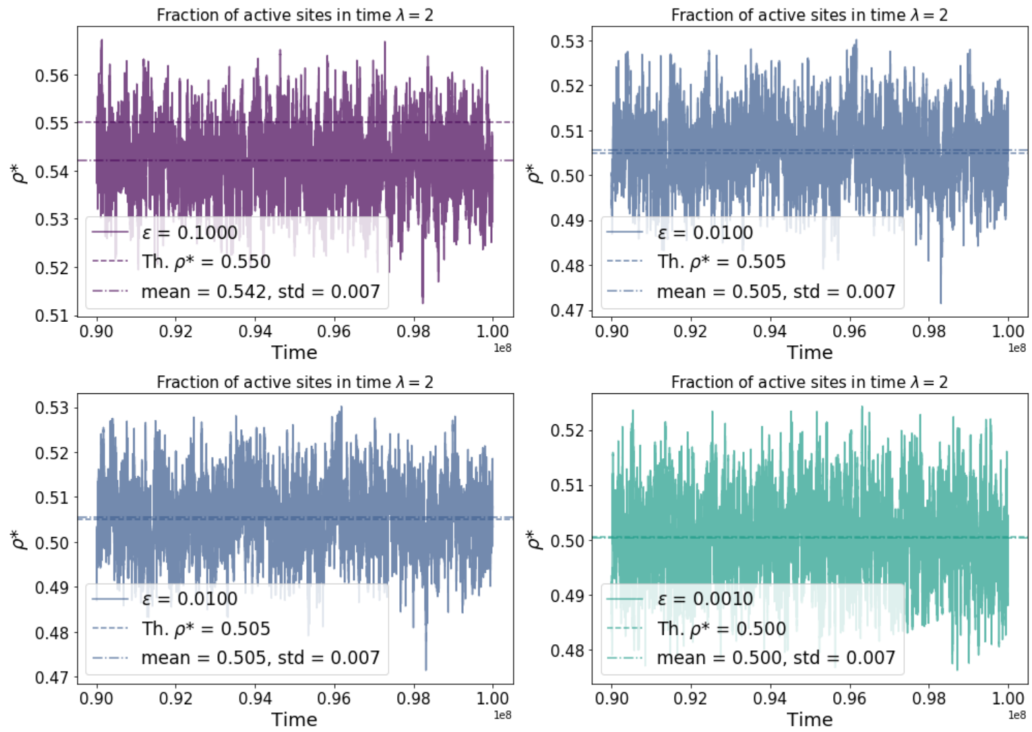


Figure 9: Fraction of active sites over time for $\lambda = 2$ at various $\epsilon$ values. Solid lines represent the simulated fraction of active sites, dash-dotted lines indicate mean values with standard deviations, and dashed lines show theoretical predictions for $\rho$.

The steady-state analysis of $\rho$ reveals:

- The mean fraction of active sites aligns well with theoretical predictions, validating the neutral dynamics framework.
- Fluctuations increase with $\epsilon$, as higher spontaneous activation rates introduce more variability.
- Higher propagation rates ($\lambda = 2$) lead to a larger fraction of active sites, demonstrating the role of $\lambda$ in sustaining activity.

These findings illustrate the interplay between spontaneous activation ($\epsilon$) and propagation rate ($\lambda$) in determining the system's steady-state behavior.

## 4.8 Avalanche Distributions for $\lambda = 1, \epsilon = 0.0001$

The avalanche time and size distributions for $\lambda = 1$ and $\epsilon = 0.0001$ are presented in Figures 10 and 11, respectively.

The avalanche time distribution (Figure 10) follows a power-law behavior, $t^\alpha$ with $\alpha = -2$, over a wide range of time durations. This indicates that the system's dynamics are scale-free for low $\epsilon$, where spontaneous activations are rare, and the propagation dynamics dominate.

Similarly, the avalanche size distribution (Figure 11) follows a power-law $s^{\tau}$ with $\tau = -\frac{3}{2}$, consistent with theoretical predictions of neutral dynamics. This highlights that avalanche sizes are distributed over a broad range without a characteristic scale.

These results demonstrate the system's adherence to scale-free dynamics under low spontaneous activation rates, validating the theoretical framework of neutral dynamics.

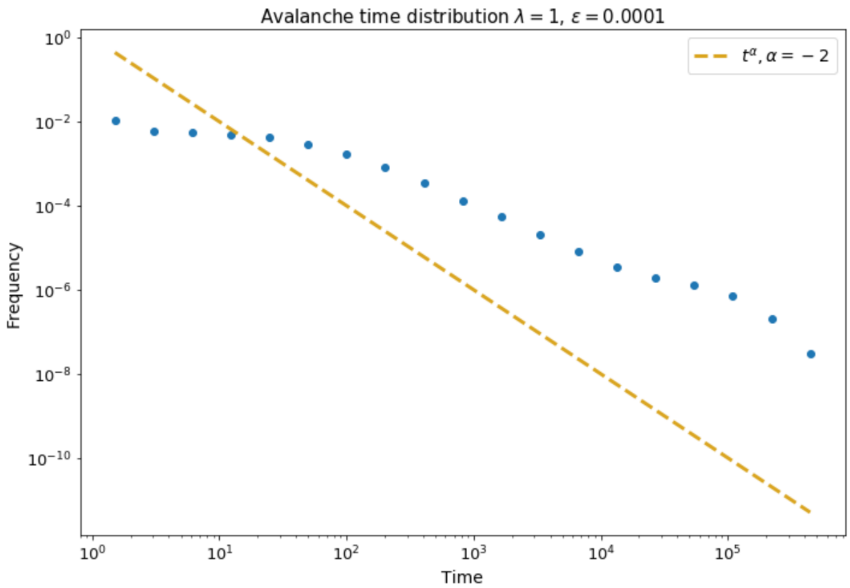


Figure 10: Avalanche time distribution for $\lambda = 1$ and $\epsilon = 0.0001$. The dashed line represents the theoretical power-law $t^{\alpha}$ with $\alpha = -2$.

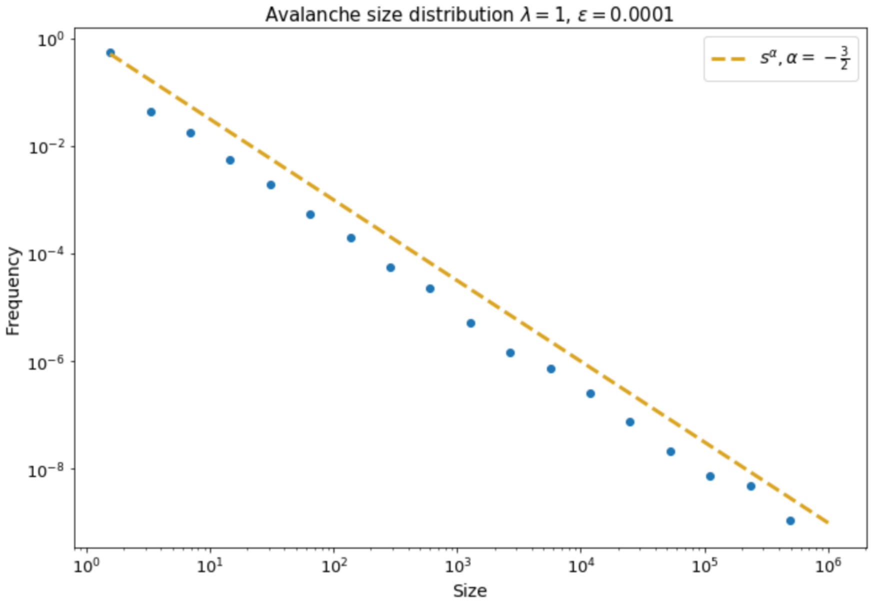


Figure 11: Avalanche size distribution for $\lambda = 1$ and $\epsilon = 0.0001$. The dashed line represents the theoretical power-law $s^{\tau}$ with $\tau = -\frac{3}{2}$.

# 5 Conclusion

# References

[1] Matteo Martinello, Jorge Hidalgo, Amos Maritan, Serena di Santo, Dietmar Plenz, and Miguel A. Muñoz, Neutral Theory and Scale-Free Neural Dynamics, Physical Review X, 7(4), 041071 (2017). Publisher: American Physical Society. DOI: 10.1103/PhysRevX.7.041071. URL: https://journals.aps.org/prx/abstract/10.1103/PhysRevX.7.041071.