SYDE 556/750

Simulating Neurobiological Systems Lecture 3: Population Representation

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cell activity



behavior

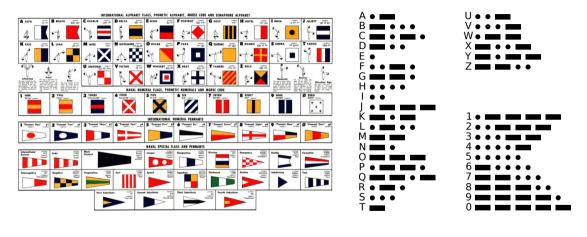
ongoing

NEF Principle 1: Representation

NEF Principle 1 – Representation

Groups ("populations", or "ensembles") of neurons *represent* represent values via nonlinear encoding and linear decoding.

Lossless Codes



Encoding: $\mathbf{a} = f(\mathbf{x})$ Decoding: $\mathbf{x} = f^{-1}(\mathbf{a})$

Binary numbers: Nonlinear encoding, linear decoding

- ▶ Represent a natural number between 0 and $2^n 1$ as n binary digits.
- ► Nonlinear encoding

$$a_i = (f(x))_i = \begin{cases} 1 & \text{if } x - 2^i \lfloor \frac{x}{2^i} \rfloor > 2^{i-1}, \\ 0 & \text{otherwise}. \end{cases}$$

► Linear decoding

ecoding
$$x = f^{-1}(\mathbf{a}) = \sum_{i=0}^{n-1} 2^i a_i = \mathbf{F} \mathbf{a} = \begin{pmatrix} 1 & 2 & \dots & 2^{n-1} \end{pmatrix} \begin{pmatrix} a_0 \\ a_1 \\ \vdots \\ a_{n-1} \end{pmatrix}.$$

► This is a **distributed code**. But, **not robust** against additive noise!

Lossy codes

► Lossy code

Inverse f^{-1} does not exist, instead approximate the represented value

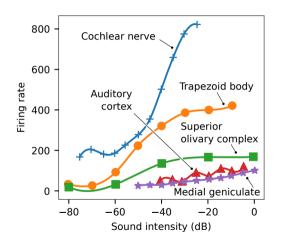
Encoding:
$$\mathbf{a} = f(\mathbf{x})$$

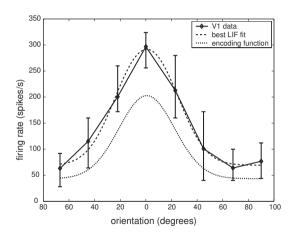
Decoding: $\mathbf{x} \approx g(\mathbf{a})$

Examples

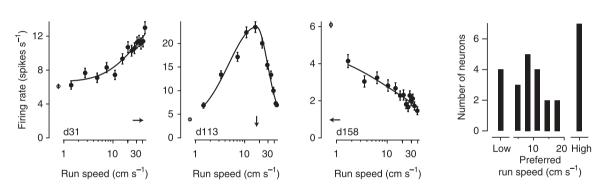
- Audio, image, and video coding schemes (MP3, JPEG, H.264)
- Basis transformation onto first n principal components (PCA)
- Neural Representations

Tuning curves (I)





Tuning curves (II)

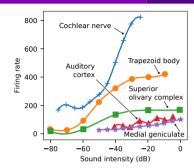


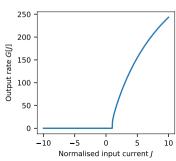
- ► Last lecture: response curves: a = G(J)
- This lecture: tuning curves: $a = f(x) = G(J_i(x))$
- ► What sort of function can we try for $J_i(x)$?
- ▶ Introduce a gain α_i and a bias J_i^{bias} :

$$J_i(x) = \alpha_i x + J_i^{\text{bias}}$$

$$a_i(x) = G(\alpha_i x + J_i^{\text{bias}})$$

- $ightharpoonup \alpha_i$ controls the slope
- $ightharpoonup J_i^{\text{bias}}$ shifts curve left and right





▶ Does this work for all tuning curves?

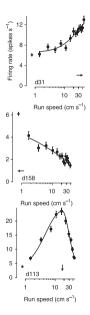
$$a_i(x) = G(\alpha_i x + J_i^{\text{bias}})$$

- ► a) increasing: Yes!
- **b** b) decreasing: Yes! (just let α_i be negative)
 - ▶ or, better yet, introduce e_i which is either 1 or -1 and keep α_i to be always positive. This keeps the two ideas (slope and increase/decreasing) separate.

$$a_i(x) = G(\alpha_i(e_ix) + J_i^{\mathrm{bias}})$$

- c) preferred stimulus: Need some sort of similarity measure
 - ▶ But it shouldn't be too complicated. So far we've only needed to introduce multiplication and addition, which are both things we're pretty sure neurons can do, so let's avoid adding anything else if we don't have to. Ideas?

$$a_i(x) = G(\alpha_i sim(e_i, x) + J_i^{\mathrm{bias}})$$



Encoders: Preferred Direction Vectors

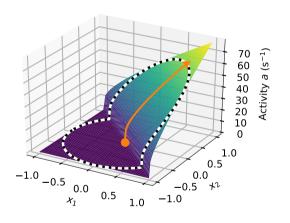
- ▶ The represented value x doesn't have to be a scalar
- ▶ What if it's a vector?
- ► There's a simple similarity-like measure for vectors: the dot product

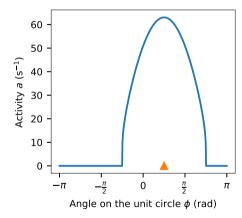
$$\langle \mathbf{x}, \mathbf{y} \rangle = \sum_{i=0}^{d} x_i y_i = \cos(\angle(\mathbf{x}, \mathbf{y})) \|\mathbf{x}\| \|\mathbf{y}\|$$

$$a_i(\mathbf{x}) = G(\alpha_i \langle \mathbf{e}_i, \mathbf{x} \rangle + J_i^{\text{bias}})$$

- Constrain e_i to be a unit vector
 - Note that for scalar x, the only two unit vectors are +1 and -1
 - ► So the increasing / decreasing scenario is a special case of this!

Preferred Directions in Higher Dimensions: Representing 2D Values





Decoding

► Non-linear Encoding and Linear Decoding

$$\mathbf{a}_i = Gig[lpha_i \langle \mathbf{x}, \mathbf{e}_i
angle + J_i^{ ext{bias}}ig],$$
 Encoding $\hat{\mathbf{x}} = \mathbf{D}\mathbf{a}$

- ightharpoonup How do we find \mathbf{D} ?
- ► Least-squares minimization

$$\arg\min_{\mathbf{D}} E = \frac{1}{|\mathbb{X}|} \int_{\mathbb{X}} \|\mathbf{x} - \hat{\mathbf{x}}\| \, d\mathbf{x} = \frac{1}{|\mathbb{X}|} \int_{\mathbb{X}} \|\mathbf{x} - \mathbf{Da}(\mathbf{x})\| \, d\mathbf{x}$$

Decoding via Least-squares Minimization

► Find the minimum decoding error

$$\arg\min_{\mathbf{D}} \mathsf{E} = \frac{1}{|\mathbb{X}|} \int_{\mathbb{X}} \|\mathbf{x} - \hat{\mathbf{x}}\| \, \mathrm{d}\mathbf{x} = \frac{1}{|\mathbb{X}|} \int_{\mathbb{X}} \|\mathbf{x} - \mathbf{D}\mathbf{a}(\mathbf{x})\| \, \mathrm{d}\mathbf{x}$$

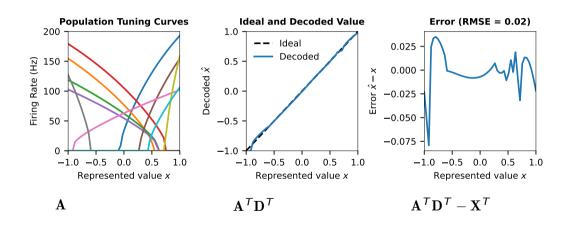
▶ We can do this analytically, or sample:

$$\arg\min_{\mathbf{D}} E = \frac{1}{N} \sum_{i=0}^{N} \|\mathbf{x}_i - \mathbf{Da}(\mathbf{x}_i)\|$$

Decoding via Least-squares Minimization

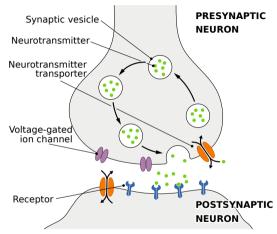
- ▶ Let's write this in matrix form, where $\mathbf{A}_{ik} = a_i(x_k)$ and $\mathbf{X} = (x_1, \dots, x_N)$
- ightharpoonup We want $\mathbf{A}^T \mathbf{D}^T = \mathbf{X}^T$
- ightharpoonup So $\mathbf{A}\mathbf{A}^T\mathbf{D}^T = \mathbf{A}\mathbf{X}^T$
- $(\mathbf{A}\mathbf{A}^T)^{-1}\mathbf{A}\mathbf{A}^T\mathbf{D}^T = (\mathbf{A}\mathbf{A}^T)^{-1}\mathbf{A}\mathbf{X}^T$
- ► In Python, D = np.linalg.lstsq(A.T, X.T, rcond=None)[0].T
- (where A is a n \times N array and X is a d \times N array)

Decoding



Sources of Noise in Biological Neural Networks

- Axonal jitterActive axonal spike propagation
- ► Vesicle release failure 10-30% of pre-synaptic events cause post-synaptic current
- Neurotransmitter per vesicle
 Varying amounts of neurotransmitter
- ► Ion channel noise Ion-channels are "binary", stochastic
- ► Thermal noise
- Network effects
 Simple, noise-free inhibitory/excitatory
 networks produce irregular spike trains



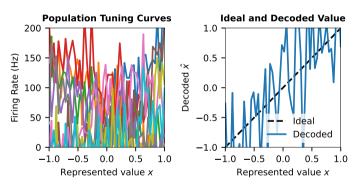
► How to model? Gaussian noise

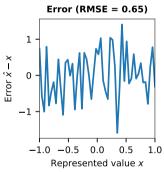
NEF Principle 0: Noise

NEF Principle 0 – Noise

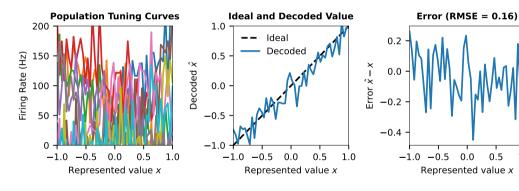
Biological neural systems are subject to significant amounts of noise from various sources. Any analysis of such systems must take the effects of noise into account.

Decoding Noisy A Without Taking Noise Into Account





Decoding Noisy A Accounting for Noise



0.5

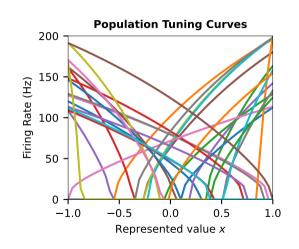
1.0

Summary: Building a model of neural representation (Encoding)

Encoding

- Select d, possible range $\mathbf{x} \in \mathbb{X}$, usually $\mathbb{X} = \{\mathbf{x} \mid ||\mathbf{x}|| \le r, \mathbf{x} \in \mathbb{R}^d\} \ (r = 1)$
- ► Select number of neurons *n*
- Select tuning curves, maximum rates $\Rightarrow \mathbf{e}_i, \ \alpha_i, \ J_i^{\text{bias}}$
 - ightharpoonup Sample e_i from unit-sphere
 - Uniformly distribute x-intercept, maximum rate
- Encoding equation:

$$a_i(\mathbf{x}) = G[\alpha_i \langle \mathbf{e}_i, \mathbf{x} \rangle + J_i^{\text{bias}}]$$



Summary: Building a model of neural representation (Decoding)

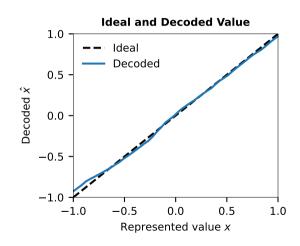
Decoding

- ► Uniformly sample *N* samples from X, $X = (x_1, ..., x_N)$
- ► Compute **A**, where $(\mathbf{A})_{ik} = a_i(\mathbf{x}_k)$
- Decoder computation:

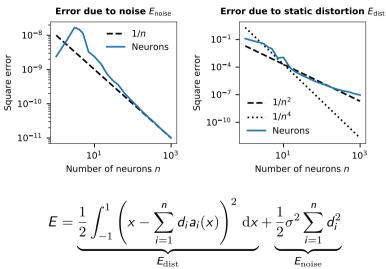
$$\mathbf{D}^{\mathsf{T}} = \left(\mathbf{A}\mathbf{A}^{\mathsf{T}} + N\sigma^{2}\mathbf{I}\right)^{-1}\mathbf{A}\mathbf{X}^{\mathsf{T}}$$

Decoding equation:

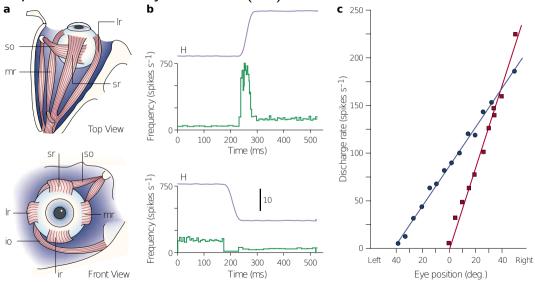
$$\hat{\mathbf{X}} = \mathbf{D}\mathbf{A}$$



Analysing Sources of Errors



Example: Horizontal Eye Position (1D)



Example: Horizontal Eye Position (1D) (cont.)

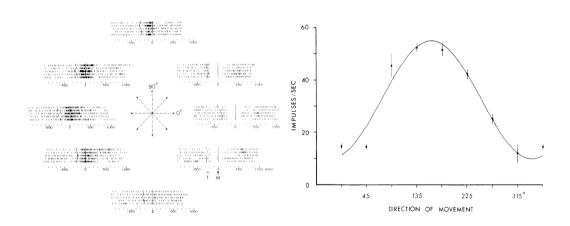
- ► Step 1: System Description
 - ► What is being represented?
 - x is the horizontal eye position
 - ► What is the tuning curve shape?
 - ▶ Linear, low $\tau_{\rm ref}$, high $\tau_{\rm RC}$
 - ▶ $e_i \in \{1, -1\}$
 - Firing rates up to $300 \, \mathrm{s}^{-1}$

- ► Step 2: Design Specification
 - Range of values

$$ightharpoonup X = [-60, 60]$$

- Amount of noise
 - ▶ About 20% of $\max(\mathbf{A})$
- ► Step 3: Implementation
 - Choose tuning curve parameters
 - Compute decoders

Example: Arm Movements (2D)



Example: Arm Movements (2D) (cont.)



- Experiment by Georgopoulos et al., 1982
- ► Preferred arm movement directions e_i
- ▶ Idea: Population Vectors, decode using

$$\hat{\mathbf{x}} = \sum_{i=1}^{n} a_i(\mathbf{x}) \mathbf{e}_i = \mathbf{E} \mathbf{A}$$

- Good direction estimate
- Cannot reconstruct magnitude

The NEF does not use population vectors!

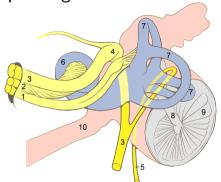
Example: Arm Movements (2D) (cont.)

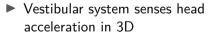
- ► Step 1: System Description
 - ► What is being represented?
 - x the movement direction (or hand position)
 - What is the tuning curve shape?
 - Bell-shaped
 - ► Encoders are randomly distributed along the unit circle
 - Firing rates up to $60 \, \mathrm{s}^{-1}$

- ► Step 2: Design Specification
 - Range of values

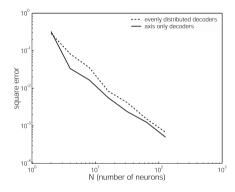
- Amount of noise
 - ▶ About 20% of max(A)
- ► Step 3: Implementation
 - Choose tuning curve parameters
 - Compute decoders

Example: Higher Dimensional Representation





► Axis aligned, must choose $\mathbf{e}_i \in \{[1,0,0],[-1,0,0],\dots,[0,0,-1]\}$



- ► Same as three 1D populations
- Slightly better precision
- **►** Encoders affect accuracy

Image sources

Title slide

"The Ultimate painting." Author: Clark Richert.

From Wikimedia.