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

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Abstract

We introduce a comprehensive retinotopic model of V1 based on ORGaNICs, a stochastic recurrent circuit framework implementing divisive normalization via modulation of recurrent amplification. Specifically, we simulate the membrane potentials and firing rates of 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. We further implement a 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 GR model accurately captures the dependence of the Fano factor and noise correlations as a function of stimulus contrast. The spike process is then filtered and fed back as input to the dynamical variables simulating the membrane potential of the neurons. Thus, using the theory of stochastic LTI systems, we demonstrate that, for a grating response, the circuit exhibits gamma frequency oscillations and accurately captures the contrast dependence of gamma activity and LFP coherence, measured across neuronal populations tuned to different spatial locations, orientation, and spatial frequency. Finally, we predict these quantities in the context of plaids, and natural images. Therefore, our framework offers a versatile tool for understanding the dynamics and noise correlation of V1 activity.

Keywords: gamma; oscillations; visual cortex; spiking activity

V1 model

We begin with a brief introduction of the setup of our problem. A common implementation of ORGaNICs (Heeger & Mackey, 2019; Heeger & Zemlianova, 2020) is given by the following set of stochastic differential equations,

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

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 described 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 an input gain, and the recurrent input gated by a recurrent gain for a given neuron. $\mathbf{b}$, 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 constant that defines the shape of the normalization curves for different principal neurons. $\mathbf{W}_r$ 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

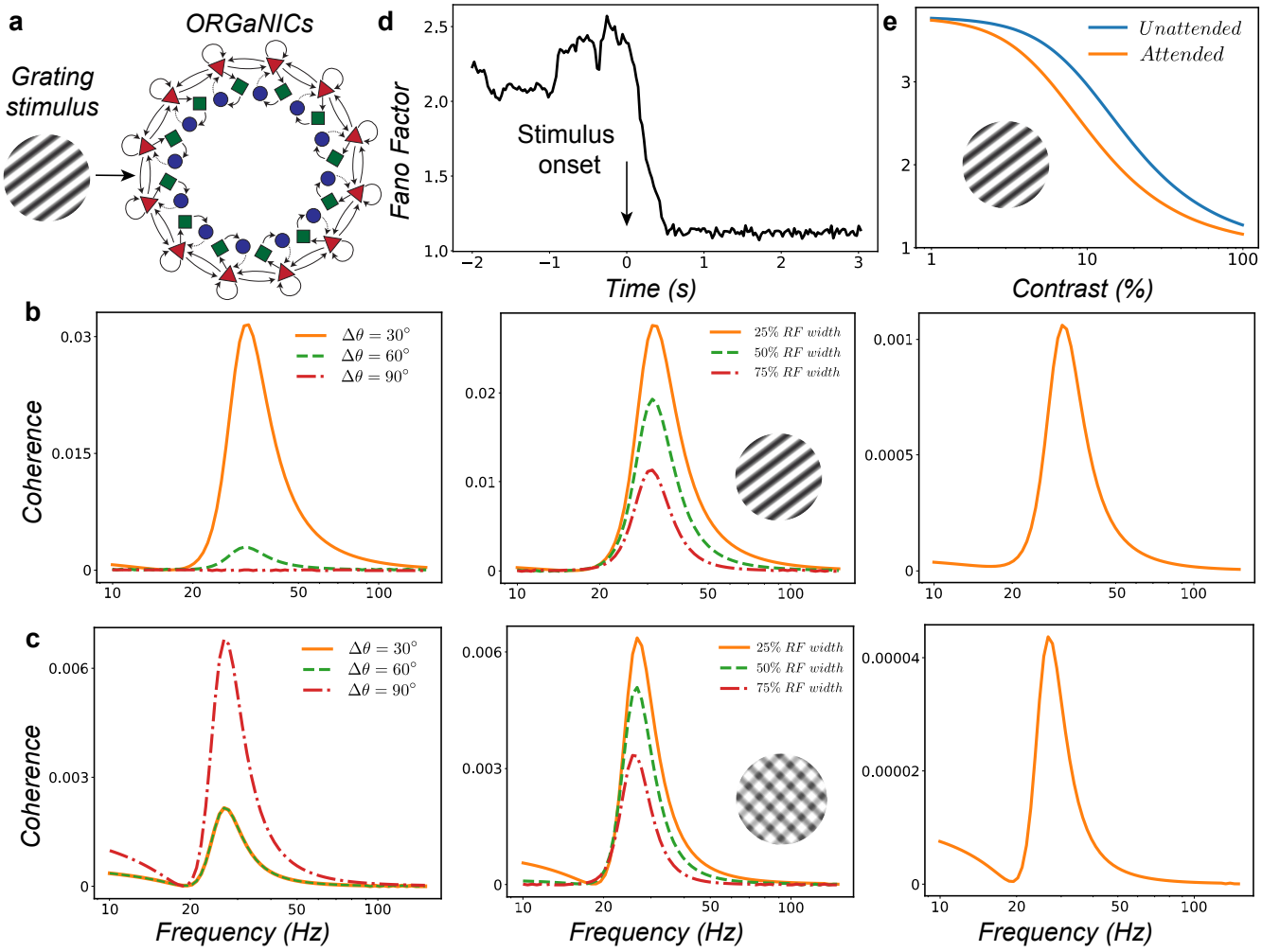

Figure 1: **a:** An illustration of the ORGaNICs model with three different types of neurons which receives a grating stimulus (z). **b:** Response to a 45-degree oriented grating stimulus. Coherence between the maximally firing neuron and neurons with the same RF location, same preferred spatial frequency (SF), but different preferred orientations (left); nearby RF location, same preferred SF, and same preferred orientations (center); same RF location, different preferred SF, and same preferred orientations (right). **c:** Same as **b**, but for a plaid stimulus. **d:** Fano factor of the maximally firing neuron, demonstrating noise quenching upon stimulus onset, presented at $t = 0$. **e:** Fano factor as a function of the contrast of a grating stimulus and a prediction of the effect of attention.

the principal neurons follow the normalization equation exactly at steady-state, $\mathbf{y}_{ss}^{+} = \lfloor \mathbf{z} \rfloor^2 / (\sigma^2 + \mathbf{W} \lfloor \mathbf{z} \rfloor^2)$ when $\mathbf{W}_r = \mathbf{I}$ and $\mathbf{b} = \mathbf{b}_0 = b_0 \mathbf{1}$, where b_0 is a scalar.

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 ~ 25000 variables.

GR model for spiking activity

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 reliable process, following (Carandini, 2004) 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 (Carandini, 2004), where the membrane potentials are assumed to have a Gaussian probability distribution with a 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 implement the GR model analytically and incorporate the time-correlations of the membrane potentials.

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 fol-

lows. 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 $Cov(I_i, I_j) \propto p e^{-\Delta\tau(j-i)/\tau_e}$, 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 and hence the Fano factor analytically.

Results

Since our system exhibits a fixed-point solution, we can calculate the power spectrum analytically, defined by the spectral density matrix which depends on the Jacobian ($\mathbf{J}$) and the noise matrix ($\mathbf{Q}$) as follows, $\mathcal{S}(\omega) = (\imath\omega\mathbf{I} + \mathbf{J})^{-1}\mathbf{Q}(-\imath\omega\mathbf{I} + \mathbf{J})^{-\top}$. From the appropriate elements of this matrix we can obtain the coherence between any two neurons as a function of frequency. We show the results for coherence between the maximally firing neuron and neurons with a different orientation tuning/ RF location/ spatial tuning frequency for grating and plaid stimuli, Fig. 1b&c. Further, our model captures the quenching of the Fano factor upon stimulus onset (Fig. 1d), a widespread cortical phenomenon (Churchland et al., 2010). Finally, 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 depending on model parameters (viz., not a fit parameter). Fig. 1e shows the FF as a function of the grating stimulus contrast, similar to experiments (Coen-Cagli & Solomon, 2019). The orange curve predicts the effect of attention, which we simulate by varying the input gains $\mathbf{b}$ (Eldar, Cohen, & Niv, 2013).

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