

## Introduction and Motivation

- Excitatory-inhibitory balance is ubiquitous in cortex
- How does balance determine the response properties of cortical circuits?
- In classical balanced network theory,  $e \leftrightarrow i$  cancellation implies a linear relationship between stimulus and firing rates (VanVreeswijk & Sompolinsky, Science, 1996)
- But cortical circuits implement non-linear stimulus representations
- We develop a theory of semi-balanced networks that implement non-linear representations by allowing for excess inhibition without excess excitation

## Semi-balanced Networks

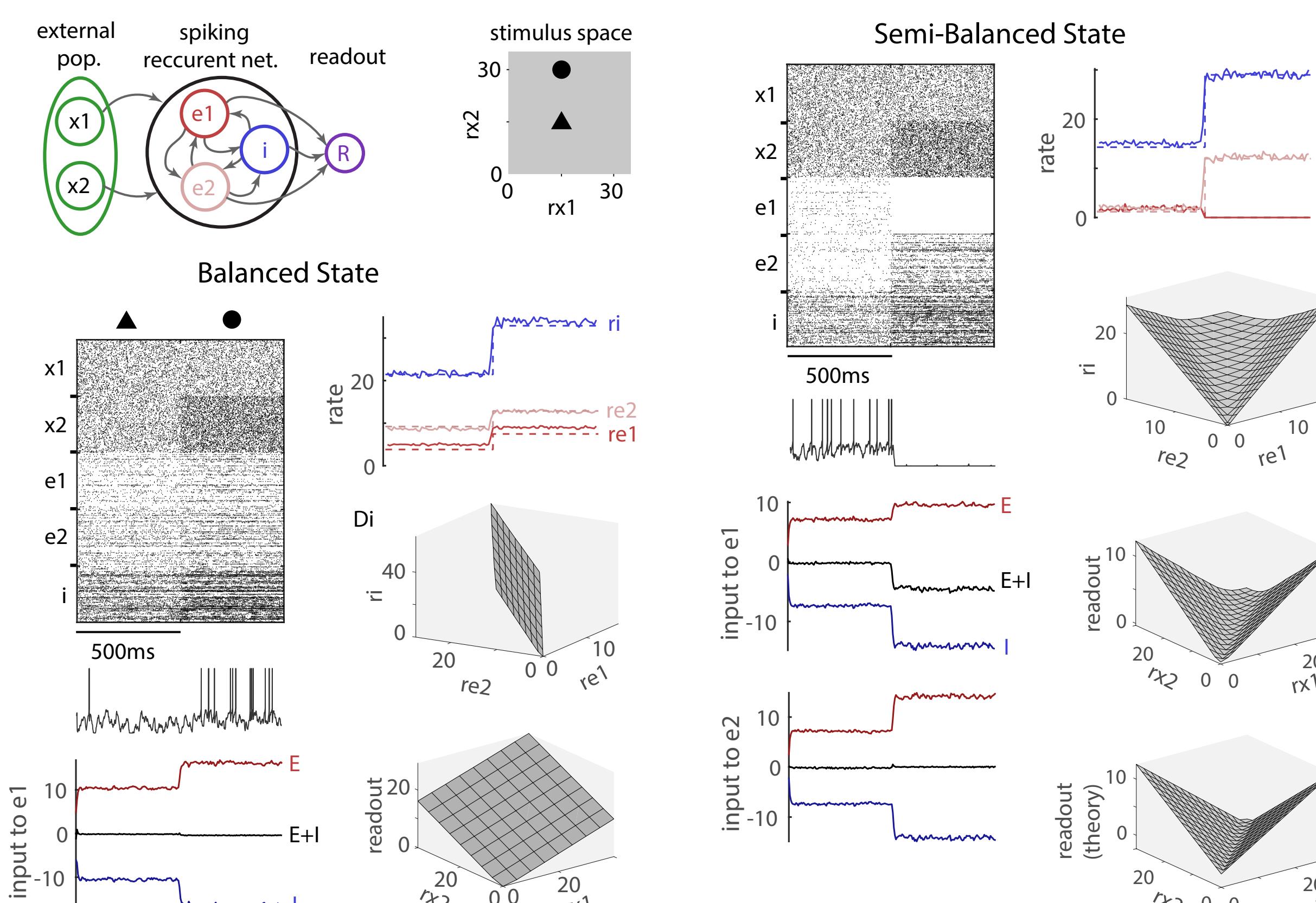
- Classic balance: total input  $\mathbf{I}$  stays  $\mathcal{O}(1)$  by cancellation of recurrent and external competition

$$\mathbf{I} = \overline{JK}(\mathbf{Wr} + \mathbf{W}_x \mathbf{r}_x) \quad \mathbf{r} = -\mathbf{W}^{-1} \mathbf{W}_x \mathbf{r}_x$$

- Semi-balance: we allow  $\mathbf{I}$  to be  $\mathcal{O}(\overline{JK})$  and negative for some neurons, which suppresses their spiking. - this yields the relation

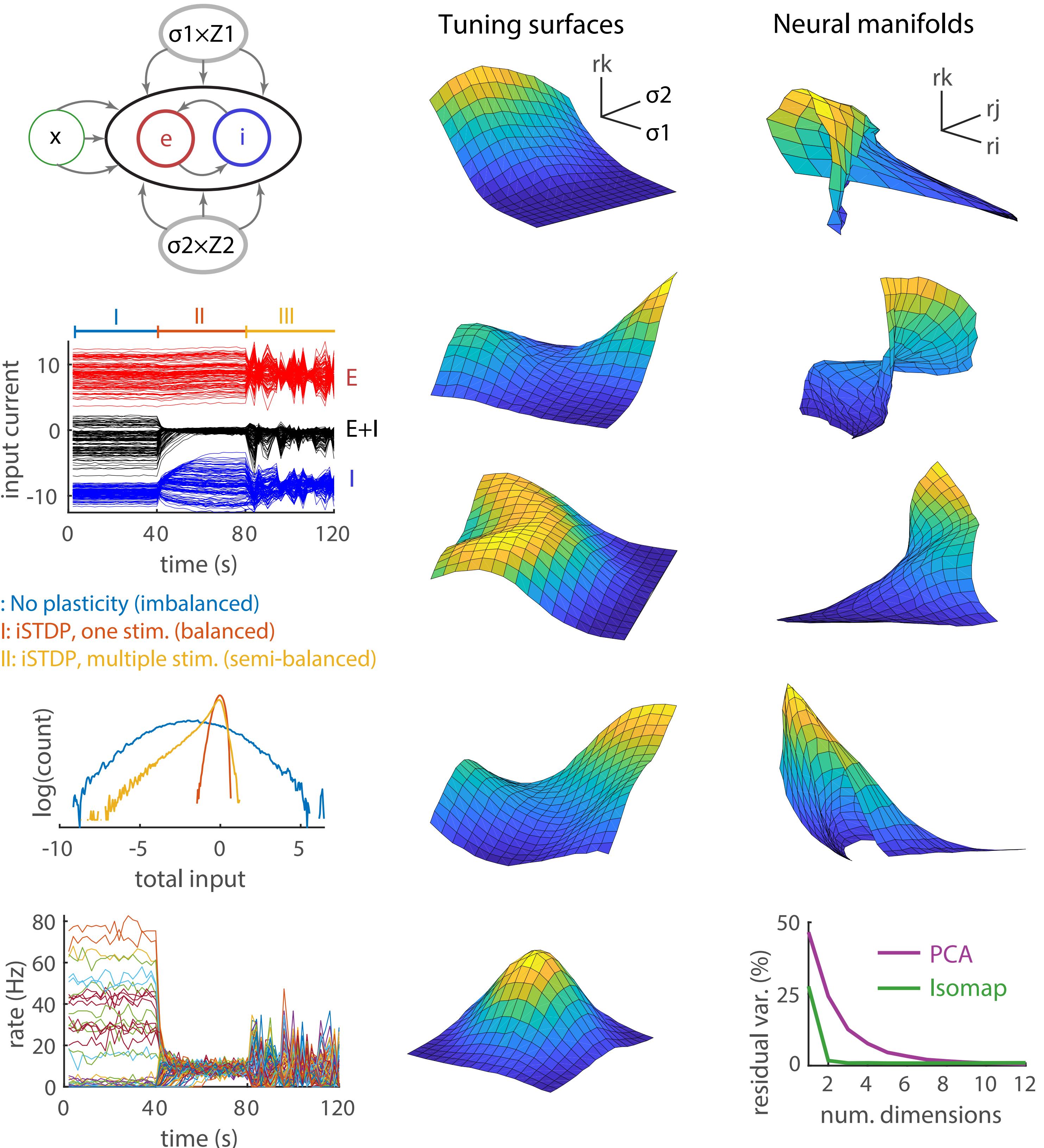
$$\mathbf{r} = [\mathbf{Wr} + \mathbf{W}_x \mathbf{r}_x + \mathbf{r}]^+$$

- This corresponds to certain subpopulations of neurons having their voltage clamped near the inhibitory reversal potential
- This directly relates semi-balanced networks to ANNs with ReLU activations and to threshold-linear networks (Curto & Morrison, Neural Comp, 2016)



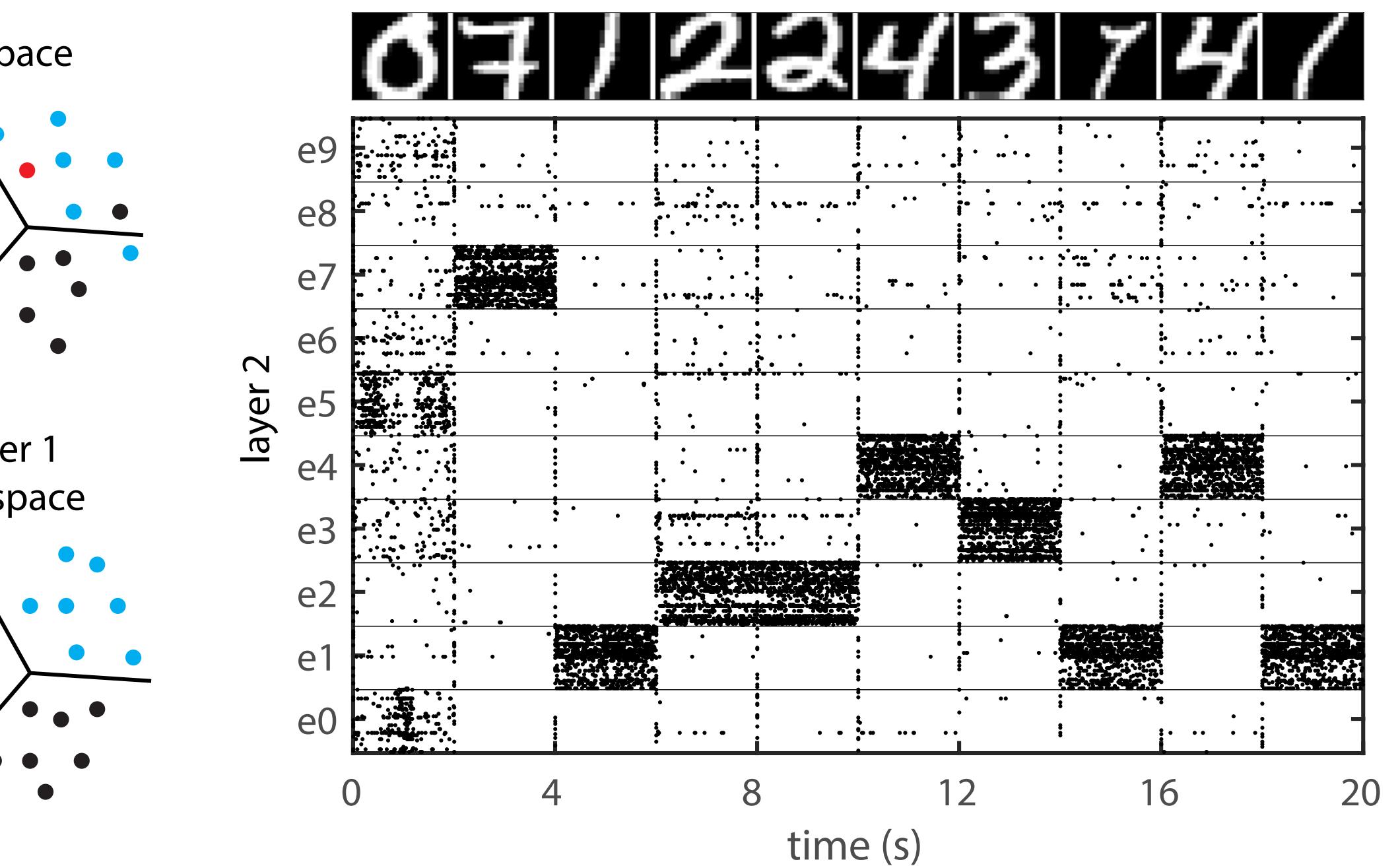
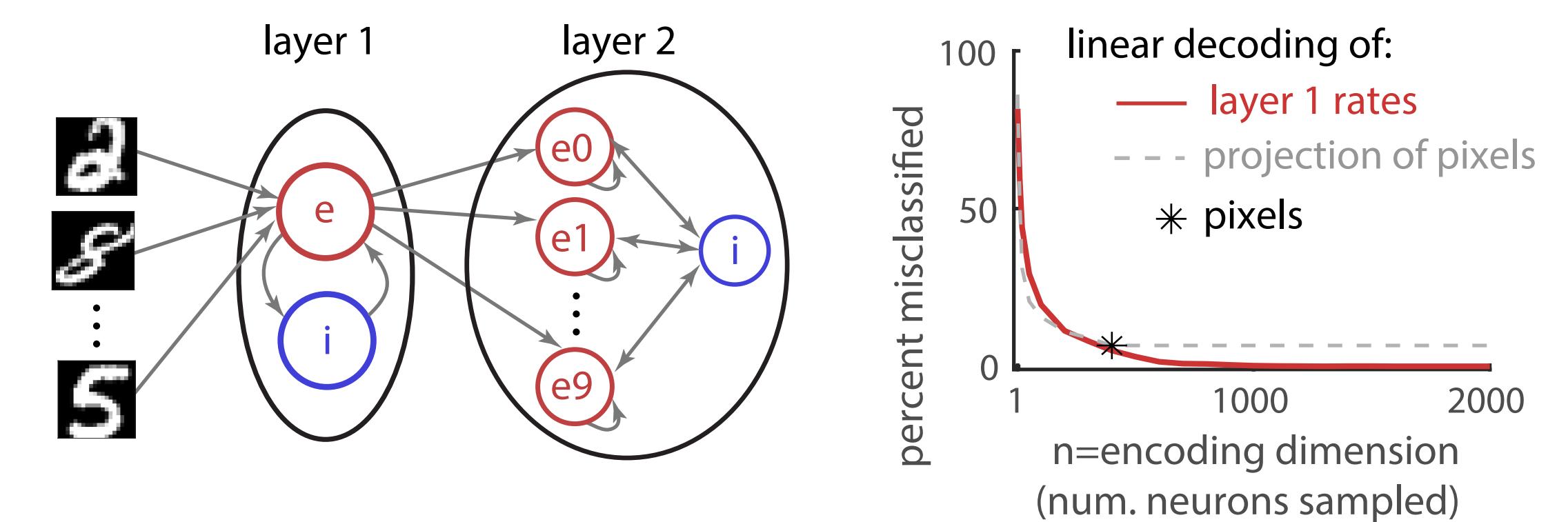
## Nonlinear Distributed Representation of Low-Dimensional Stimuli

- A time-constant two-dimensional stimulus is distributed over the population as  $\vec{Z} = \sigma_1 \vec{Z}_1 + \sigma_2 \vec{Z}_2$
- During the first 40s (stage I), synaptic weights and stimulus magnitude were fixed
  - Currents were imbalanced at single-neuron resolution
- During the next 40s (stage II), homeostatic inhibitory spike-timing dependent plasticity (iSTDP; Vogels, et al., Science, 2011) was turned on
  - This balanced the network with respect to the fixed stimulus value
- During the last 40s (stage III), iSTDP was still active but stimulus magnitudes were selected randomly and switched every 2s
  - This resulted in an excess of inhibition, but not excitation (semi-balanced)



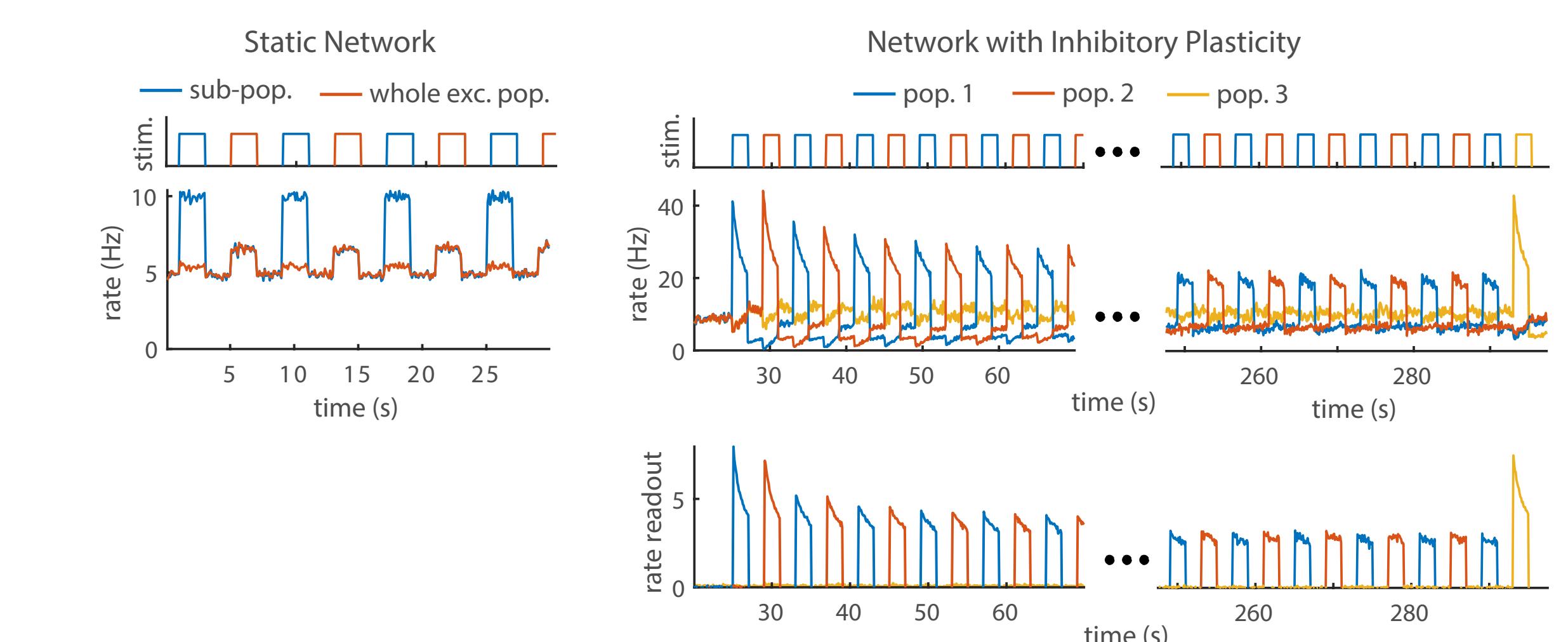
- The neural representation of the two-dimensional stimulus has a rich, nonlinear structure useful for performing computations

## Nonlinear Representations Improve Computations



## Surprise Detection

- Periodic switching between two common stimuli  $\sigma_1 \vec{Z}_1$  and  $\sigma_2 \vec{Z}_2$  while iSTDP is active
- Novel stimulus  $\sigma_3 \vec{Z}_3$  is introduced after an extended period of time



- Thus, unfamiliar or ‘surprising’ stimuli evoke a disproportionate firing rate response from the population