Analytic model of response statistics in noisy neural populations with divisive normalization

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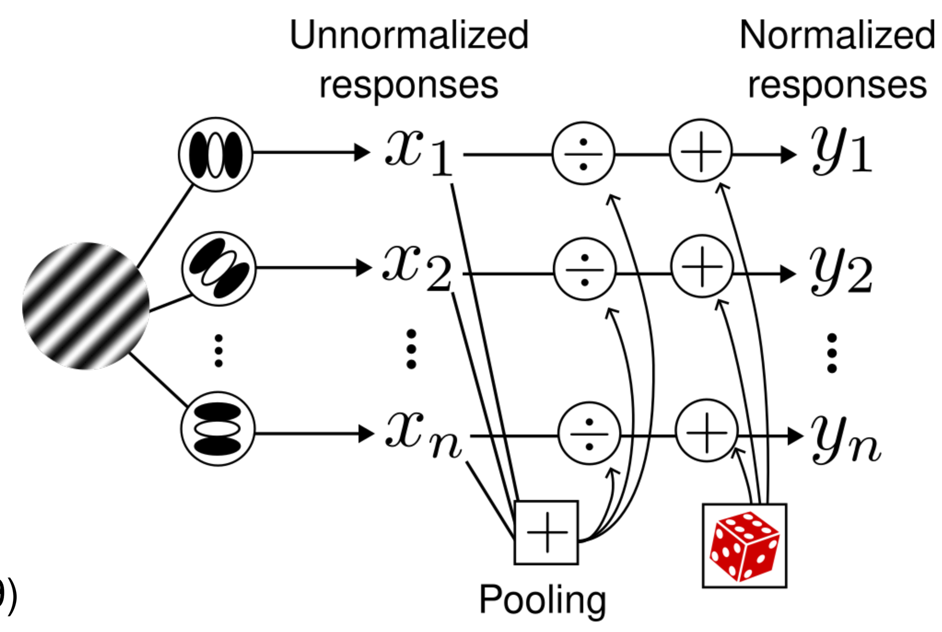
Background

Divisive normalization and neural noise interact in complex ways

Population response depends on noise-normalization interaction

However, this interaction is poorly understood

(Robbe et al. 2024, Coen-Cagli, Solomon 2019)



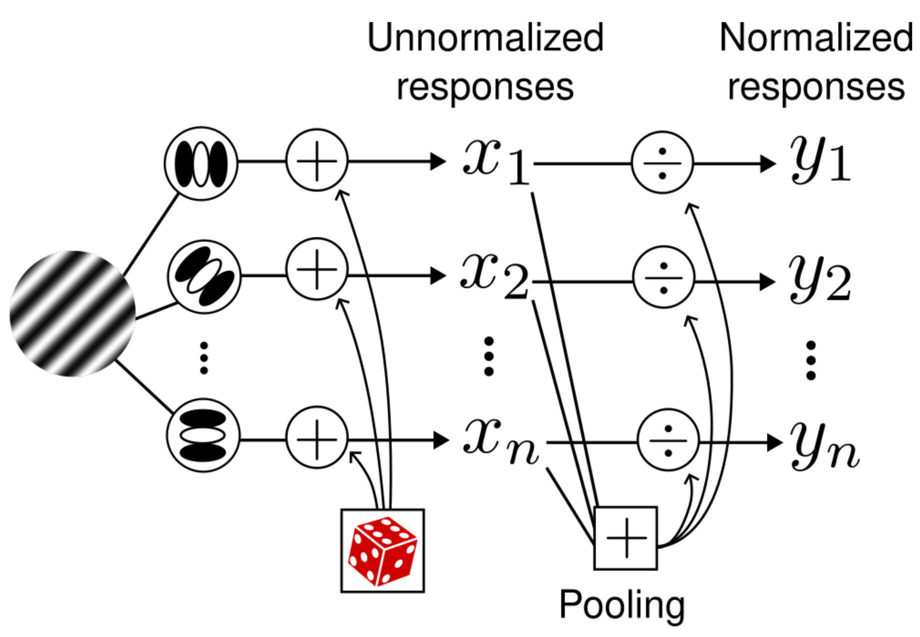
Goal

Analytic model of response statistics with noise-normalization interaction

Model

Input noise added pre-normalization

Normalization signal depends on input mean and noise structure



$$\mathbf{x} \sim \mathcal{N}(\boldsymbol{\mu}, \boldsymbol{\Sigma})$$
$$\mathbf{y} = \frac{\mathbf{x}}{\sqrt{\mathbf{x}^T \mathbf{B} \mathbf{x}}}$$

Parameters
$\boldsymbol{\mu} \in \mathbb{R}^n$
$\boldsymbol{\Sigma} \in \mathbb{R}^{n \times n}$
$\mathbf{B} \in \mathbb{R}^{n \times n}$

Output response statistics

$$\mathbb{E}[y_i] = \mathbb{E}\left[\frac{x_i}{\sqrt{x_i^2 B_{ii} + v_i}}\right] \approx \frac{\mu_i}{\sqrt{\mu_i^2 B_{ii} + \widehat{v}_i}} + \mathrm{tr}\left(\mathbf{H}_{y_i}(\mu_i, \widehat{v}_i) \cdot \begin{bmatrix} \sigma_{x_i}^2 & \rho_{x_i,v_i} \\ \rho_{x_i,v_i} & \sigma_{v_i}^2 \end{bmatrix}\right)$$

$$\mathbb{E}[y_i y_j] = \mathbb{E}\left[\frac{x_i x_j}{\mathbf{x}^T \mathbf{B} \mathbf{x}}\right] = \mathbb{E}\left[\frac{N}{D}\right] \approx \frac{\mu_N}{\mu_D}\left(1 - \frac{\rho(N,D)}{\mu_N \mu_D} + \frac{\sigma_D^2}{\mu_D^2}\right)$$

Auxiliary variables: $v_i = \sum_{j \neq i} x_j^2 B_{jj} \quad N = x_i x_j \quad D = \mathbf{x}^T \mathbf{B} \mathbf{x}$

Final expressions

$$\mathbb{E}[\mathbf{y}] \approx f(\boldsymbol{\mu}, \boldsymbol{\Sigma}, \mathbf{B})$$
$$\mathrm{Cov}[\mathbf{y}] \approx g(\boldsymbol{\mu}, \boldsymbol{\Sigma}, \mathbf{B})$$

Efficient and differentiable
Can be fit to neural response statistics
Can be optimized for computational goals

Output response statistics: Exact formulas for isotropic case

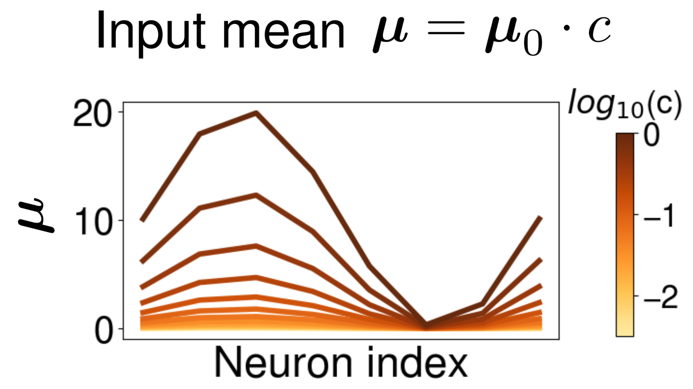
$$\mathbb{E}[\mathbf{y}] = a \cdot \boldsymbol{\mu} \qquad \mathrm{Cov}[\mathbf{y}] = b \cdot \boldsymbol{\mu}\boldsymbol{\mu}^T + c \cdot \mathrm{I}$$

$$a = \frac{\Gamma\left(\frac{n+1}{2}\right)}{\sqrt{2\sigma^2}\,\Gamma\left(\frac{n+2}{2}\right)} {}_1F_1\left(\frac{1}{2}; \frac{n+2}{2}; \frac{-||\boldsymbol{\mu}||^2}{2\sigma^2}\right) \quad b = \frac{1}{(n+2)\sigma^2} {}_1F_1\left(1; \frac{n+4}{2}; \frac{-||\boldsymbol{\mu}||^2}{2\sigma^2}\right) - a^2 \quad c = \frac{1}{n} {}_1F_1\left(1; \frac{n+2}{2}; \frac{-||\boldsymbol{\mu}||^2}{2\sigma^2}\right)$$

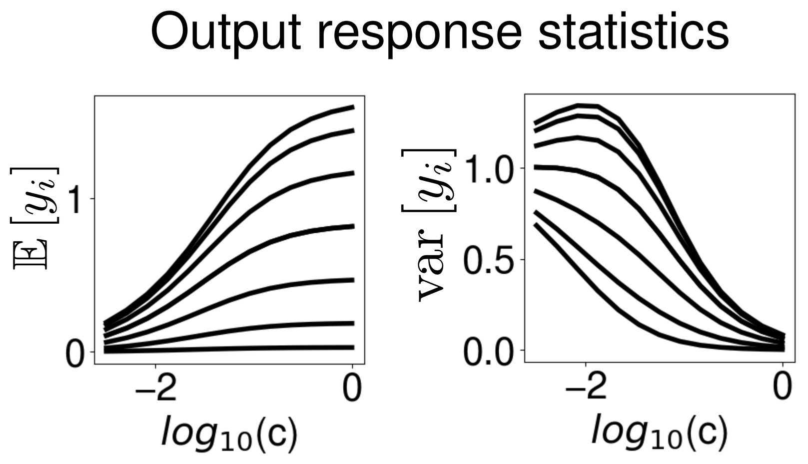
Effect of input mean ($\boldsymbol{\mu}$)

Response saturation

Input mean $\boldsymbol{\mu} = \boldsymbol{\mu}_0 \cdot c$

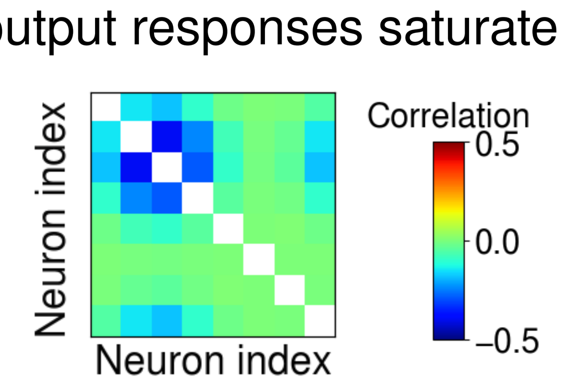


Output response statistics



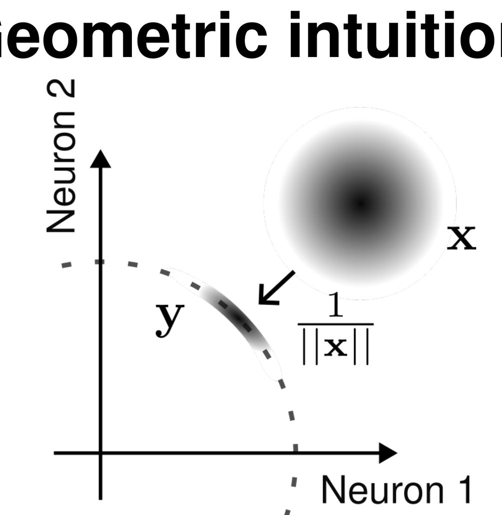
Mean output responses saturate

(fixed c)



Normalization induces output correlations from independent input noise

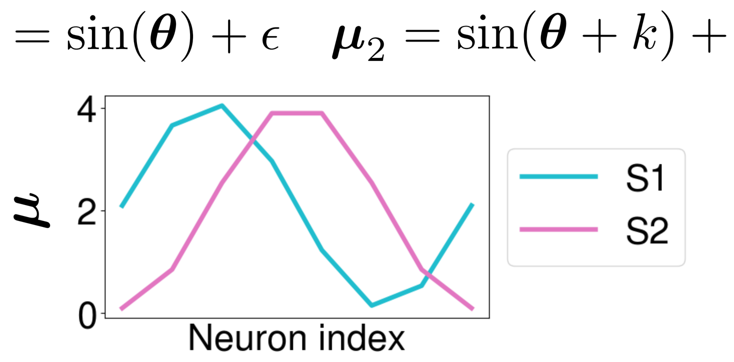
Geometric intuition

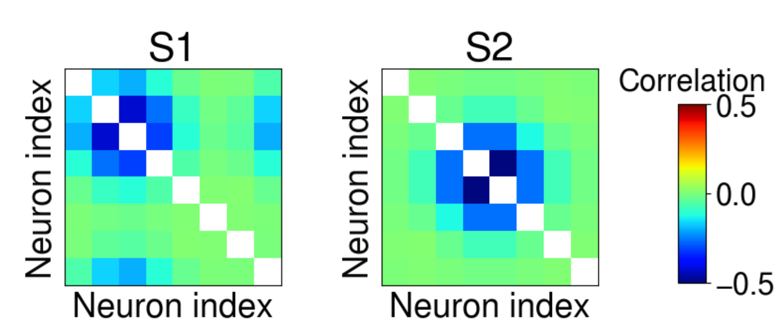


Stimulus dependence

Output correlations depend on $\boldsymbol{\mu}$

$\boldsymbol{\mu}_1 = \sin(\boldsymbol{\theta}) + \epsilon \quad \boldsymbol{\mu}_2 = \sin(\boldsymbol{\theta} + k) + \epsilon$





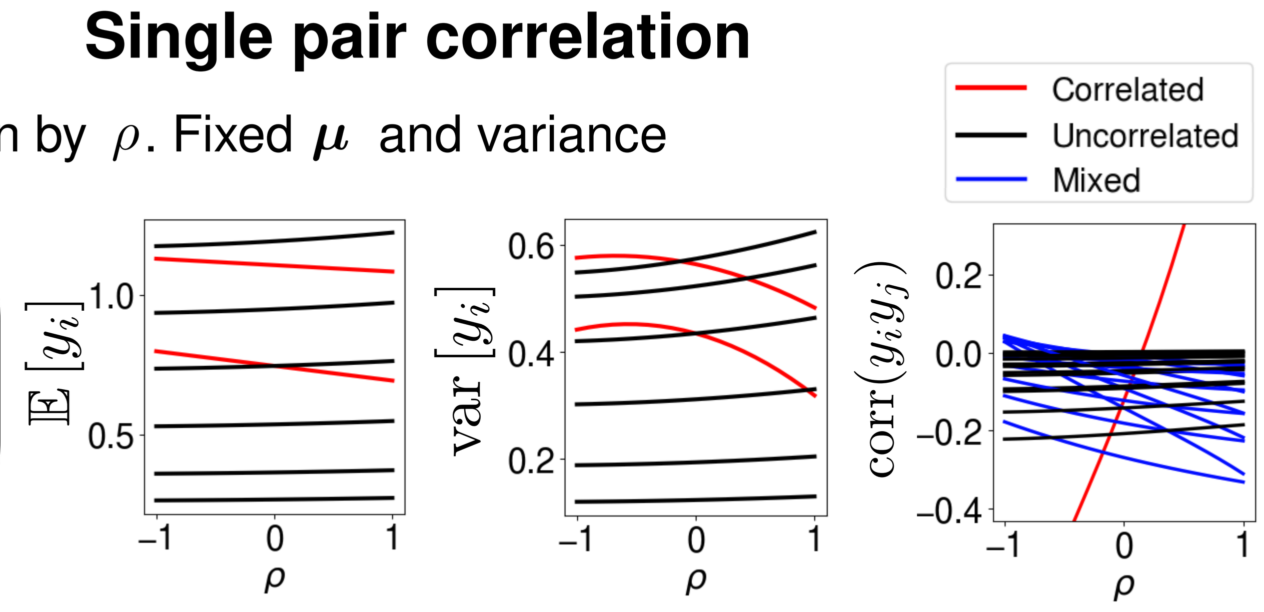
Normalization induces stimulus-dependent output correlations

Effect of input noise (Σ)

Single pair correlation

Input correlation given by ρ. Fixed $\boldsymbol{\mu}$ and variance

$$\mathrm{corr}(\mathbf{x}) = \begin{pmatrix} 1 & \rho & 0 & \cdots & 0 \\ \rho & 1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 1 \end{pmatrix}$$

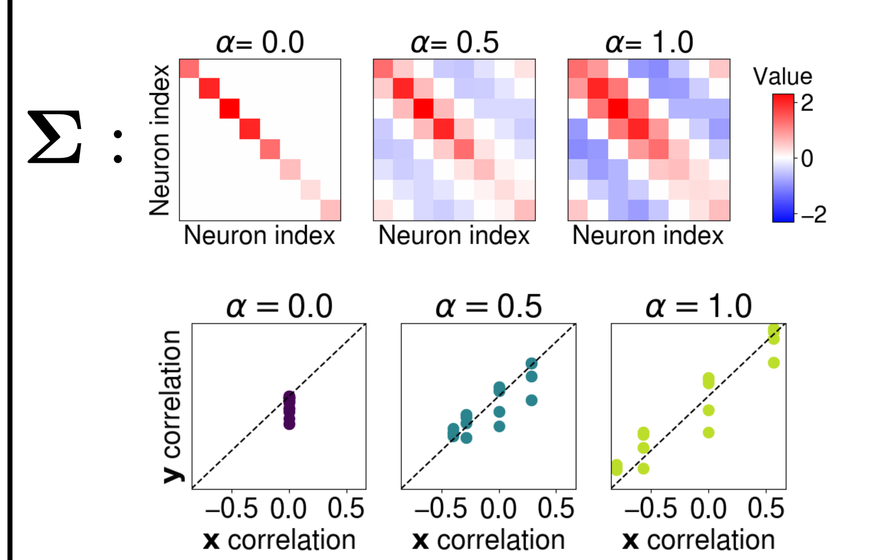


A single input noise correlation can affect all output statistics via normalization.

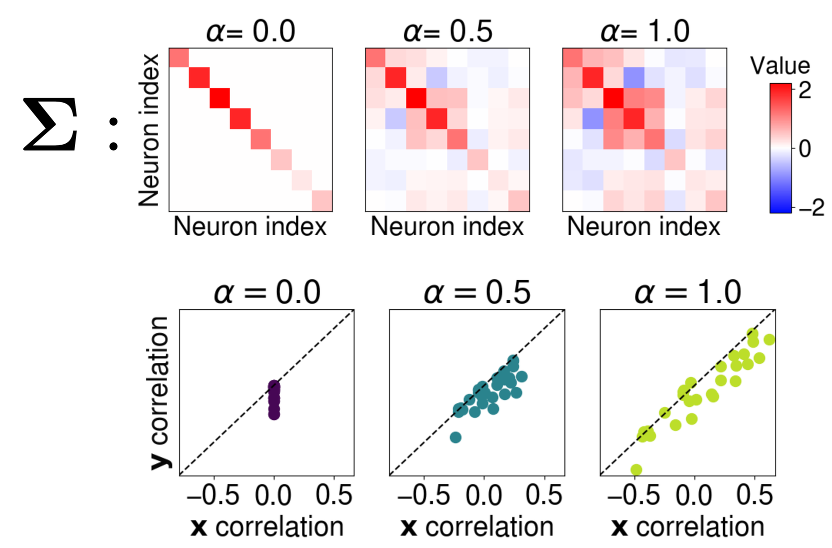
Population correlations

$\boldsymbol{\Psi}_s$ structured input correlations. α parametrizes $\boldsymbol{\Sigma}$: $\boldsymbol{\Psi} = \mathbf{I}(1-\alpha) + \alpha \cdot \boldsymbol{\Psi}_s$

Distance dependent correlations



Random correlations



Output covariance is correlated with input covariance.
Pre-normalization correlations can be inferred from output correlations.

Effect of normalization matrix ($\mathbf{B}$)

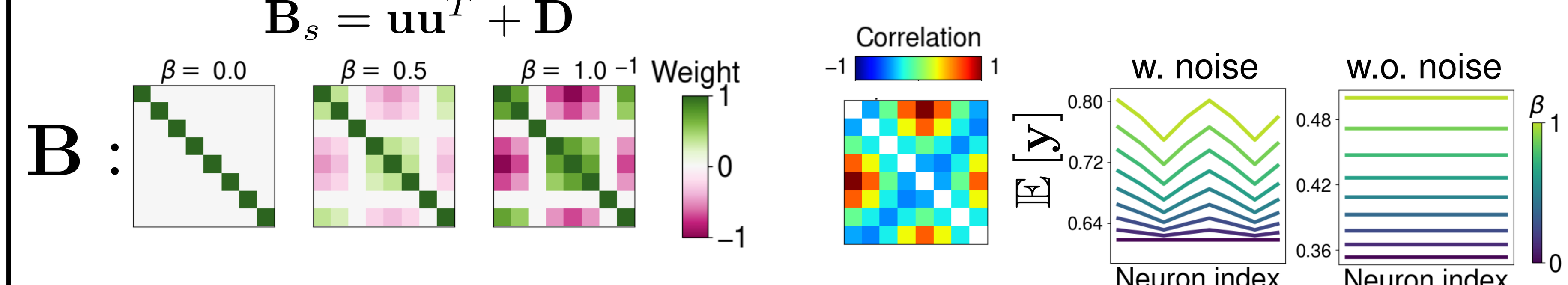
Structured normalization weights

$\mathbf{B}$ can instantiate diverse forms of normalization (e.g. feature specific)

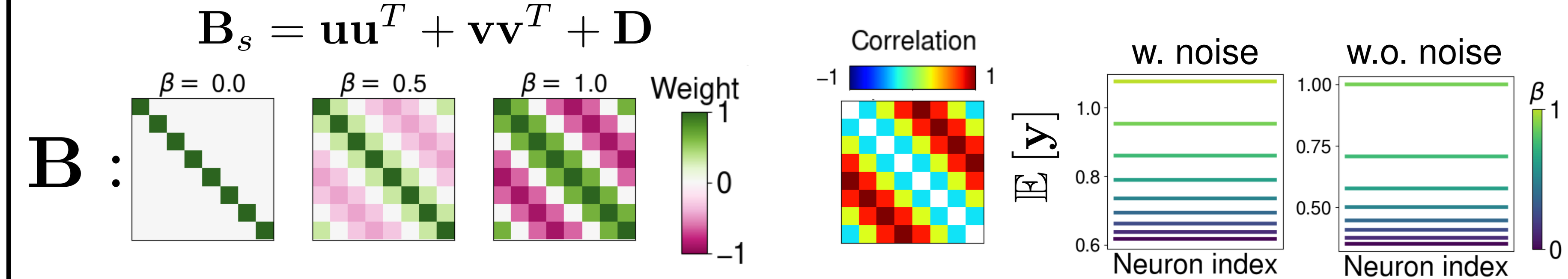
$\mathbf{B}_s$ has structured weights. β parametrizes $\mathbf{B}$: $\mathbf{B} = \mathbf{I}(1-\beta) + \beta \cdot \mathbf{B}_s$

$\boldsymbol{\mu} = \mathbf{1}$

$\mathbf{B}_s = \mathbf{u}\mathbf{u}^T + \mathbf{D}$



$\mathbf{B}_s = \mathbf{u}\mathbf{u}^T + \mathbf{v}\mathbf{v}^T + \mathbf{D}$



Structured normalization can transform uncorrelated input noise into structured output mean and structured output correlations

Noise-normalization interaction alters output response statistics differently than normalization without noise.

Conclusions

Complex neural response properties emerge from noise-normalization interaction:
- Saturating responses
- Stimulus-dependent correlations
- Spontaneous activity differences

Both input noise and normalization affect output mean and covariance due to their interaction

Potential contributor to observed neural response properties

Future work

Implement model variants (half-saturation constant, exponent, stochastic gain) $\frac{\mathbf{x}}{\sqrt{\mathbf{x}^T \mathbf{B} \mathbf{x} + c_{50}^2}}$

Normative modeling of noise and normalization interactions for specific functions and tasks

Fit model to neuronal response data

Goris RLT et al. (2024) Nat Rev Neurosci; **Coen-Cagli R; Solomon SS**(2019) J. Neurosci; **Weiss O; Bounds HA; Adesnik H; Coen-Cagli R** (2023) PLoS Comput Biol; **Carandini M; Heeger, DJ** (2012) Nat Rev Neurosci; **Schwartz O; Simoncelli EP** (2001) Nat Rev Neurosci; **Verhoef BE; Maunsell JHR** (2017) Nat Neurosci