How Behavioral Constraints May Determine Optimal Sensory Representations

by Salinas (2006)

CPSC 644

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Motivation

- Neural response is typically characterized in terms of a tuning curve: Change in response (firing rate, etc.) as a particular stimulus parameter is varied.
- Efficient coding hypothesis: Response should maximize information, i.e., sensory neurons should represent the sensory world as efficiently as possible.
- Problem: *"Such a principle cannot completely account for the response characteristics of cortical neurons, particularly beyond early sensory areas, because* ***it does not consider how the encoded information will be used, if at all****."* Also, the ubiquity of monotonic tuning curves is not well explained.

Research Questions

- "Early receptor neurons seem to be highly specialized for describing a rather small set of [stimuli] that are **relevant for a specific behavior**, ..."
- Questions:
  - **"Does an animal's behavior influence the shapes of its sensory tuning curves?"**
  - "What features would be most sensitive to behavioral constraints?"

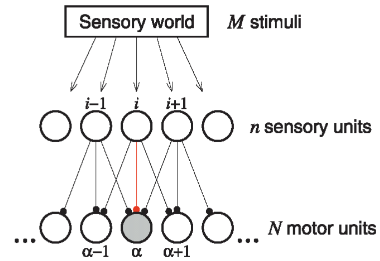
Monotonic Tuning Curves

- Quite prevalent, in somatosensory system, etc.: Peaked tuning curves are not the only kind!
- No analysis so far based on efficient coding hypothesis, or any other principle (except for learning, which is not clear if it is the case).
- What promotes monotinic tuning properties?

Approach

- Treat tuning curves as basis functions, based on which other functions of the stimulus parameters can be easily constructed.
- "If something can be said about the statistics of the downstream motor activity, then we should be able to say something about the sensory tuning curves that are optimal for driving such activity."

Network Model

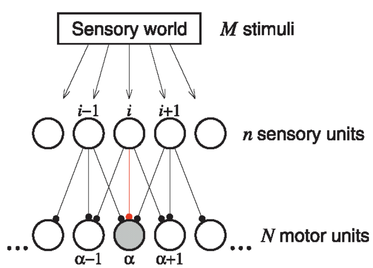


- Response matrix $\mathbf{r}$:

  r_{ik} is the firing rate of basis neuron i evoked by stimulus k.

  $\mathbf{r}_k$ is a response vector for stimulus k.
- Mean response over trials $\langle r_{ik} \rangle$.
- Motor response $\mathbf{R}$, target response $\mathbf{F}$.

Tuning Curve



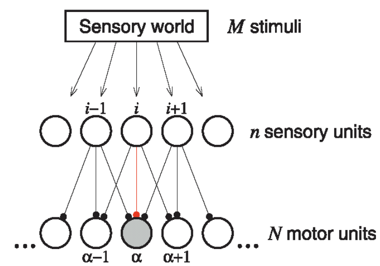
- To deal with variability in response, we use the average over trials (presentation of the same stimulus k):

$$\langle r_{ik} \rangle$$

- Tuning curve of sensory cell i:

$\langle r_{ik} \rangle$, plotted as a function of k

Motor Neuron Activation



- Motor neuron response to stimulus k:

$$R_{\alpha k} = \sum_{i=1}^{n} w_{\alpha i} r_{ik}$$

where $w_{\alpha i}$ is the connection from sensory unit i to motor unit α. This can be written as

$$\mathbf{R} = \mathbf{w}\mathbf{r}.$$

E_B: Error Measure for $\mathbf{F}$ vs. $\mathbf{R}$

- $E_B = 0$ if sensory neurons are most accurate and driven responses are equal to the desired ones.
- $E_B = 1$, driven activity has no resemblance to the target, and the error is maximal.
- E_B depends on four quantities: $E_B = f(\langle \mathbf{r} \rangle, \boldsymbol{\sigma}, \{s_k\}, \boldsymbol{\phi})$.
  1. $\langle \mathbf{r} \rangle$: sensory tuning curves
  2. $\boldsymbol{\sigma}$: noise in sensory tuning curves
  3. $\{s_k\}$: probability of observing stimulus k
  4. $\boldsymbol{\phi}$: correlation across $\mathbf{F}_k$

$$\phi_{kl} = \frac{1}{N} \sum_{\alpha=1}^{N} F_{\alpha k} F_{\alpha l}$$

What Determines the Optimal Tuning Curve?

- What tuning curve $\langle \mathbf{r} \rangle$ minimize E_B?
- The solution is not unique (problem is underconstrained):

$$\mathbf{R} = \mathbf{w}\mathbf{r} \quad \text{and}$$

$$\mathbf{R} = (\mathbf{w}\mathbf{A})(\mathbf{A}^{-1}\mathbf{r})$$

  give equivalent results with different factors (for an arbitrary invertible matrix $\mathbf{A}$).
- Additional constraints are needed.

Additional Constraints

- $\vec{F}_\alpha$: target function of motor unit α for all k stimuli.
- If all $\vec{F}_\alpha$ are different from each other, a lot of tuning curves will be necessary. This means $\vec{F}_\alpha$ should be uncorrelated, i.e., $\boldsymbol{\phi}$ should be close to diagonal.
- Thus how big N is, and how correlated the functions $\vec{F}_\alpha$ affect the design of the sensory tuning curves.
- Basic idea: use the eigenvector of $\boldsymbol{\phi}$ to design the tuning curves.

Properties of ϕ

- With s_k equal for all k, the M eigenvalues are nonnegative and sum to 1.
- When $\boldsymbol{\phi}$ results from averaging just a few functions ($<< M$) or many functions with similar shapes, only a few eigenvalues are significantly larger than 0.
- When the average involves many different functions, most eigenvalues are close to 1 and $\boldsymbol{\phi}$ itself is close to diagonal.

Optimal Tuning Curve and ϕ: Single Neuron

- If tuning curve is proportional to an eigenvector of $\boldsymbol{\phi}$ with eigenvalue λ:

$$E_B(n=1) = \frac{\left(1 - \frac{\lambda}{M}\right)\rho + 1}{\rho + 1},$$

where ρ is signal-to-noise ratio.

- With high variability of neural activity, ρ tends to 0, and error to 1.
- Worst case scenario is when $\lambda = 0$: max error, regardless of ρ.
- Lowest error when λ is max: Tuning curve is equal to the first principal component of $\boldsymbol{\phi}$.

Optimal Tuning Curve and ϕ: Multiple Neuron

- For n basis neurons and no noise, the minumum error reachable is:

$$min(E_B) = 1 - \frac{1}{M}\sum_{i=1}^{n}\lambda_i,$$

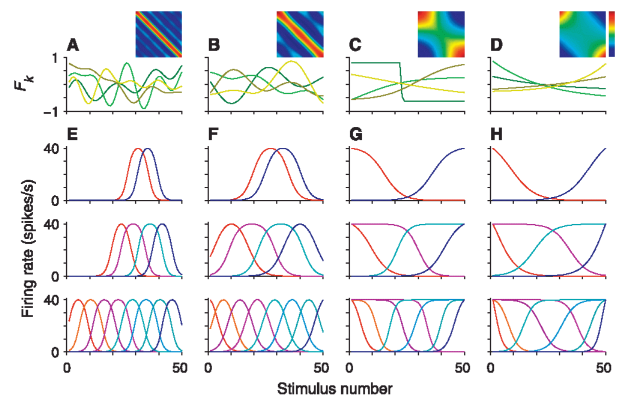
for n largest eigenvalues λ_i.

- If only a few eigenvalues are large so that it sums up to M, then $n << M$.

Monotonic vs. Nonmonotonic Tuning Curves

- What sets of tuning curves are optimal when there is variability and when specific downstream functions are considered?
- Four parameters to generate tuning curves, both monotonic or unimodal. Use optimization function to tune the parameters to minimize E_B.

Results for Four Classes of Downstream Target

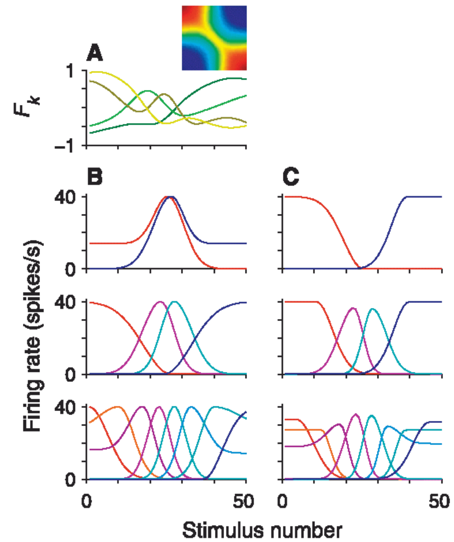


- Top row: $\mathbf{F}_k$ and their correlation matrix $\boldsymbol{\phi}$.
- Rows below: 2, 4, and 8 tuning curves that minimize E_B for those targets.
- A,B: nonmonotonic target, nonmonotonic tuning curve; C,D: monotonic target, monotonic tuning curve

Interpretation of the Results

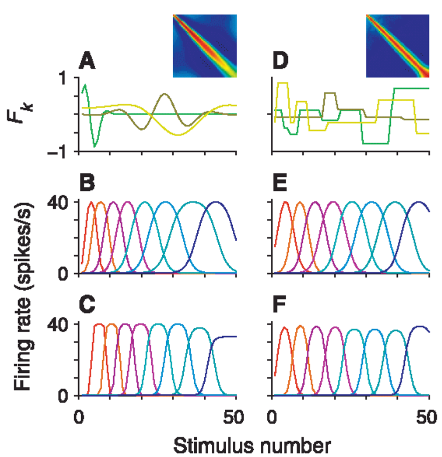
- "The detailed features of the optimal tuning curves clearly depend on the specifics of the target class."
- "Two types of responses [nonmonotonic and unimodal] may arise not because of information-coding considerations but because of differences in the actions that various types of stimuli ultimately trigger."
- "For example, some stimulus parameters, such as the orientation of a bar, should lead to approximately the same sorts of movements regardless of the parameter's value. But other parameters or features, such as image contrast or sound intensity, haven an obvious directionality, in that salient stimuli of high contrast or high intensity are more likely to lead to action."
- "Sensory neurons might respond in a qualitatively different way to features with and without such a behavioral bias."

Mixed Tuning Curves



- Binocular disparity: Typical actions vary depending on disparity:
  1. Zero: lots of possible actions.
  2. Negative: converging eye movement to make disparity 0.
  3. Positive: diverging eye movement to make disparity 0.
- Mixed monotone and unimodal tuning curves: Such tuning curves have been reported in V4.

Widening Tuning Curves



- Bat's echolocation:
  1. Far from the target: want to track smoothly
  2. Close to the target: want to turn sharply to make the final catch
- Unimodal tuning curves with different widths: Similar properties found in bat auditory system.

Discussion

- Considering downstream requirements helped explain curious sensory tuning properties.
- Classical approach of information maximization is not enough.
- Previous theoretical studies of sensory neurons were based on: (1) optimality assumption (efficient coding) and (2) statistics of the inputs.
- Appraoch presented here goes backwards.
- Estimating input statistics is straight-forward, but not so for motor statistics associated with specific stimuli.

Discussion (YC)

- This is a remarkable paper.

References

Salinas, E. (2006). How behavioral constraints may determine optimal sensory representations. *PLoS Biology*, 4:2383.