Assignment 3

1. **Population Coding**

Consider a population of N neurons, responsible for estimating a continuous stimulus parameter $\theta \in [0, 2\pi)$. Let the mean firing rate of neuron i be:

$$f_i(\theta) = r_{max} e^{\gamma(cos(\theta-\phi_i)-1)}.$$

Further, let the population be evenly tiled in stimulus space with $\phi_i = (i-1)\Delta\phi + \frac{\Delta\phi}{2}$, where $\Delta\phi = \frac{2\pi}{N}$. Let the population response $\mathbf{r} = [r_1, \ldots, r_N]$ to a single trial presentation of stimulus θ obey the following density function:

$$P(\mathbf{r}|\theta) = \prod_{i=1}^{N} \frac{(f_i(\theta)T)^{r_i T}}{(r_i T)!} e^{-f_i(\theta)T},$$

where $T = 1$s is the duration of the trial and $r_{max} = 50$ Hz. We discretize the stimulus θ into $\{0, \Delta\theta, 2\Delta\theta, \ldots, M\Delta\theta\}$ with $M = \frac{2\pi}{\Delta\theta}$ and $\Delta\theta = 0.01$. For a fixed θ and a single stimulus trial we let the stimulus estimate be

$$\theta_{est} = \frac{\sum_{i=1}^{N} r_i \phi_i}{\sum_{i=1}^{N} r_i}.$$

The `MATLAB` code `population_code.m` simulates the above system, where for each fixed θ 10^3 trials are performed and $\langle\theta_{est}\rangle(\theta)$ and $\sigma^2_{est}(\theta) = \langle(\theta - \theta_{est})^2\rangle$ are computed, where $\langle\cdot\rangle$ is an expectation over trials[1].

(a) Plot $\langle\theta_{est}\rangle$ and σ^2_{est} as a function of θ for $N = 5, 10, 50$. Let $\gamma = 10$.

(b) Compute the Fisher information $\mathrm{FI}(\theta) = -\langle \frac{\partial^2}{\partial\theta^2} \ln(P(\mathbf{r}|\theta))\rangle$. Compare $\sigma^2_{est}(\theta)$ computed in a) to the lower bound estimate obtained from $\mathrm{FI}(\theta)$ for $N = 5, 10, 50$.

(c) Let $N = 6$. Let the total error be $E = \int_0^{2\pi} \sigma_{est}(\theta)^2 d\theta \approx \sum_i^M \sigma^2_{est}(\theta_i)\Delta\theta$. Numerically show that E is non-monotonic in the tuning curve slope γ for $\gamma \in (1, 15)$. Plot $\sigma^2_{est}(\theta)$ for γ that minimizes E and for γ on either side of the minimum. Give an intuitive description of why there is an optimal tuning curve slope (i.e. one that minimizes E).

[1] To model a true periodic stimulus estimate we construct θ_{est} from ϕ_i's that are possibly $\pm 2\pi$ shifted value so that $\min[\phi_i - \theta, (\phi_i + 2\pi) - \theta, (\phi_i - 2\pi) - \theta]$ is used. This may look like the system uses knowledge of θ to construct its estimate, however, in reality it is just hardwiring that the stimulus is periodic.

2. **Balanced excitation and inhibition in recurrent cortical networks**

Consider a network of coupled leaky-integrate-and-fire neurons that obey the following dynamics:

$$\tau \frac{dV_i^\alpha}{dt} = -V_i^\alpha + J^{\alpha 0} + \tau \left(\sum_{j=1}^{N_E} J_{ij}^{\alpha E} \sum_k \delta(t - t_{jk}^E) - \sum_{j=1}^{N_I} J_{ij}^{\alpha I} \sum_k \delta(t - t_{jk}^I) \right).$$

Here $\alpha \in \{E, I\}$ denote an excitatory (E) and an inhibitory (I) population. Population α has N_α neurons, and V_i^α is the membrane potential of neuron i from population α. The time t_{jk}^α is the time of the k^{th} spike from neuron j in population α. Each neuron obeys the spike-reset rule $V_i^\alpha(t_{ik}^\alpha) = V_t \to V_i^\alpha(t_{ik}^\alpha + dt) = V_r$ for $dt \to 0$. Take $N_E = N_I \equiv N = 1000$, $V_t = 1$, $V_r = 0$, $\tau = 15$ ms. The parameter $J_{ij}^{\alpha\beta}$ is the coupling between neuron j of population β to neuron i of population α. Let $J_{ij}^{\alpha\beta} = J^{\alpha\beta} > 0$ with probability $p^{\alpha\beta}$ and zero otherwise. For simplicity we consider homogeneous connectivity statistics with $p^{\alpha\beta} \equiv p$ for all α and β. Population α also receives the constant input $J^{\alpha 0}$.

The average number of excitatory (inhibitory) connections that a neuron receives is $K = pN$. Balanced networks as proposed by van Vreeswijk and Sompolinsky[2] scale synaptic strength as $J^{\alpha\beta} = j^{\alpha\beta}/\sqrt{K}$, so that interactions between neurons are very strong (compared to the more classic $1/K$ scaling). For the external input to be of comparable magnitude we also consider $J^{\alpha 0} = j^{\alpha 0}\sqrt{K}$. In what follows we take $j^{EE} = 1$, $j^{IE} = 2$, $j^{EI} = 3$, $j^{II} = 2.5$, $j^{E0} = 1.2$, $j^{I0} = 0.7$, and $p = 0.2$. The `MATLAB` code `balanced_net.m` simulates the above system with random initial conditions (uniform on $[V_r, V_t]$). The output of the program is the network raster – a scatter plot of the spike times and neuron indices.

(a) Consider the population activity over time interval $t \in (0, T)$. Let the average firing rate across population α be:

$$r^\alpha = \lim_{N^\alpha \to \infty} \lim_{T \to \infty} \frac{10^3}{N^\alpha T} \sum_{i=1}^{N^\alpha} \sum_k \delta(t - t_{ik}) \approx \frac{\text{\# of spikes from entire population}}{(\text{\# of neurons})(\text{time interval of simulation})}.$$

Here the $\approx$ holds for large N^α and large T, and the 10^3 converts the time units from ms to s. For large K (hence large N^α) a pair of balance conditions will be

[2] Neural Computation, 10, 1321–1371, 1998.

satisfied by the network, amounting to the following pair of linear equations:

$$\begin{aligned} j^{EE}r^E - j^{EI}r^I + j^{E0} &= \mathcal{O}(1/\sqrt{K}), \\ j^{IE}r^E - j^{II}r^I + j^{I0} &= \mathcal{O}(1/\sqrt{K}). \end{aligned}$$

Show that for $K \to \infty$ we have the following solution for the firing rates.

$$r^E_{\text{theory}} = \frac{j^{E0}j^{II} - j^{I0}j^{EI}}{j^{EI}j^{IE} - j^{EE}j^{II}}, \qquad r^I_{\text{theory}} = \frac{j^{E0}j^{IE} - j^{I0}j^{EE}}{j^{EI}j^{IE} - j^{EE}j^{II}}.$$

Modify `balanced_net.m` to compare r^α estimated from simulations to r^α_{theory} (set $T = 2000$ ms). Do this for $N = 100 \times l^2$ for $l = 1, \ldots, 7$ (this sweep should take 10 minutes). Note that for r^α measured in Hz we require the dimensioned theoretical rate $r^\alpha_{\text{theory}} \to \frac{10^3}{\tau} r^\alpha_{\text{theory}}$. Discuss any discrepancies between r^α_{theory} and r^α and how they depend on N.

We remark that the expressions for r^α_{theory} ignore any details about the spike generating mechanism. More to the point, the firing rates of all models (LIF, Hodgkin-Huxley, etc.) in a balanced network will converge to r_{theory} for $K \to \infty$. What are the consequences for interpreting how single cell physiology impacts large network dynamics.

(b) Modify `balanced_net.m` so that $J^{\alpha\beta} = j^{\alpha\beta}/K$ and $J^{\alpha 0} = j^{\alpha 0}$ for $\alpha, \beta \in \{E, I\}$[3]. This weakly coupled network will show dynamics that are quite distinct from the strongly coupled balanced network. Set $T = 1000$ ms and compare the network raster plots for the classic $1/K$ and balanced $1/\sqrt{K}$ couplings. Discuss the results with respect to the idea that correlated activity between spike trains can be used to infer the strength of synaptic connectivity between neurons.

(c) i. Modify `balanced_net.m` to run two realizations of the simulation with the exact same coupling matrix and initial conditions ($T = 1000$ ms). In the second realization force $V_1^E(t = 500ms) \to V_t$, in other words artificially insert a single extra spike in the second realization at $t = 500$ ms[4]. Plot the network rasters for the two simulations on top of one another with the dots in different colors. What do your findings imply for neural coding schemes that rely on precise spike timing from specific neurons? What about neural codes based on firing rates, computed either over time or population.

[3] With $p = 0.2$ and $N = 1000$ we have that $K = 200$, making the shift to $1/K$ scaling amounting to a reduction of all inputs by a factor of $1/\sqrt{200} \approx 1/14$.

[4] Without loss of generality we assume that neuron 1 of the E population is the source of the extra spike.

ii. Repeat the exercise in (a) but now have $V_1^E(t = 500ms) \to V_1^E(t = 500ms) + \eta$, in other words simply perturb the membrane voltage by η (which may or may not cause a spike). Let $\eta = 0.5$. Save $V_1^E(t)$ for the two realizations and plot their difference $\Delta(t) = [V_1^E(t)]_{\text{r2}} - [V_1^E(t)]_{\text{r1}}$. Run your simulations several times until you have an example where $\Delta(t) \to 0$ and one where $\Delta(t)$ fluctuates widely. Prove that if $V_1^E(t)$ does not spike for $t > 500$ ms then $\Delta(t) \to 0$ for $t \to \infty$ and $\Delta(t) > 0$ for $t < \infty$.