RESEARCH ARTICLE | OCTOBER 18 2018

Robust entropy requires strong and balanced excitatory and inhibitory synapses

Vidit Agrawal; Andrew B. Cowley; Qusay Alfaori; ... et. al

Chaos 28, 103115 (2018)
https://doi.org/10.1063/1.5043429

CHAOS **28**, 103115 (2018)

Robust entropy requires strong and balanced excitatory and inhibitory synapses

Vidit Agrawal,[1,a)] Andrew B. Cowley,[2,a)] Qusay Alfaori,[1] Daniel B. Larremore,[3,4]
Juan G. Restrepo,[2] and Woodrow L. Shew[1,b)]
[1]*Department of Physics, University of Arkansas, Fayetteville, Arkansas 72701, USA*
[2]

tends to result in a regime with higher firing rates and strong correlations. Two studies in particular have shown that entropy can be increased by tuning the E/I balance to the tipping point between these two distinct dynamical regimes.[11,12] However, a more systematic understanding of how E/I balance impacts entropy is difficult to obtain experimentally because pharmacological manipulations are rather difficult to precisely control. Moreover, with a few interesting exceptions,[15,16] experiments do not vary the numbers of excitatory or inhibitory neurons. Computational models offer an alternative approach in which the number of excitatory and inhibitory neurons, as well as strength of excitatory and inhibitory synapses, can easily be controlled. Previous computational studies have addressed similar topics but typically have neglected inhibition[12,17] or have not considered the effects of changing the E/I ratio.[18,19] Thus, theoretical and experimental understanding of the relationship between the entropy of ongoing dynamics and the balance of excitation and inhibition—mediated by both relative strengths of excitatory and inhibitory synapses and relative numbers of excitatory and inhibitory cells—remains unresolved.

Here, we attempt to improve the theoretical understanding of entropy of ongoing dynamics by studying a network model of binary neurons in detail. We consider how entropy of the population firing rate depends on the fraction of inhibitory neurons α and the strengths of E and I interactions, W_E and W_I, respectively. We find maximal entropy near the tipping point between the low and high firing rate dynamical regimes, as seen in experiments.[12] We also find that, for a given choice of W_E and W_I, the tipping point can be achieved by adjusting

iterations of Eq. (8). The entropy is then calculated directly from Eq. (4).

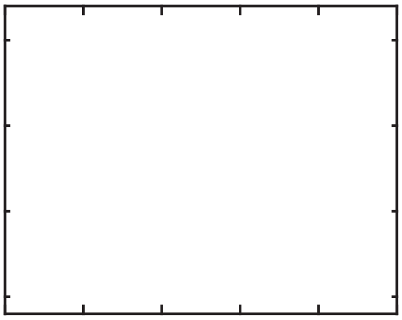
III. RESULTS

Our primary goal is to determine how the entropy of a network varies with the relative numbers of E and I neurons and the relative strength of E and I synapses. We first describe our results from numerical simulations of the binary model and then describe results from the theory.

First, we show in Fig. 1 that the system network activity visits the widest variety of states when excitation and inhibition are balanced at the tipping point between high and low firing rate regimes. This is visible in time series [Fig. 1(a)] as well as empirical distributions $P(S)$ of network activity (based on 10^4 time steps of simulation). Correspondingly, entropy H is greatest along the boundary between low and high firing regimes (Fig. 2). In the three-dimensional (W_E, W_I, α) parameter space, this boundary forms a curved surface, which we henceforth refer to as the *maximum entropy surface*.

As discussed in Sec. II A, we expect that the transition from the low to the high firing regimes occurs at the *critical surface* of parameters where $\lambda = 1$. While we find this is usually an excellent approximation to our numerical results, the maximum entropy and critical surfaces differ slightly for high values of α, and therefore, we will only use the critical surface as a qualitative guide to the location of the maximum entropy surface.

To numerically identify the maximum entropy surface, for each fixed value of (W_E, W_I), we compute entropy across a wide range of values of α, finding the value $\alpha^{\star}$ that maximizes $H(W_E, W_I, \alpha)$. In Fig. 3(a), we show $\alpha^{\star}$ as a function of W_E and W_I. As one might expect, higher values of W_E require a larger number of I neurons (higher $\alpha^{\star}$) in order to maintain a balanced network and vice versa. This agrees qualitatively with the estimate using the critical surface, $\alpha^{\star} \approx$ $(W_E$



A second prediction from our work is that size of the drop in entropy due to a manipulation of inhibition or excitation will be correlated with the entropy before the manipulation. This prediction supposes that the cortex is sometimes operating with a weak-synapse E/I balance where entropy is higher and the drop in entropy would be greater and at other times is operating with a strong-synapse E/I balance where entropy is lower and the drop in entropy would be less.

[35]F. Fernandez and C. C. Garner, "Over-inhibition: A model for developmental intellectual disability," Trends Neurosci.