Testing the Efficiency of Sensory Coding with Optimal Stimulus Ensembles

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Presented by Tomoki Tsuchida
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Agenda

- Efficient Coding Hypothesis
- Response Function and Optimal Stimulus Ensemble
- Firing-Rate Code
- Spike-Timing Code
- OSE vs Natural Stimuli
- Conclusion
Efficient Coding Hypothesis

- “[Sensory systems] recode sensory messages, extracting signals of high relative entropy from the highly redundant sensory input” (Barlow, 1961)

- Neurons should encode information to match the statistics of natural stimuli
  - Use fewer bits (and higher resolution) for common stimuli

- Is this true?
  - What are the “natural stimuli?”
  - Behavioral relevance should be considered
  - “Supernatural” stimuli sometimes drive neurons best
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Response and OSE

- **Stimulus and response**

  - Neural system = “channel”

  - Channel capacity: maximum mutual information between signal and response

  - Optimal stimulus ensemble: stimulus ensemble that saturates the channel capacity.
When there is no noise, best RF is the integral (cdf) of the stimulus distribution.

Conversely, we can calculate the stimulus distribution for which the RF is optimal – “OSE.”

Is OSE = Natural stimulus ensemble?
Response and OSE

- With noisy responses, OSE changes
  - OSE avoids response regions that are noisy
- Still contains most of the probability at 25-55 dB SPL (most useful region)
Response and OSE

- This result is from constant intensity stimuli
  - What about time-varying stimuli?
  - What if information is encoded in spike timing?

- Two experiments:
  1. Experiment with time-varying stimuli, assuming rate-coding
  2. Experiment with time-varying stimuli, and consider information from precise timing of spikes.
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OSE for Time-Varying Stimuli

- Question: what kind of time-varying stimuli are those neurons optimized for?

- Checking for “all” time-varying stimuli is impossible, so assume distribution of OSE is parameterized

- Ensemble “member”: characterized by two parameters, $a$ (sample average) and $b$ (standard deviation) of the sine wave

\[ p(s) \propto \mathcal{N}(\mu_a, \sigma_a) \mathcal{N}(\mu_b, \sigma_b) \]

- OSE: want to find the best parameters such that $p(s)$ maximizes the mutual information.
Online algorithm

Draw $a$ and $b$ from the Gaussians. Construct the signal with $a$ and $b$.

Update estimate of $p(s)$

(This is for a single neuron.)
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Firing-Rate Code

- What information is encoded in the firing rate?
  - Consider the firing rates from 80ms windows (segments in the previous slide)
Firing-Rate Code

- Multiple OSEs possible
- Covers 30 – 300 Hz of firing rate
- Invariant along the y-axis (since iso-FRs don’t change either)
  ➞ Variance (fluctuations around mean) doesn’t matter much
OSEs do vary in the variance of “mean” axis

But: with clipped stimulus mean…

All OSEs have the same variance

Conclusion: neurons are optimized for ensembles whose clipped stimulus mean look like D.
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Spike-Timing Code

- What information is encoded in spike timing of response?

- If information is encoded in spike timing, the timing code should be *reliable* (low noise) and *distinctive* (high entropy – many distinct symbols.)

- Look at binary strings of ten 2-ms bins (2ms ≅ refractory period.)

- Repeat each stimulus 25 times

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Spike-Timing Code

- t-OSE is much narrower in x-axis and firing rate range; centered at higher STD (y-axis.)

- Why?
Spike-Timing Code

- Need to balance between response variety (high entropy) and reliability (low noise)
- Large fluctuations trigger reliable spikes

Want this to be **high**…
… but this to be **low**.
Spike-Timing Code

- Examples of stimuli snippets with different probabilities
  - High-probability stimuli elicit reliable responses.

- Using spike-timing code can increase information rates 8-fold.
Population Data

- **r-OSE**
  - Uses full dynamic range of the receptor
  - Expands along with iso-FR lines for higher STD

- **t-OSE**
  - Narrower along stimulus means
  - Does not use STD < 10 dB
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OSE vs Natural Stimuli

- How does the natural sound ensemble (environmental sounds) of grasshoppers compare to the OSEs?
  - How do the environmental sounds and communication signals differ?
OSE vs Natural Stimuli

- Environmental sounds vs songs: on its own, neither ensemble fully employ information capacity
OSE vs Natural Stimuli

- However, what *subset* of song ensemble matches t-OSE?

- Transient onset of song “syllables” matches t-OSE

- Behaviorally relevant signals

- Neurons are optimized for encoding of strong transients, but can still provide information about other stimuli.
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Conclusion

- Rate code or time code?
  - Depends on how downstream neurons use the output

- To make full use of the information capacity, we need to rely on the spike-timing read-out.

- Receptors maximize the information gained about specific (but less often occurring) aspects of the stimuli. (Even for some supernatural stimuli!)

- Coding strategy of sensory neurons is matched to the ensemble of natural stimuli, weighted by the behavioral relevance.