

Statistical framework for encoding and decoding grid cell population activity

KiJung Yoon

Generalized linear model

The spiking activity is modeled as an inhomogeneous Poisson process with the firing rate a function of various covariates that modulate spiking activity:

$$p(Y|X, \Theta) = \prod_t \text{Pois}(\lambda_{full}(t)dt)$$

$$\log p(Y|X, \Theta) = \sum_t y_t \log \lambda_{full}(t) - \lambda_{full}(t)dt + \text{const.}$$

$$\lambda_{full}(t) = \lambda_{space}(t) \cdot \lambda_{speed}(t) \cdot \lambda_{direction}(t) \cdot \lambda_{history}(t) \quad (1)$$

$$\log(\lambda_{space}(t)) = \sum_i \alpha_i \cos(2\pi \langle \mathbf{b}_i, \mathbf{x}(t) \rangle) + \beta_i \sin(2\pi \langle \mathbf{b}_i, \mathbf{x}(t) \rangle) \quad (2)$$

$$\log(\lambda_{speed}(t)) = c + \gamma s(t) \quad (3)$$

$$\log(\lambda_{direction}(t)) = \sum_i \kappa_i B_i(\theta(t)) \quad (\text{cardinal cubic spline basis}) \quad (4)$$

$$\log(\lambda_{history}(t)) = \sum_i \eta_i \langle \mathbf{h}_i, \mathbf{n} \rangle \quad (5)$$

$$\mathbf{h}_i = \frac{1}{2} (\cos(a \log[t + b] - \phi_i) + 1) \quad (6)$$

where $\lambda_{full}(t)$ is the probability of a spike within each 1 ms time bin. In equation (2), $\mathbf{x}(t)$ refers to the spatial position of an animal at time t , \mathbf{b}_i 's specify sinusoidal waveforms of different wavelengths and orientations, and α_i, β_i specify the influence of 2D Fourier basis functions. In equation (3), c is a constant representing the mean firing rate, $s(t)$ refers to the speed of the animal at time t , and γ specifies the influence of speed on spike rate. In equation (5), \mathbf{n} is a neuron's past spike history up to some point, \mathbf{h}_i specifies the spike history filter basis, and η_i represents the influence of the past spike activity around the time when \mathbf{h}_i is not zero.

Here, we presumed a multiplicative model whose nonlinearity function is represented by $\exp(\cdot)$, but other functions like $\log(1 + e^x)$ or $\max(0, x)$ will be compared as an additive model.

A single-neuron-based GLM with only a spatial tuning

$$\log \lambda_{full}(t) = X \cdot \Theta \quad (7)$$

$$= \underset{(10^5 \sim 10^6)}{T} \begin{bmatrix} \vdots & \vdots & \vdots & \vdots & \vdots \\ 1 & \cos(2\pi \langle \mathbf{b}_1 \rangle \mathbf{x}(t)) \cdots \cos(2\pi \langle \mathbf{b}_{N_{fb}} \rangle \mathbf{x}(t)) & \sin(2\pi \langle \mathbf{b}_1 \rangle \mathbf{x}(t)) \cdots \sin(2\pi \langle \mathbf{b}_{N_{fb}} \rangle \mathbf{x}(t)) & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \end{bmatrix} \begin{bmatrix} c_1 \\ \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \end{bmatrix}$$

$1 + 2N_{fb}$

Multiple-neuron-based GLM with only a spatial tuning

i) Distinct spatial tuning between cells:

$$\log \lambda_{full}(t) = X \cdot \Theta \quad (8)$$

$$= \begin{bmatrix} \text{cell 1} & & & \\ & \text{cell 2} & & \\ & & \ddots & \\ & & & \text{cell N} \end{bmatrix} \begin{bmatrix} c_1 \\ \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \\ \hline c_1 \\ \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \\ \hline \vdots \\ \hline c_1 \\ \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \end{bmatrix}$$

ii) Distinct spatial tuning, but shared bias:

$$\log \lambda_{full}(t) = X \cdot \Theta \quad (9)$$

$$= \begin{bmatrix} \begin{array}{|c|c|} \hline \text{cell 1} \\ \hline \end{array} & & & \\ & \begin{array}{|c|c|} \hline \text{cell 2} \\ \hline \end{array} & & \\ & & \ddots & \\ & & & \begin{array}{|c|c|} \hline \text{cell N} \\ \hline \end{array} \end{bmatrix} \begin{bmatrix} c_1 \\ \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \\ \hline \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \\ \hline \vdots \\ \hline \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \end{bmatrix}$$

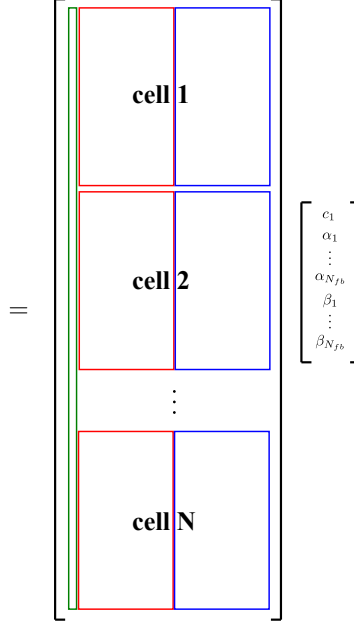
iii) Same spatial tuning by imposing fixed relative phases:

$$\log \lambda_{full}(t) = X \cdot \Theta \quad (10)$$

$$= \begin{bmatrix} \begin{array}{|c|c|} \hline \text{cell 1} \\ \hline \end{array} & & & \\ \begin{array}{|c|c|} \hline \text{cell 2} \\ \hline \end{array} & & & \\ \vdots & & \ddots & \\ \begin{array}{|c|c|} \hline \text{cell N} \\ \hline \end{array} & & & \end{bmatrix} \begin{bmatrix} \alpha_1 \\ \vdots \\ \alpha_{N_{fb}} \\ \beta_1 \\ \vdots \\ \beta_{N_{fb}} \\ c_1 \\ \vdots \\ c_N \end{bmatrix}$$

iv) Same spatial tuning by imposing fixed relative phases, and shared bias:

$$\log \lambda_{full}(t) = X \cdot \Theta \quad (11)$$



How to impose relative phase information into the model?

Given a set of animal's position $\{\mathbf{x}(t)|t = 1 \cdots T\}$ and spatial relative phase $\vec{\delta}^{ij}$ between cell i and j , the predictor matrix X_j is determined by shifting $\{\mathbf{x}(t)\}$ by $-\vec{\delta}^{ij}$ followed by feeding it into (2). Here, the i^{th} reference cell's X_i is assumed to be constructed from $\{\mathbf{x}(t)\}$, and we named cell 1 as a reference cell. In this way, X_j 's in (10, 11) are concatenated to build a tall predictor matrix X . After training the encoding model, we can reconstruct the animal's trajectory without $X_{2:N}$, but

Fourier basis for stimulus filter

Spatial modulation in grid cell activity is parameterized by Fourier basis that is general and flexible enough to represent any triangular lattice of diverse grid periods, orientations, and even irregularity. The 2D Fourier transform of a spatially periodic pattern is predominantly composed of a small number of Fourier components, which is equivalent to the wavelengths and orientations of periodic spatial bands. The hexagonal lattice in grid cell responses is the sum of three significant periodic bands, therefore, the power spectral density (PSD) of any hexagonally arranged pattern shows three significant Fourier components with additional symmetry of themselves (see **Figure 1**). Identification of the Fourier components together with phase angles enables to recover the original spatial response (see **Figure 1**). Equation (2) is depicted in **Figure 2** for better understanding the structure of $\lambda_{space}(t)$.

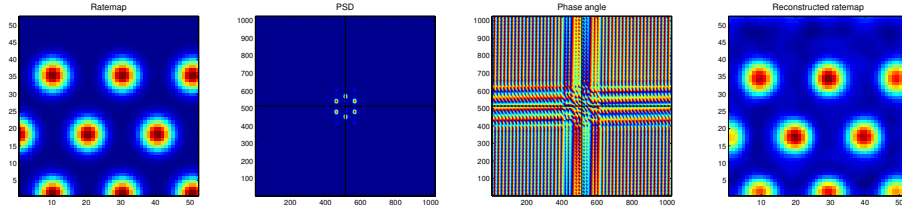


Figure 1: **Spectral analysis of grid cell responses.** (a) Simulated spatial response of a grid cell. (b) Power spectral density of (a). (c) Phase angle of each Fourier component ranging from $-\pi$ to $+\pi$. (d) Reconstructed spatial response from significant Fourier components whose power is greater than a pre-defined threshold.

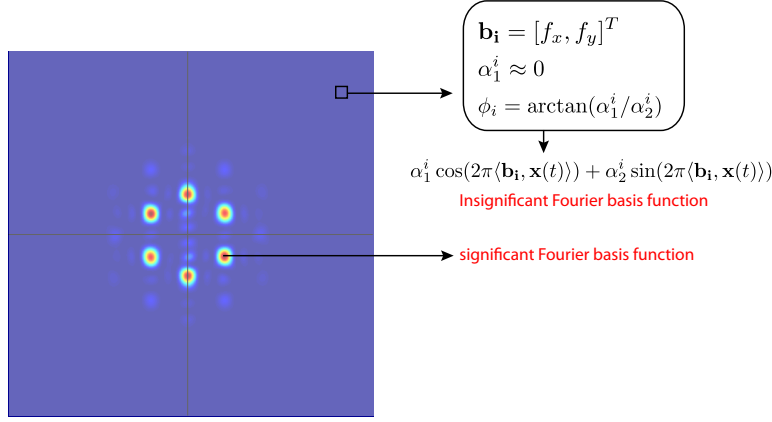


Figure 2: **Fourier basis functions.** An individual pixel in PSD represents a single Fourier basis function characterized by the frequency \mathbf{b}_i (position of the pixel), the magnitude $\sqrt{(\alpha_1^i)^2 + (\alpha_2^i)^2}$ (intensity of the pixel), and the phase angle $\phi_i = \arctan(\alpha_1^i / \alpha_2^i)$ (the same pixel value in Figure 1c).

Raised cosine bumps for spike history filter

Spike history filter \mathbf{h}_k could account for the refractory effect of neurons as well as their burstiness, bistability of responses, and firing-rate adaptation [?]. The temporal components of \mathbf{h}_k were represented by raised cosine basis of the form (6). This basis allows for the representation of fine temporal structure near the time of a spike and coarser/smooth dependency at later times [?]. The \mathbf{h}_k filter was represented with eleven such basis functions (see **Figure 3**).

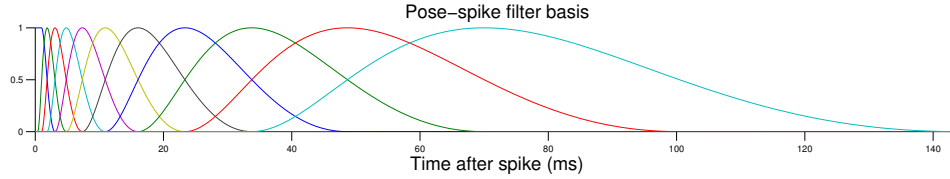


Figure 3: **Raised cosine bumps.** Eleven basis functions for representing spike-history filter. Basis vectors have the form of raised cosine bumps, so they sum to a constant and have log-scaling of the time axis, which enables to represent fine temporal structure near the time of a spike but is constrained to be smooth at longer time scales [?].

Particle filter for decoding grid cells

Under the assumption that the individual grid cells are conditionally independent Poisson processes and that the path of the rat during foraging in an environment is a Gaussian random walk, the system model is described by the following two equations:

- state space equation

$$\begin{aligned} x_t &= f(x_{t-1}, v_{t-1}) \\ &= \mathcal{N}(x_{t-1}, \Sigma) \end{aligned}$$

- observation equation

$$\begin{aligned} y_t &= h(x_t, w_t) \\ &\sim \text{Poisson}(\lambda_{full}(t)dt) \end{aligned}$$

The posterior probability of the current position from the spike train data measured up to the current position time, $p(x_t|y_{1:t})$, can be computed recursively in two steps:

- prediction step

$$p(x_t|y_{1:t-1}) = \int \textcolor{red}{p}(x_t|x_{t-1})p(x_{t-1}|y_{1:t-1})dx_{t-1} \quad (12)$$

- update step

$$p(x_t|y_{1:t}) \propto \textcolor{blue}{p}(y_t|x_t)p(x_t|y_{1:t-1}) \quad (13)$$

(7) can be thought of as a prior over x_t before receiving the most recent observation y_t , and the prior is updated in (8) with the new observation y_t using Bayes' rule to obtain the posterior over x_t . In general, the computation in the prediction and update steps cannot be carried out analytically. Thus, the approximate method such as Monte Carlo sampling is needed and we will exploit the standard SIR particle filter with unconditional resampling [?], where the proposal distribution is taken to be the state transition distribution.

$$x_t \rightarrow \phi_t \rightarrow r_t \rightarrow \hat{\phi}_t \rightarrow \hat{x}_t$$