SYDE 556/750

Simulating Neurobiological Systems Lecture 3: Population Representation

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September 18 & 20, 2023

- ► Slide design: Andreas Stöckel
- ► Content: Terry Stewart, Andreas Stöckel, Chris Eliasmith





Visua'**,** ∩ortex

Mapping receptive fields

cell activity





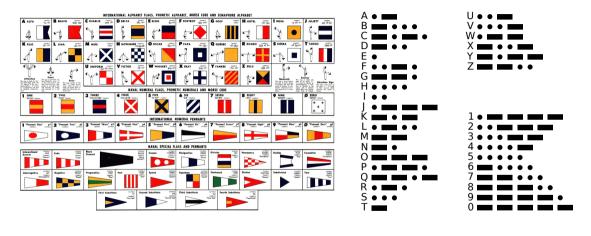


NEF Principle 1: Representation

NEF Principle 1 – Representation

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

Lossless Codes



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

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

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

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

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▶ Linear decoding

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

- ▶ Represent a natural number between 0 and $2^n 1$ as n binary digits.
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► This is a **distributed code**.

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

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

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

Lossy codes

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

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Examples

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

Lossy codes

► Lossy code

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

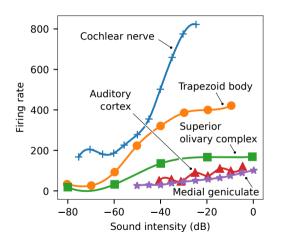
Encoding:
$$\mathbf{a} = f(\mathbf{x})$$

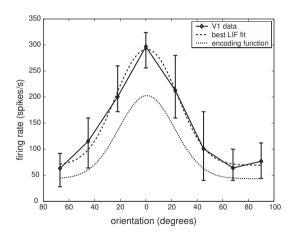
Decoding: $\mathbf{x} \approx g(\mathbf{a})$

Examples

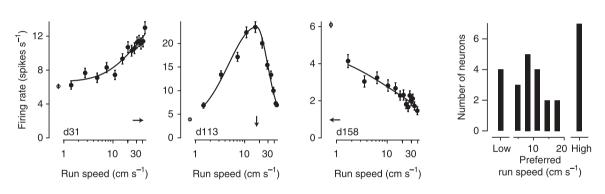
- Audio, image, and video coding schemes (MP3, JPEG, H.264)
- Basis transformation onto first n principal components (PCA)
- ► Neural Representations

Tuning curves (I)

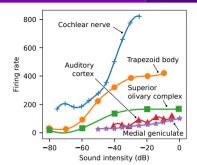


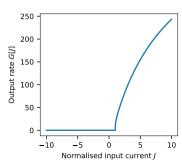


Tuning curves (II)



- 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 $J_i(x)$?



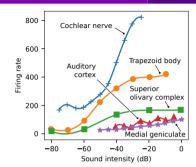


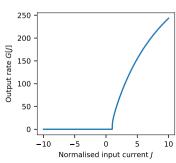
- ► Last lecture: response curves: a = G(J)
- This lecture: tuning curves: $a = f(x) = G(J_i(x))$
- ► What sort of function can we try for $J_i(x)$?
- ▶ Introduce a gain α_i and a bias J_i^{bias} :

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

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

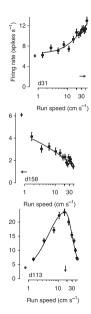
- $ightharpoonup \alpha_i$ controls the slope
- $ightharpoonup J_i^{\text{bias}}$ shifts curve left and right





Does this work for all tuning curves?

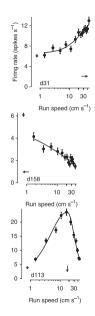
$$a_i(x) = G(\alpha_i x + J_i^{\text{bias}})$$



▶ Does this work for all tuning curves?

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

▶ a) increasing: Yes!

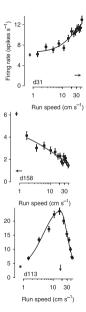


Does this work for all tuning curves?

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

- ▶ a) increasing: Yes!
- \blacktriangleright b) decreasing: Yes! (just let α_i be negative)
 - ightharpoonup 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.

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



▶ Does this work for all tuning curves?

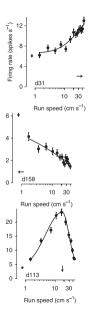
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- ▶ a) increasing: Yes!
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 - ▶ or, better yet, introduce e_i which is either 1 or -1 and keep α_i to be always positive. This keeps the two ideas (slope and increase/decreasing) separate.

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

- 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

- ightharpoonup The represented value x doesn't have to be a scalar
- ► What if it's a vector?

Encoders: Preferred Direction Vectors

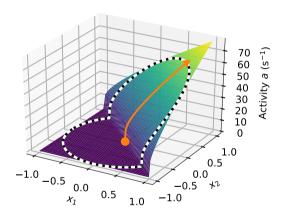
- ▶ The represented value x doesn't have to be a scalar
- ▶ What if it's a vector?
- ► There's a simple similarity-like measure for vectors: the dot product

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

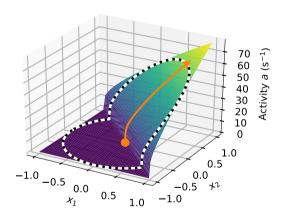
$$a_i(\mathbf{x}) = G(\alpha_i \langle \mathbf{e}_i, \mathbf{x} \rangle + J_i^{\text{bias}})$$

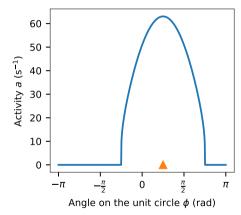
- Constrain e_i to be a unit vector
 - Note that for scalar x, the only two unit vectors are +1 and -1
 - ► So the increasing / decreasing scenario is a special case of this!

Preferred Directions in Higher Dimensions: Representing 2D Values



Preferred Directions in Higher Dimensions: Representing 2D Values





Decoding

► Non-linear Encoding and Linear Decoding

$$\mathbf{a}_i = G[\alpha_i \langle \mathbf{x}, \mathbf{e}_i \rangle + J_i^{ ext{bias}}],$$
 Encoding $\hat{\mathbf{x}} = \mathbf{D}\mathbf{a}$ Decoding

ightharpoonup How do we find \mathbf{D} ?

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

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

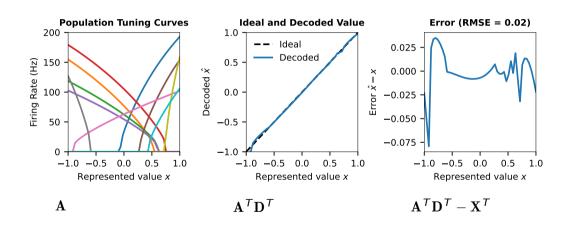
► We can do this analytically, or sample:

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

Decoding via Least-squares Minimization

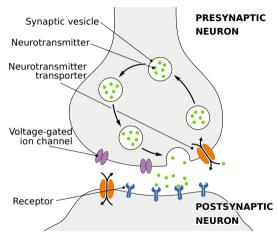
- ▶ Let's write this in matrix form, where $\mathbf{A}_{ik} = a_i(x_k)$ and $\mathbf{X} = (x_1, \dots, x_N)$
- ightharpoonup We want $\mathbf{A}^T \mathbf{D}^T = \mathbf{X}^T$
- ightharpoonup So $\mathbf{A}\mathbf{A}^T\mathbf{D}^T = \mathbf{A}\mathbf{X}^T$
- $(\mathbf{A}\mathbf{A}^T)^{-1}\mathbf{A}\mathbf{A}^T\mathbf{D}^T = (\mathbf{A}\mathbf{A}^T)^{-1}\mathbf{A}\mathbf{X}^T$
- ► 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



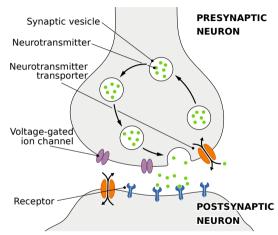
Sources of Noise in Biological Neural Networks

- 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



Sources of Noise in Biological Neural Networks

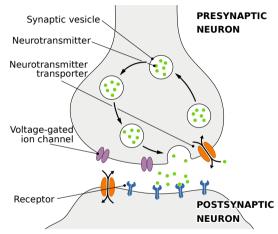
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► How to model?

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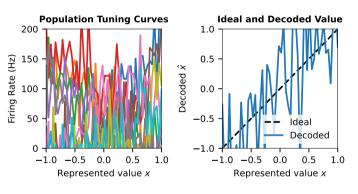
► How to model? Gaussian noise

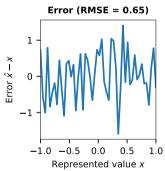
NEF Principle 0: Noise

NEF Principle 0 – Noise

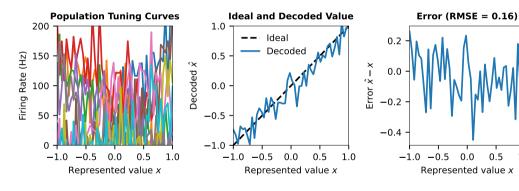
Biological neural systems are subject to significant amounts of noise from various sources. Any analysis of such systems must take the effects of noise into account.

Decoding Noisy A Without Taking Noise Into Account





Decoding Noisy A Accounting for Noise



0.5

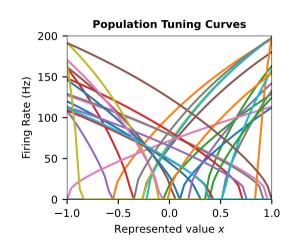
1.0

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)

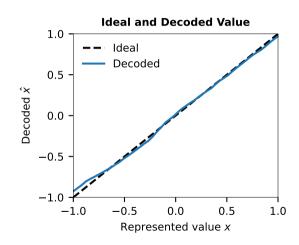
Decoding

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

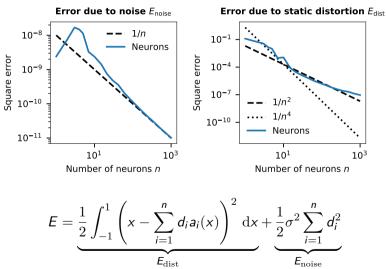
$$\mathbf{D}^{\mathsf{T}} = \left(\mathbf{A}\mathbf{A}^{\mathsf{T}} + \mathcal{N}\sigma^{2}\mathbf{I}\right)^{-1}\mathbf{A}\mathbf{X}^{\mathsf{T}}$$

Decoding equation:

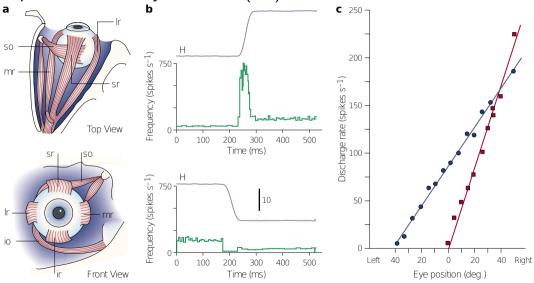
$$\hat{\mathbf{X}} = \mathbf{D}\mathbf{A}$$



Analysing Sources of Errors



Example: Horizontal Eye Position (1D)



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

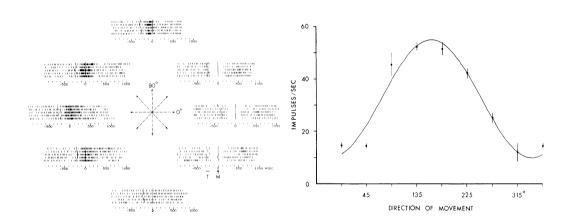
- ► Step 1: System Description
 - ► What is being represented?
 - x is the horizontal eye position
 - ► What is the tuning curve shape?
 - ▶ Linear, low $\tau_{\rm ref}$, high $\tau_{\rm RC}$
 - ▶ $e_i \in \{1, -1\}$
 - ightharpoonup Firing rates up to $300\,\mathrm{s}^{-1}$

- ► 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

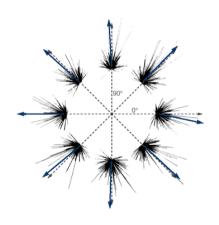
Example: Arm Movements (2D)





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

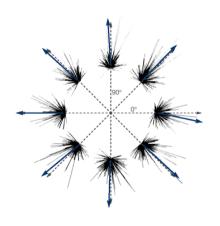
$$\hat{\mathbf{x}} = \sum_{i=1}^{n} a_i(\mathbf{x}) \mathbf{e}_i = \mathbf{E} \mathbf{A}$$



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

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

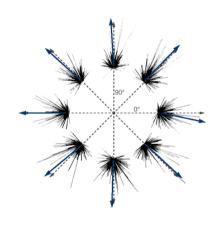
Good direction estimate



- 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



- 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

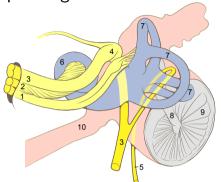
The NEF does not use population vectors!

- ► 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
 - ightharpoonup Firing rates up to $60\,\mathrm{s}^{-1}$

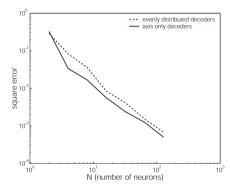
- ► Step 2: Design Specification
 - Range of values

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

Example: Higher Dimensional Representation

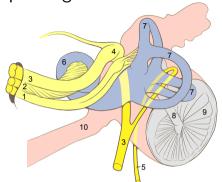


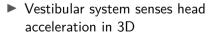
- ► Vestibular system senses head acceleration in 3D
- ▶ Axis aligned, must choose $\mathbf{e}_i \in \{[1,0,0],[-1,0,0],\dots,[0,0,-1]\}$



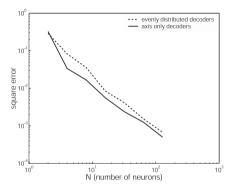
- ► Same as three 1D populations
- Slightly better precision

Example: Higher Dimensional Representation





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



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

Administration

Assignment 1 has been released.

Image sources

Title slide

"The Ultimate painting." Author: Clark Richert.

From Wikimedia.