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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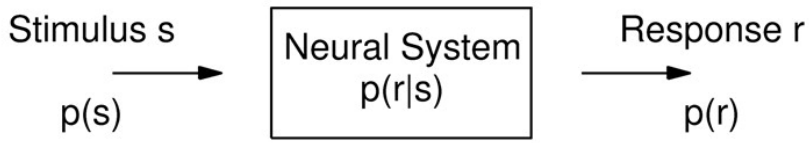
Response and OSE

- Stimulus and response



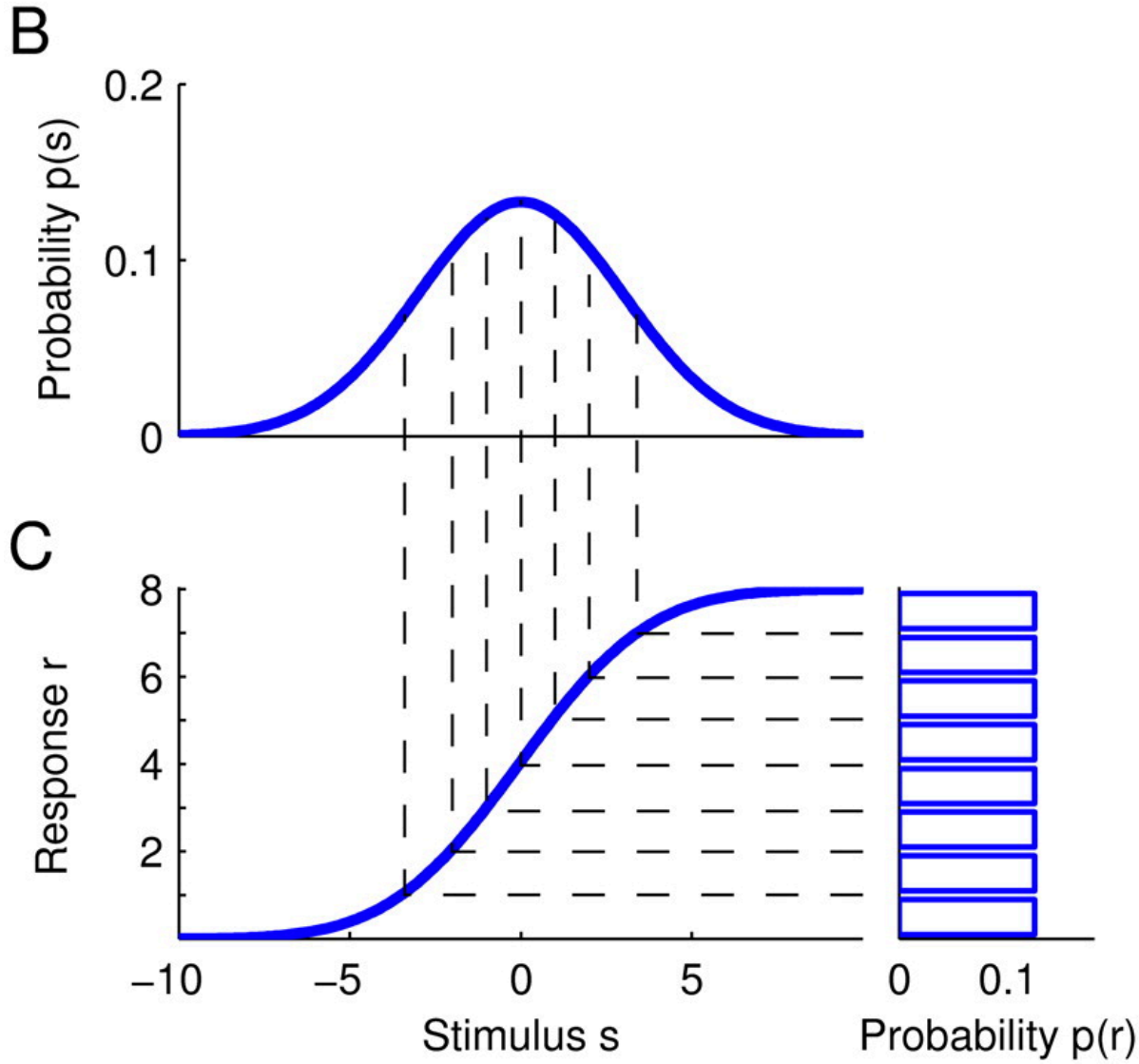
- Neural system = “channel”
- Channel capacity: maximum mutual information between signal and response
- Optimal stimulus ensemble: stimulus ensemble that saturates the channel capacity.

Response and OSE

❖When there is no noise, best RF is the integral (cdf) of the stimulus distribution.

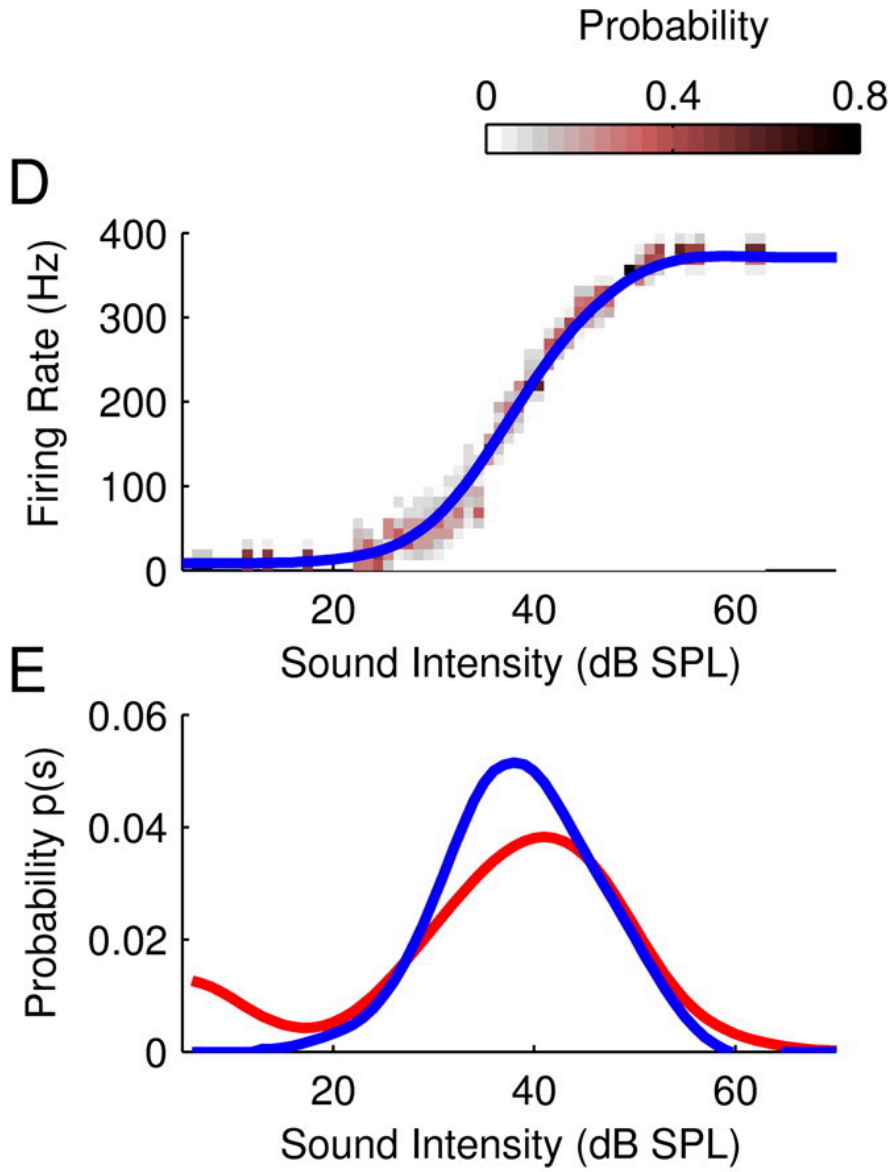
❖Conversely, we can calculate the stimulus distribution for which the RF is optimal – "OSE."

❖ 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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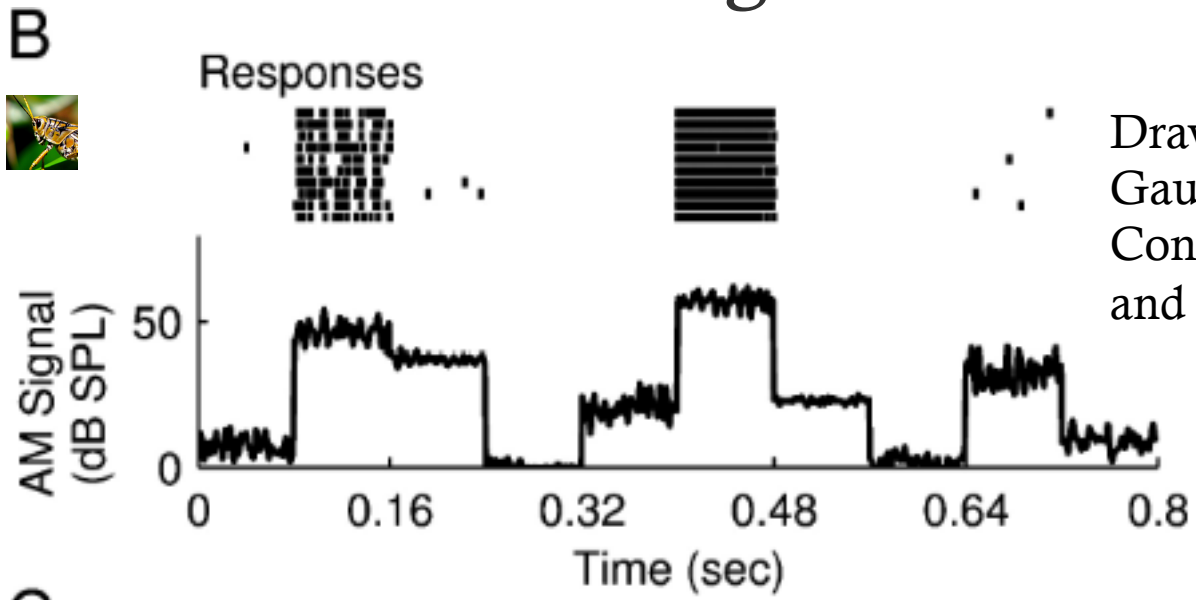
OSE for Time-Varying Stimuli

- 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*

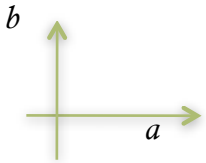
$$p(\mathbf{s}) \propto \mathcal{N}(\mu_a; \sigma_a)\mathcal{N}(\mu_b; \sigma_b)$$

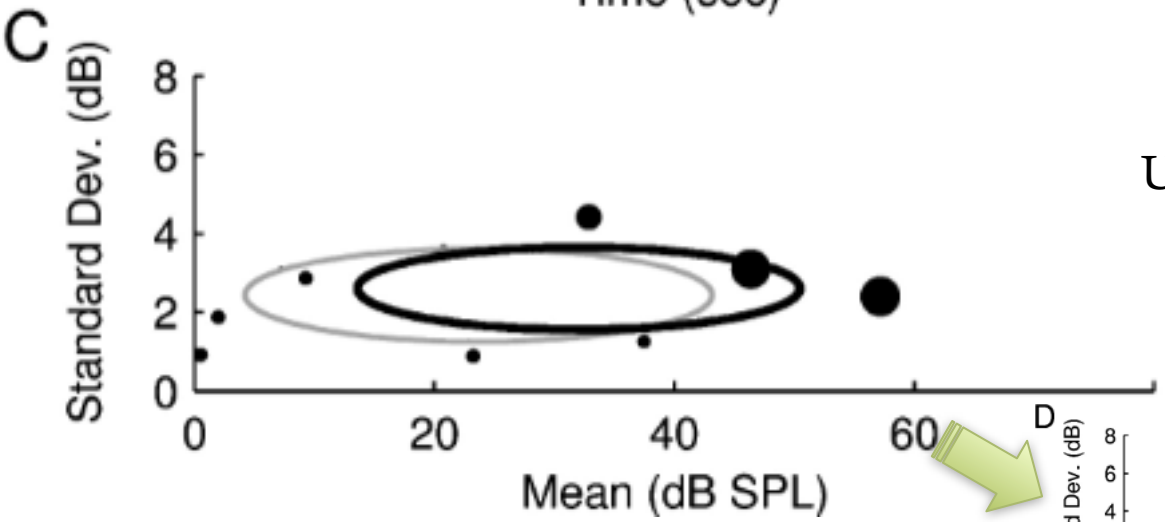
- OSE: want to find the best parameters such that $p(\mathbf{s})$ maximizes the mutual information.

Online algorithm

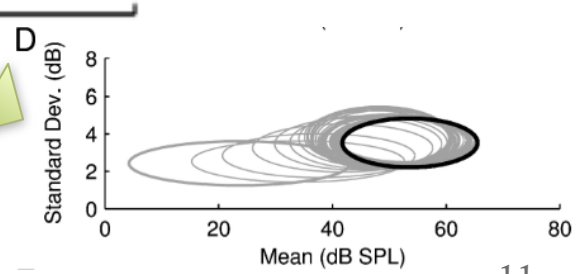


Draw a and b from the Gaussian.
Construct the signal with a and b.





Update estimate of $p(\mathbf{s})$



(This is for a single neuron.)

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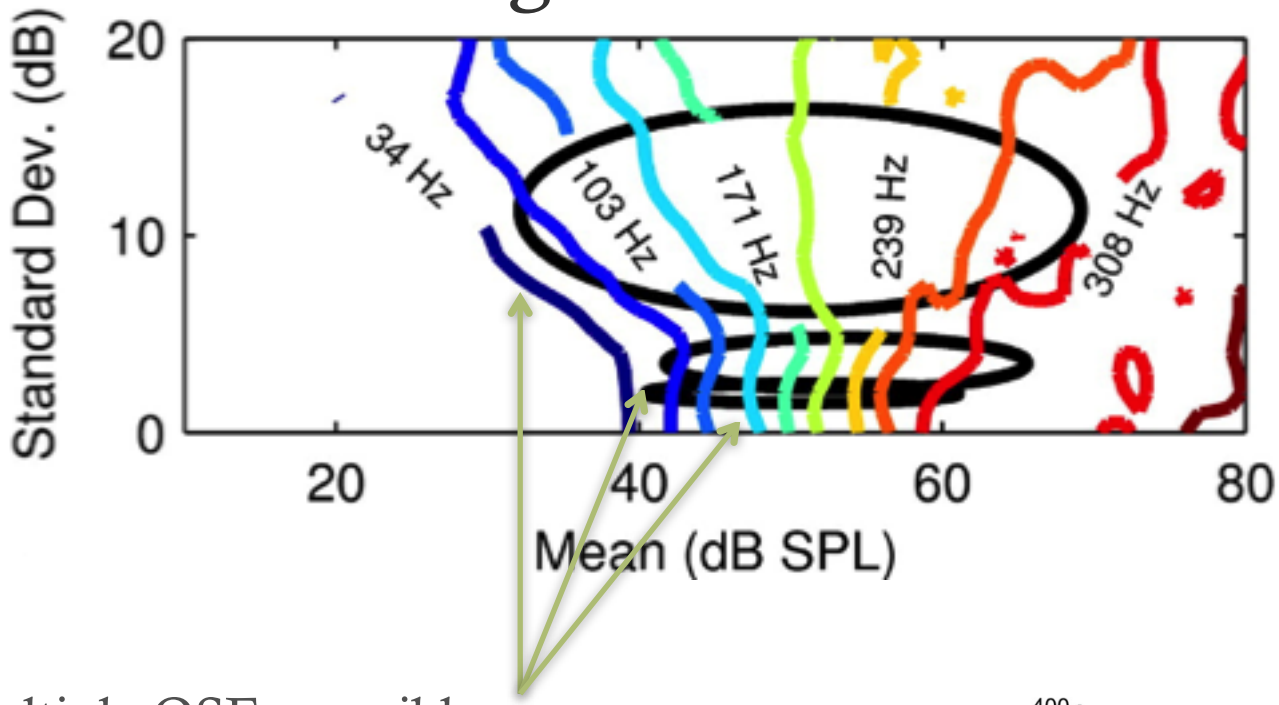
Firing-Rate Code

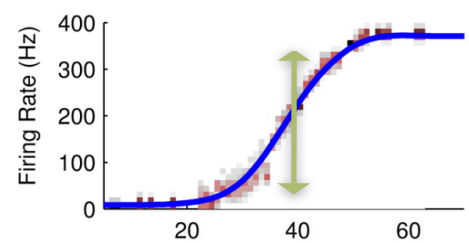
- What information is encoded in the firing rate?
  - Consider the firing rates from 80ms windows (segments in the previous slide)

Firing-Rate Code



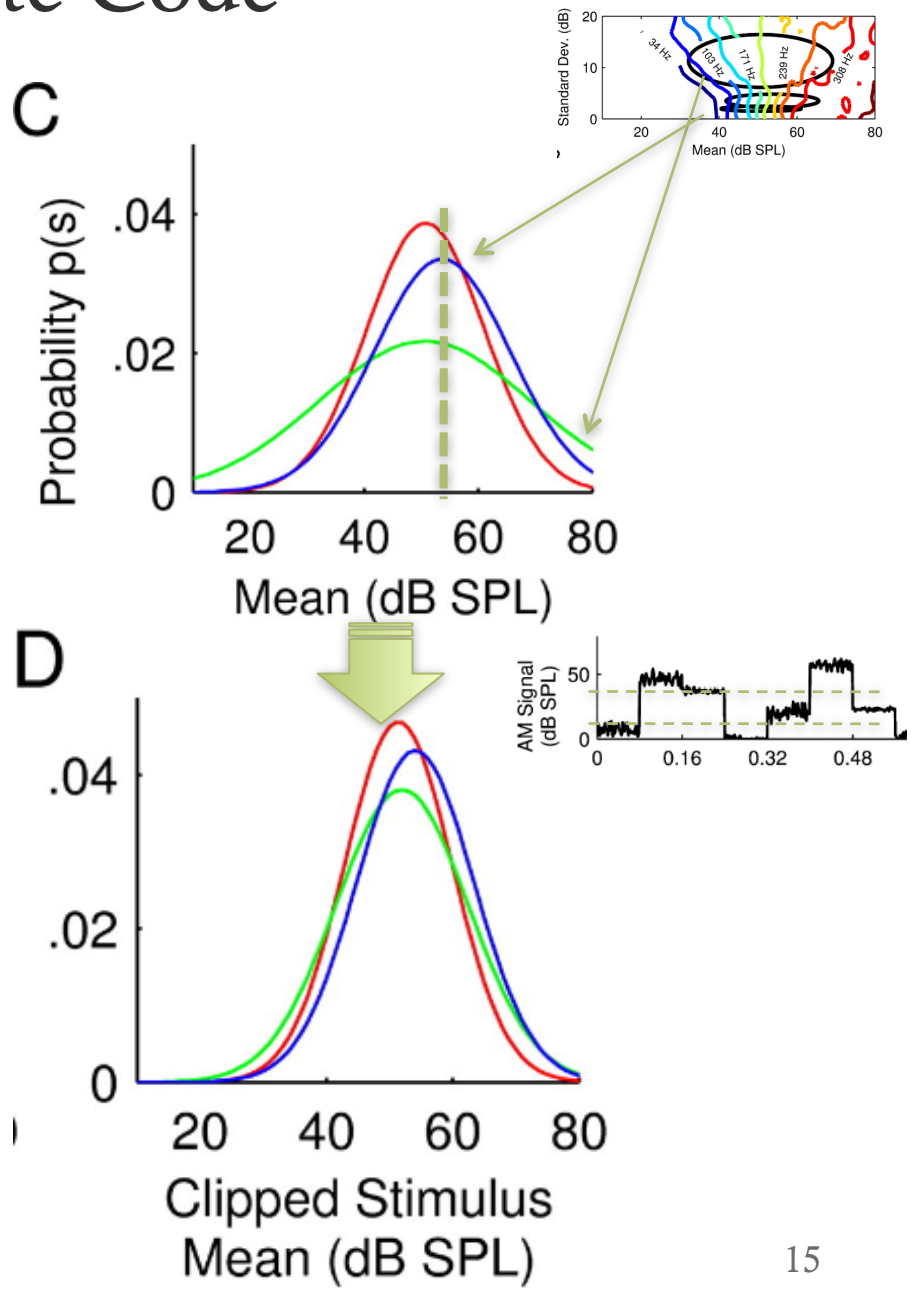
- Multiple OSEs possible
- Covers 30 – 300 Hz of firing rate
- Invariant along the y-axis
  (since iso-FRs don't change either)

  ➔ Variance (fluctuations around mean) doesn't matter much



Firing-Rate Code

- 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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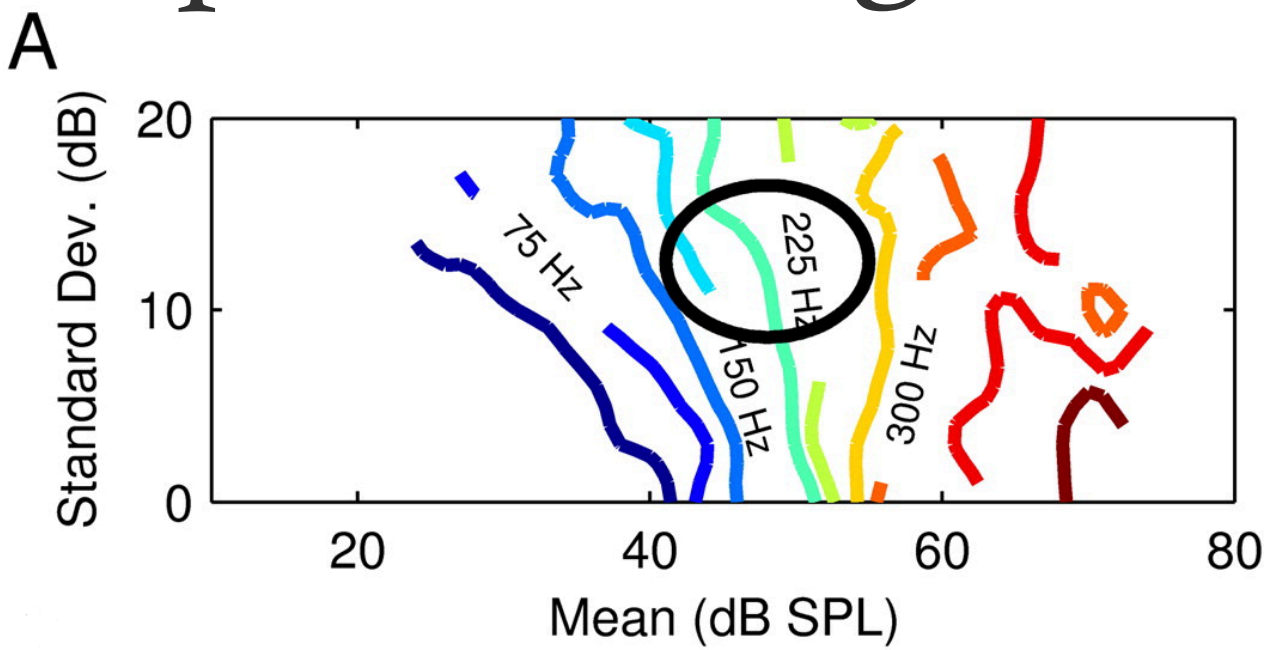
Spike-Timing Code

- 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 strings of ten 2-ms bins (2ms ≈ refractory period.)
  - Repeat same stimulus 25 times

Reliable	Unreliable
0010001100	0010001100
0010001100	1000010001
0010001100	0100100100
…	…

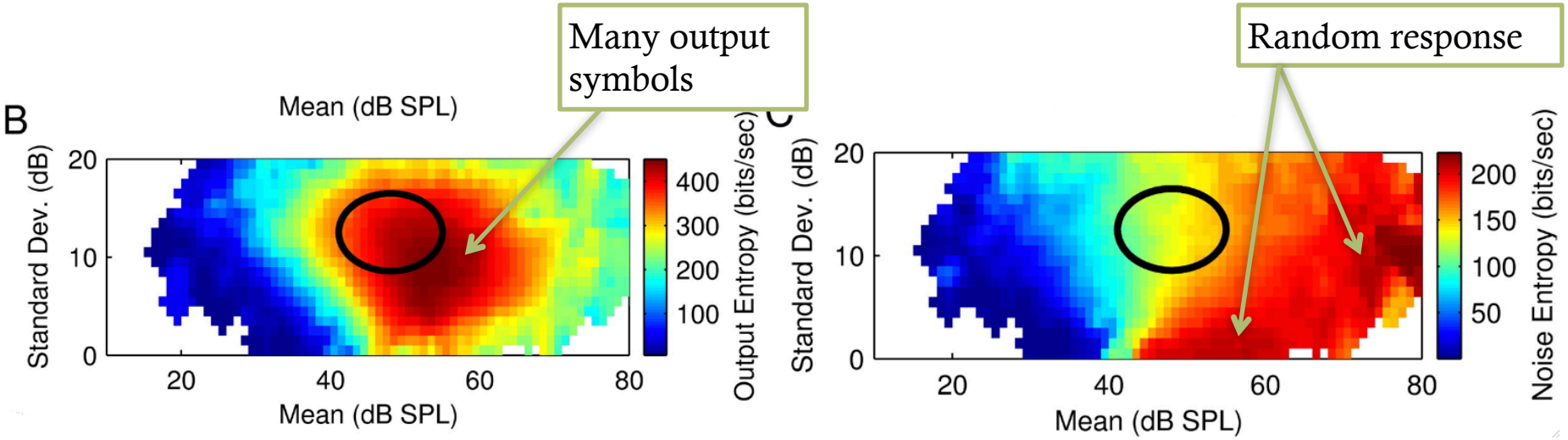
Spike-Timing Code



- 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

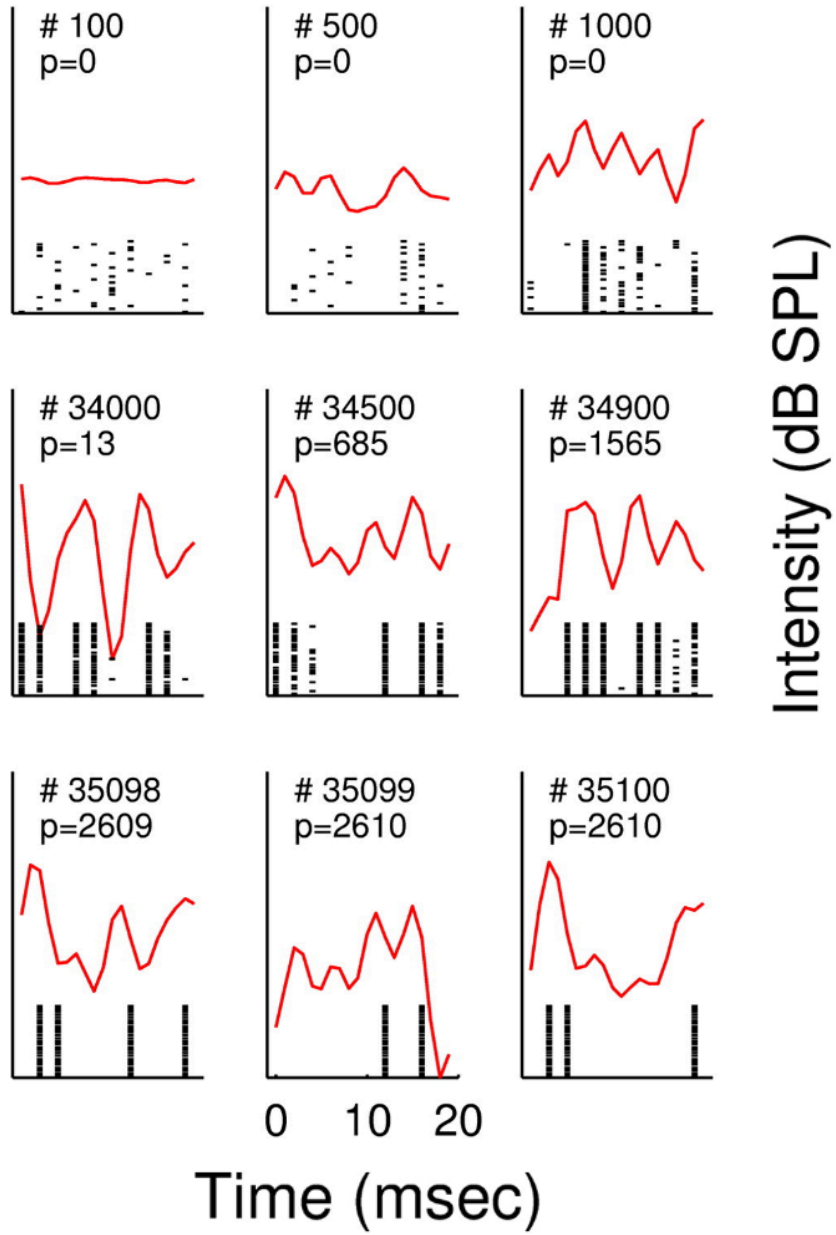


Want this to be **high**…

… but this to be **low**.

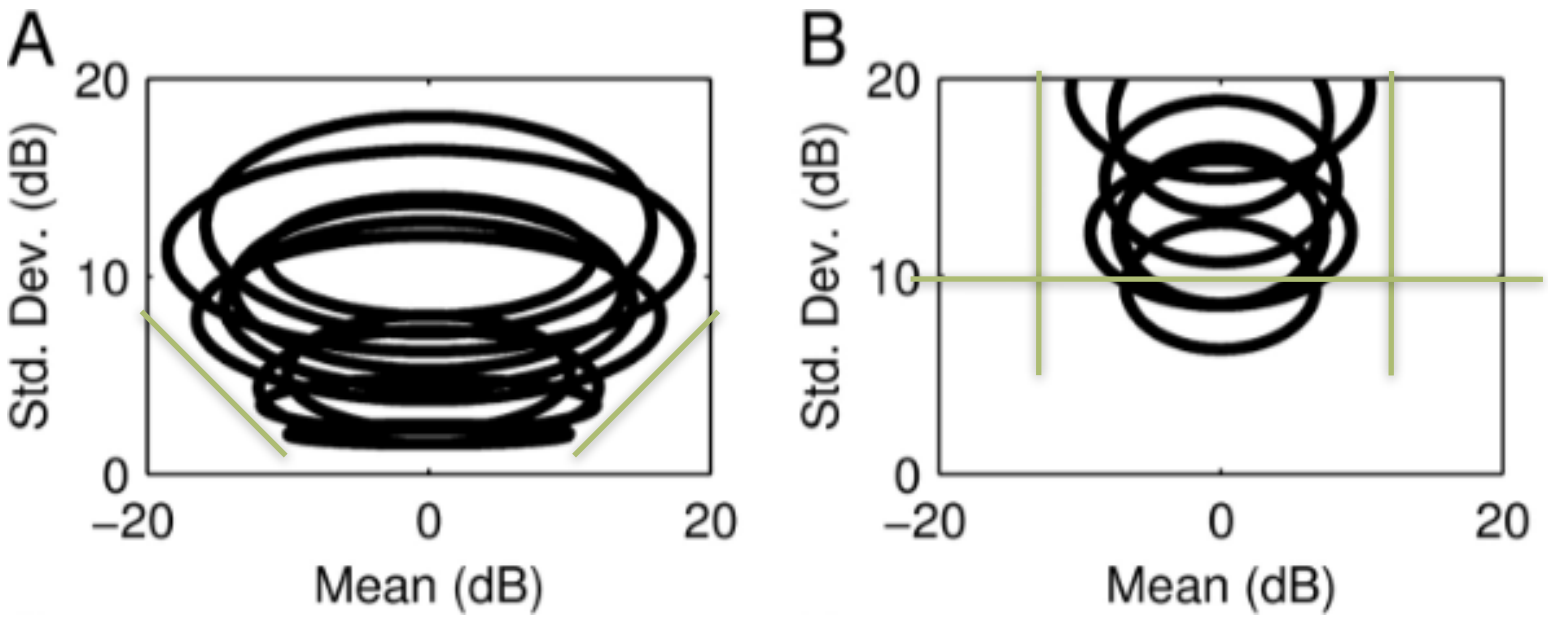
Spike-Timing Code

- 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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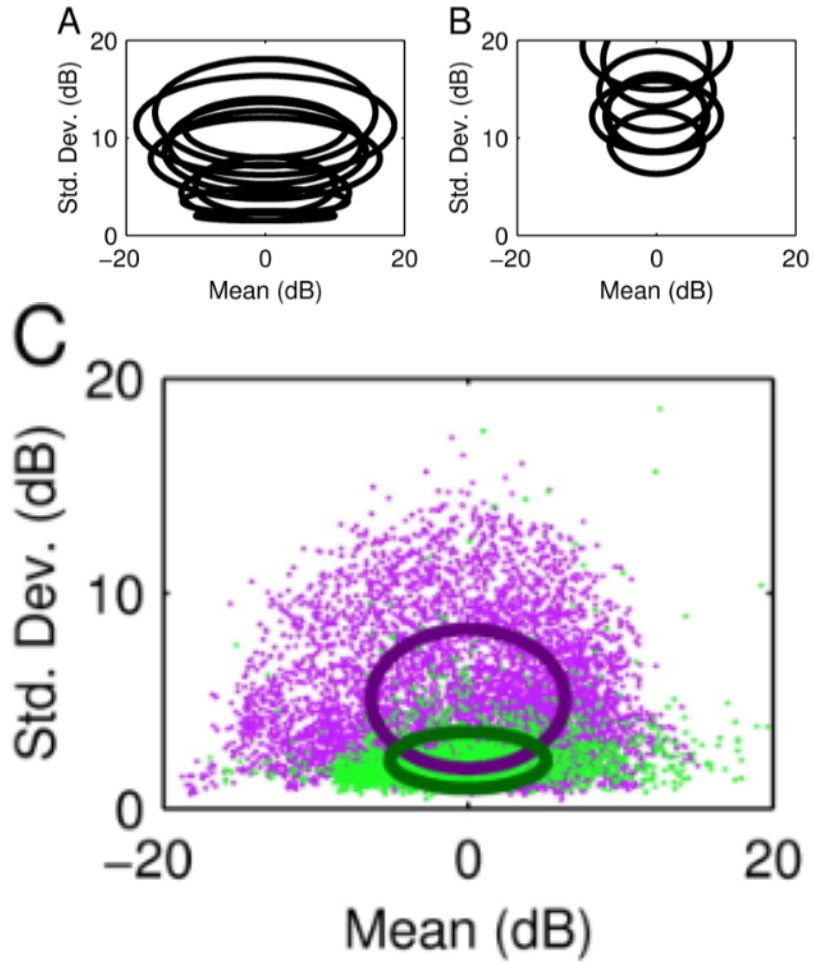
OSE vs Natural Stimuli

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

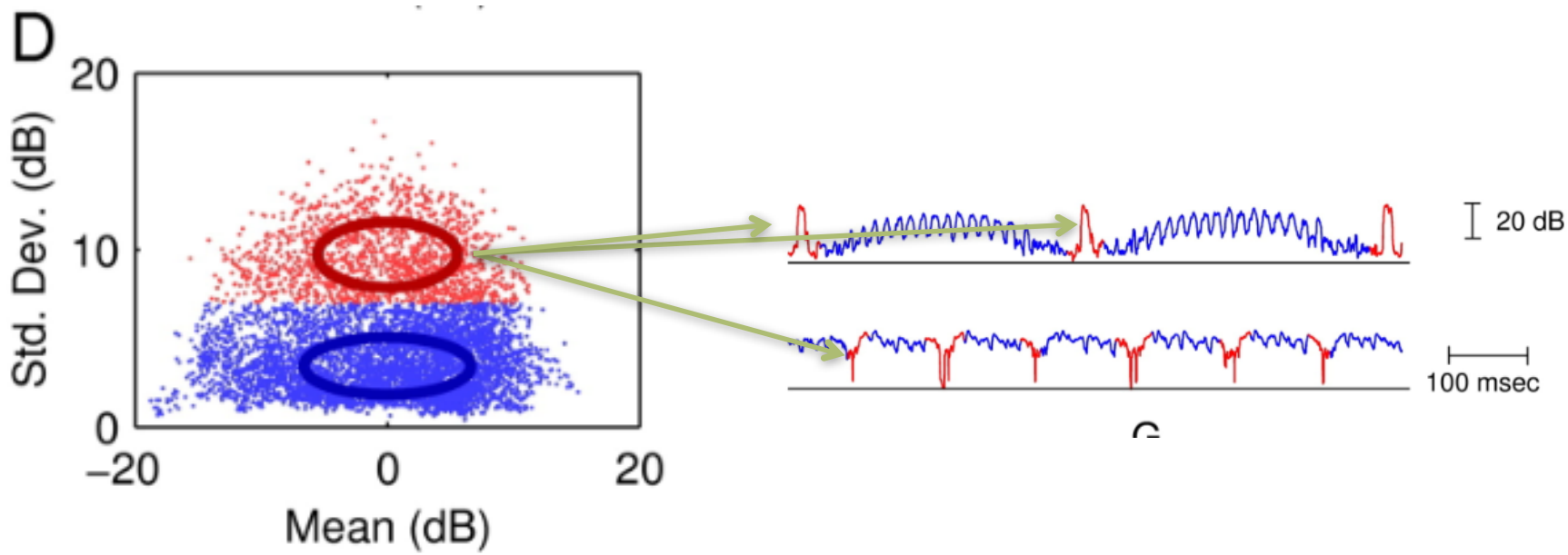
OSE vs Natural Stimuli



- 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**.