A comprehensive large-scale model of primary visual cortex (V1)

Summary: We introduce a comprehensive retinotopic model of V1 based on ORGaNICs, a stochastic recurrent circuit framework implementing divisive normalization via recurrent amplification. Specifically, we simulate the membrane potentials and firing rates of simple and complex V1 neurons driven by the outputs of a steerable pyramid, thus capturing the retinotopy, spatial frequency, receptive field size, and orientation-tuning selectivity of the neurons. Then, using the theory of stochastic LTI systems, we demonstrate that, for a grating response, the circuit oscillates at the observed (gamma) frequency and accurately captures the contrast dependence of gamma activity and LFP coherence, measured across neuronal populations at different spatial locations, with different orientation tuning and receptive field size.

We further design a modified Gaussian-Rectification (GR) model for the generation of spiking activity that takes into account the time-correlations of the membrane potentials. We demonstrate that this framework accurately captures the dependence of the Fano factor and noise correlations as a function of stimulus contrast and provides an analytical expression, depending on circuit parameters, for deviations from the Poisson-like behavior of the spiking activity. This spiking activity is then filtered (simulating synaptic filtering) and fed back as input to the dynamical variables simulating the membrane potential of neurons. Finally, we predict these quantities in the context of realistic stimuli: Gabor, plaids, and natural images. Therefore, our framework offers a versatile tool for understanding the dynamics and noise correlation of V1 activity.

Additional detail: We begin with a brief introduction of the setup of our problem. A common implementation of ORGaNICs [1, 2] is given by the following set of stochastic differential equations,

$$\begin{aligned}
\tau_y \dot{\mathbf{y}} &= -\mathbf{y} + \mathbf{b}_1 * \mathbf{z} + \left(\frac{1}{1+\mathbf{a}^+}\right) * \mathbf{W}' \left(\sqrt{\mathbf{y}^+} - \sqrt{\mathbf{y}^-}\right) + \eta_{\mathbf{y}} \\
\tau_a \dot{\mathbf{a}} &= -\mathbf{a} + \alpha * \dot{\mathbf{u}}^+ + \mathbf{u}^+ + \mathbf{u}^+ * \mathbf{a}^+ + \eta_{\mathbf{a}} \\
\tau_u \dot{\mathbf{u}} &= -\mathbf{u} + \mathbf{b}_0^2 * \sigma^2 + \mathbf{W}\left(\mathbf{y}^+ * \mathbf{u}^{+2}\right) + \eta_{\mathbf{u}}
\end{aligned} \tag{1}$$

Here, $\mathbf{z}$ is the input drive to the circuit; $\mathbf{y}$, $\mathbf{a}$, and $\mathbf{u}$ are the membrane potentials of the principal excitatory neurons, inhibitory neurons, and excitatory modulatory neurons, respectively, that evolve according to the dynamical equations defined above. $\mathbf{y}^{\pm}$, $\mathbf{u}^+$, and $\mathbf{a}^+$ are the firing rates of the corresponding neurons, found by applying rectification ($\lfloor . \rfloor$) and a power function on the corresponding membrane potentials. Each of these firing rate variables is defined by a differential equation of the form $\tau_s \dot{\mathbf{x}}^+ = -\mathbf{x}^+ + \lfloor \mathbf{x} \rfloor^\beta + \eta_{\mathbf{x}^+}$, simulating synaptic filtering, where β is the exponent of the nonlinearity equal to 2, 1, 0.5 for $\mathbf{y}$, $\mathbf{a}$, and $\mathbf{u}$, respectively. The variance of $\eta_{\mathbf{x}^+}$ is defined by a modified GR model in the next section. $\eta_{\mathbf{y}}$, $\eta_{\mathbf{a}}$ and $\eta_{\mathbf{u}}$ are uncorrelated Gaussian white noise modeling stochastic inputs for the membrane potentials. Terms highlighted in green and blue in Eq. 1 represent, in turn, the external input gated by input gain, and the recurrent input gated by recurrent gain to a given neuron. $\mathbf{b}_1$, α, and $\mathbf{b}_0$ and are the input gains for the external inputs $\mathbf{z}$, $\dot{\mathbf{u}}^+$ and σ fed to neurons $\mathbf{y}$, $\mathbf{a}$, and $\mathbf{u}$, respectively. Additionally, σ is a semi-saturation

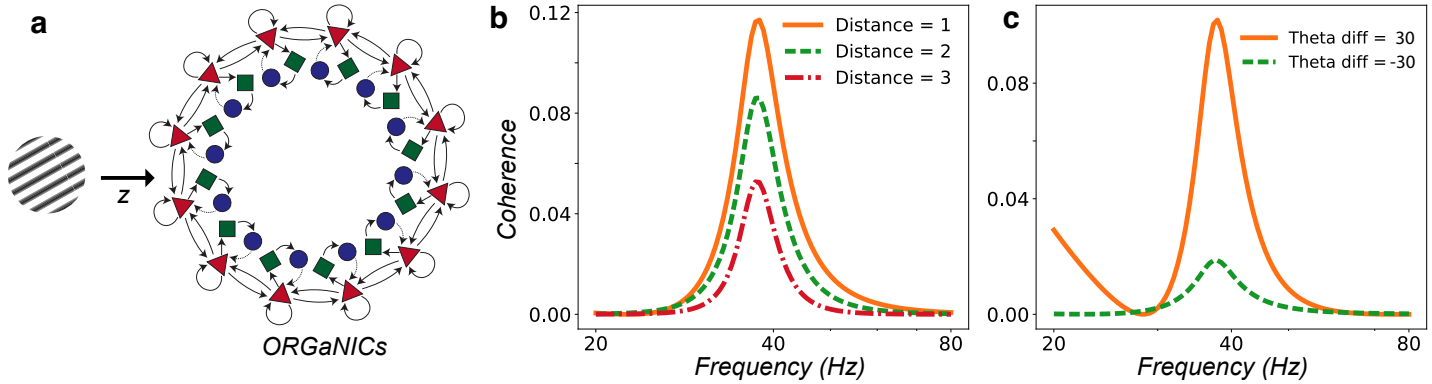

Figure 1: **a:** An illustration of the ORGaNICs model with three different types of neurons which receives a grating stimulus (z). **b, c:** Response to a 45-degree oriented grating stimulus. **b:** Coherence between maximally firing neuron (orientation tuning 30 deg.) and neurons with the same orientation and size tuning, but different location tuning (distance in pixels). **c:** Coherence between maximally firing neuron and neurons with the same location and size, but different orientation preferences.

constant that defines the shape of the normalization curves for different principal neurons. $\mathbf{W}'$ is the recurrent weight matrix that captures lateral connections among the principal neurons. This recurrent input is gated by the inhibitory $\mathbf{a}$ neurons, via the term $1/(1+\mathbf{a}^+)$. Similarly, the normalization weight matrix, $\mathbf{W}$, encapsulates the recurrent inputs received by the $\mathbf{u}$ neurons. Here, since the neurons are arranged according to the 2-dimensional retinotopic structure, we designed $\mathbf{W}$ to have spatially local connections (viz., the normalization pool is local) to implement surround-suppression in V1. The specific forms of the terms appearing in the dynamical system are designed in such a way that the principal neurons follow the normalization equation exactly at steady-state, $\mathbf{y}^+_{ss} = \lfloor \mathbf{z} \rfloor^2/(\sigma^2 + \mathbf{W}\lfloor \mathbf{z} \rfloor^2)$.

We use Eq. 1 to simulate the activity of the complex cells in V1. We take the input drive, $\mathbf{z}$, to be the output of a Steerable pyramid, thus capturing the spatial frequency, receptive field size, and orientation-tuning selectivity of the neurons. This gives a large-scale stochastic dynamical system of ~ 20000 variables.

Modified GR model for spike generation: Now we define the dynamical equations for the firing rates, $\mathbf{y}^+$, $\mathbf{u}^+$, and $\mathbf{a}^+$. Since the generation of spikes from the membrane potential is a very reliable process, following [3] we assume that the trial-to-trial variability in the spiking process arises entirely because of the variability in the neuron's membrane potential. We consider the spikes to be generated by a model similar to GR [3], visualized in Fig. 2a, where the membrane potentials are assumed to have a Gaussian probability distribution with given variance. At each time step, the probability of firing is equal to the probability of sampling the membrane potential beyond the firing threshold. This model has been successful in capturing the variability observed experimentally in V1, but such a model always predicts Poisson-like spiking (viz., Fano factor equal to 1). Since, experimentally, Fano factors larger than 1 are observed for low contrast grating stimuli, we extend the GR model to incorporate the time-correlations of the membrane potentials.

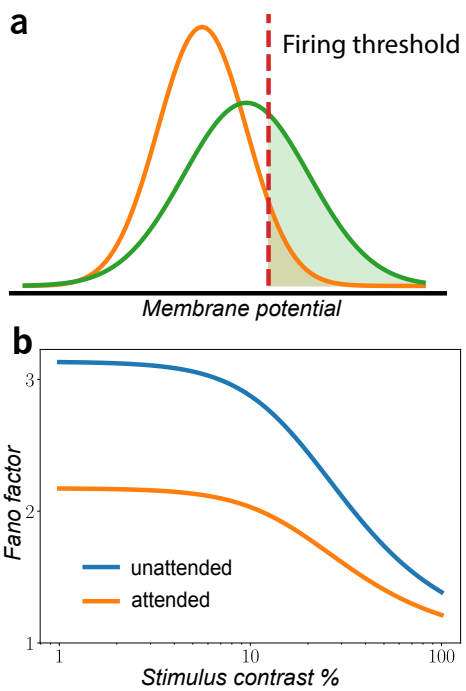

Figure 2: **a:** GR model: the membrane potentials (V) are Gaussian distributed. A spike is generated when the sampled V is beyond the firing threshold. **b:** Analytical Fano factor calculated using modified GR model as a function of contrast for the maximally firing neuron.

Specifically, we assume the spike train ($S_t = I_1 + I_2 + ... + I_n$), generated by the membrane potentials, to be a sum of correlated Bernoulli indicator random variables, I_j, with probability $p\Delta t$ of firing in time Δt, where p is the probability mass above the threshold. We approximate the firing rates by the first and second moments in the dynamical system, as follows. The normalization equation defines the mean of the spike train, $E[S_t] = \lfloor y \rfloor^2 t$, hence we have that $p = \lfloor y \rfloor^2$. To calculate the variance, we use the fact that the indicator variables are correlated in time, so that $Var(S_t) = \sum_i Var(I_i) + \sum_{i \neq j} Cov(I_i, I_j)$. Since the membrane potentials are described by Eq. 1, we know that $Cov(I_i, I_j) \propto pe^{-\Delta\tau(j-i)/\tau_e}$, where τ_e is the effective time constant of the neuron which can be defined analytically for our system at steady-state in terms of the circuit parameters. Thus, we can evaluate the variance of the spike train analytically.

Results: We find that the Fano factor (FF) can be written in terms of the effective time constant, τ_e, as $FF = 1 + \gamma\tau_e$, where γ is a known constant (viz., not a fit parameter). Fig. 2b shows the FF as a function of the grating stimulus contrast; the two curves correspond to different values for the input gains $\mathbf{b}_1$, which we know from previous work models the modulatory effect of attention on sensory-evoked activity in visual cortex. Finally, since our system exhibits a fixed-point solution, we can calculate the power spectrum and coherence analytically (Fig. 1) defined by the spectral density matrix which depends on the Jacobian ($\mathbf{J}$) and the noise matrix ($\mathbf{Q}$) as follows, $\mathcal{S}(\omega) = (\iota\omega\mathbf{I} + \mathbf{J})^{-1}\,\mathbf{Q}\,(-\iota\omega\mathbf{I} + \mathbf{J})^{-\top}$.

References:

1. Heeger, D. J. & Mackey, W. E., *PNAS*, 116(45), 22783-22794 (2019).
2. Heeger, D. J. & Zemlianova, K. O., *PNAS*, 117(36), 22494-22505 (2020).
3. Carandini, M. & Zemlianova, K. O., *PLoS biology*, 2(9), e264 (2004).