## Calculating information in spike trains

#### Two methods:

- Information in spike patterns
- Information in single spikes

# Calculating mutual information

Mutual information is the difference between the total response entropy and the mean noise entropy:

$$I(S;R) = H[R] - \Sigma_s P(s) H[R|s)].$$

#### Grandma's famous mutual information recipe

Take one stimulus s and repeat many times to obtain P(R|s).

Compute variability due to noise: noise entropy H[R|s]

Repeat for all s and average:  $\Sigma_s P(s) H[R|s)$ ].

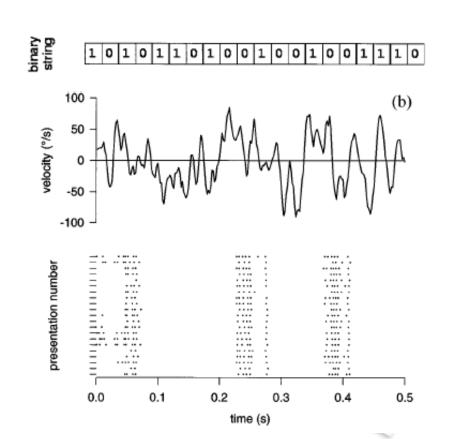
Compute  $P(R) = \Sigma_s P(s) P(R|s)$  and the total entropy H[R]

### Calculating information in spike patterns

So far only dealt with single spikes, or firing rates.

What information is carried by patterns of spikes?

Analyze patterns of the code: how informative are they?

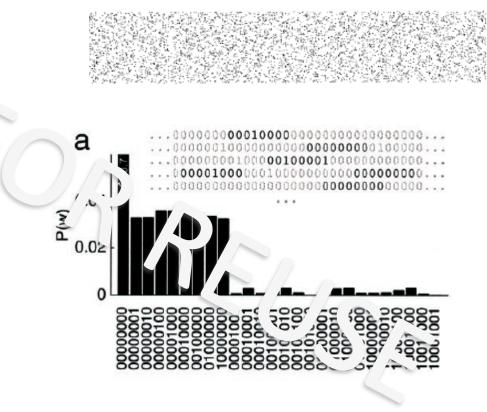


## Calculating information in spike trains

#### Entropy:

- Binary words w with letter size  $\Delta t$ , length T.
- Compute  $p(w_i)$

 $H[w] = -\sum p(w_i) \log_2 p(w_i)$ 

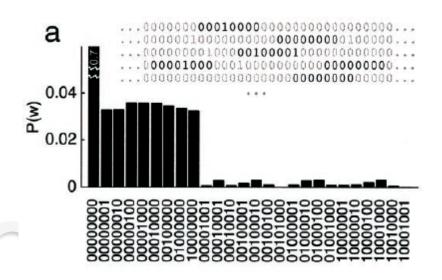


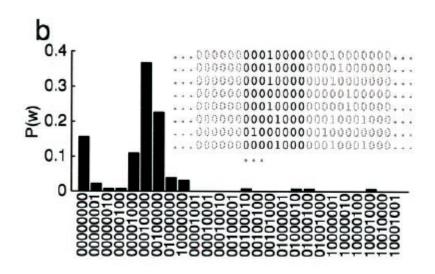
Strong et al., 1997; Reinagel and Reid, 2000

#### Calculating information in spike trains

Information:
difference between the total
variability driven by stimuli
and that due to noise, averaged

over stimuli.





# Apply grandma's recipe

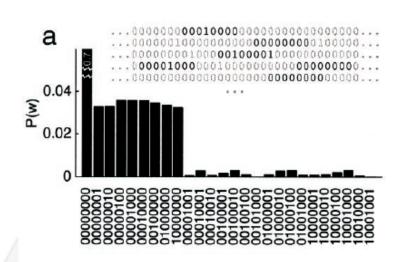
Take a stimulus sequence and repeat many times.

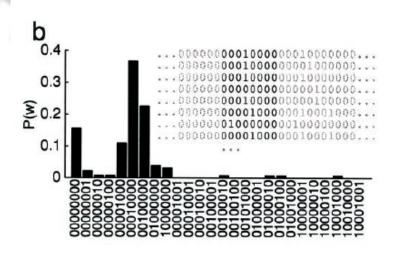
How to sample P(s)? Average over  $s \rightarrow$  average over time:

For each time in the repeated stimulus, get a set of words P(w|s(t)).

$$H_{\text{noise}} = \langle H[P(w|s_i)] \rangle_i$$

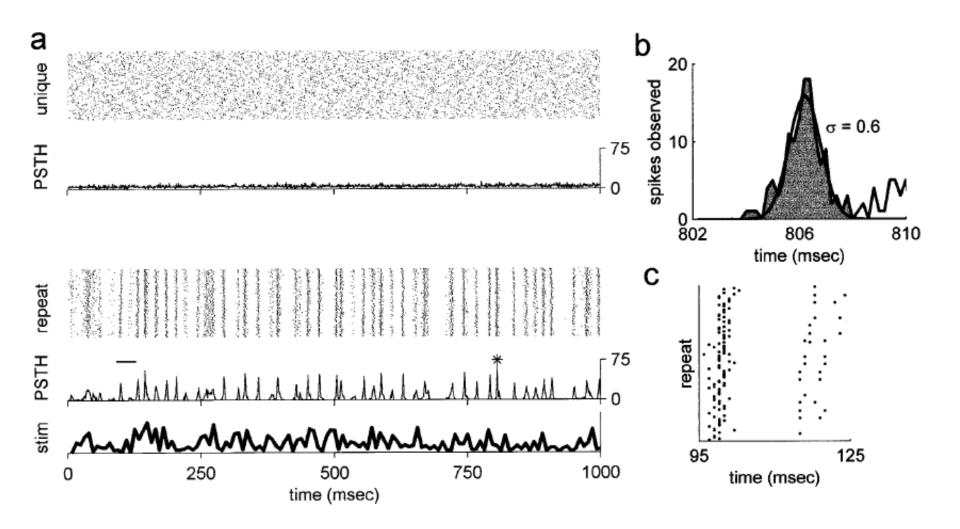
Choose length of repeated sequence long enough to sample the noise entropy adequately.





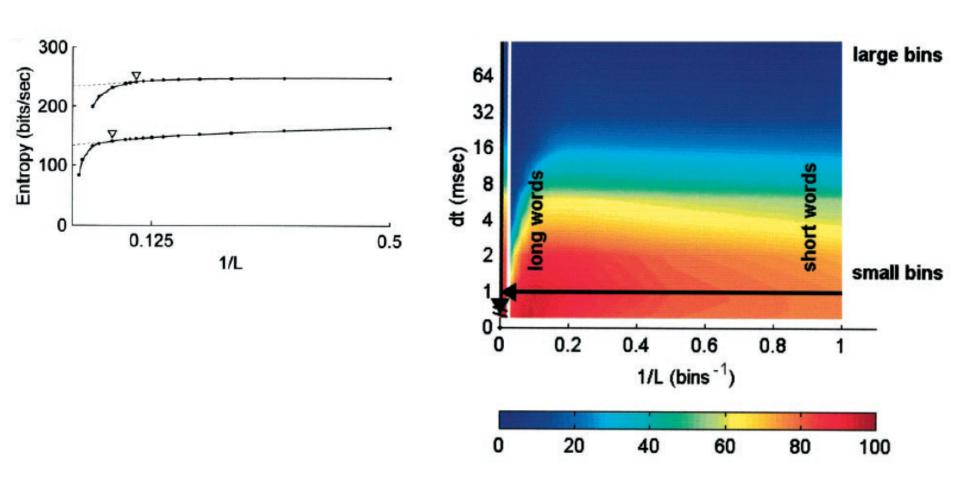
Reinagel and Reid (2000)

# Calculating information in the LGN



Reinagel and Reid (2000)

# Learning about the LGN's code

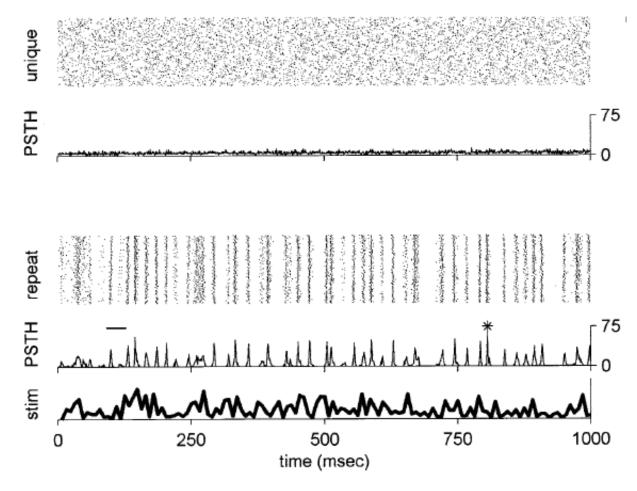


Reinagel and Reid (2000)

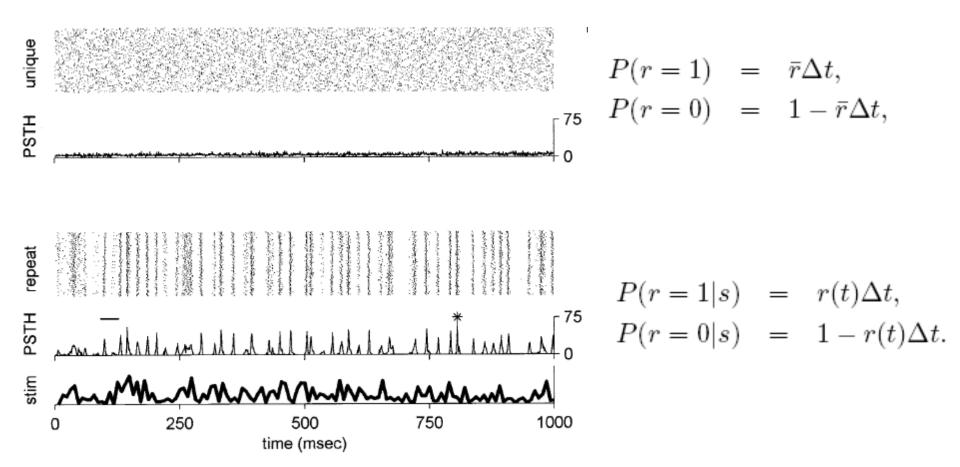
## Sampling and bias

- Never enough data!
- Corrections for finite sample size
- Panzeri, Nemenman, ...

By how much does knowing that a particular stimulus occurred reduce the entropy of the response?



Brenner et al. (2000), data Reinagel and Reid (2000)



Now compute the entropy difference:  $p = \bar{r}\Delta t$   $p(t) = r(t)\Delta t$ 

$$\begin{split} I(r,s) &= -p \log p - (1-p) \log (1-p) + \\ &+ \frac{1}{T} \int_0^T dt \, \left[ p(t) \log p(t) + (1-p(t)) \log (1-p(t)) \right]. \quad \ \leftarrow \text{Noise} \end{split}$$

Every time *t* stands in for a sample of *s* 

A time average is equivalent to averaging over the *s* ensemble.

Ergodicity

$$I(r,s) = -p\log p - (1-p)\log(1-p) + \qquad \qquad \leftarrow \text{Total}$$
 
$$+ \frac{1}{T} \int_0^T dt \, \left[ p(t)\log p(t) + (1-p(t))\log(1-p(t)) \right]. \qquad \leftarrow \text{Noise}$$

Assuming  $p \ll 1 \log(1-p) \sim p$  and using  $\frac{1}{T} \int_0^T dt \, p(t) \to p$ 

$$I(r,s) = \frac{1}{T} \int_0^T dt \, \Delta t \, r(t) \log \frac{r(t)}{\bar{r}} + Var(p(t))/2ln2 + O(p^3).$$

To get *information per spike*, divide by  $\bar{r}\Delta t$ :

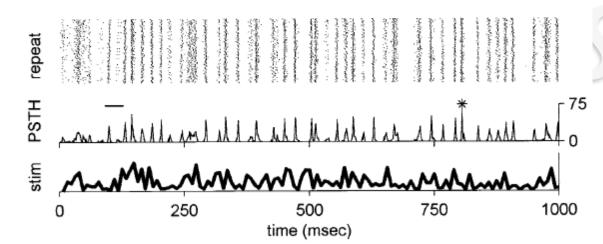
$$I(r,s) = \frac{1}{T} \int_0^T dt \, \frac{r(t)}{\bar{r}} \log \frac{r(t)}{\bar{r}}$$

Information per spike: 
$$I(r,s) = \frac{1}{T} \int_0^T dt \, \frac{r(t)}{\bar{r}} \log \frac{r(t)}{\bar{r}}$$

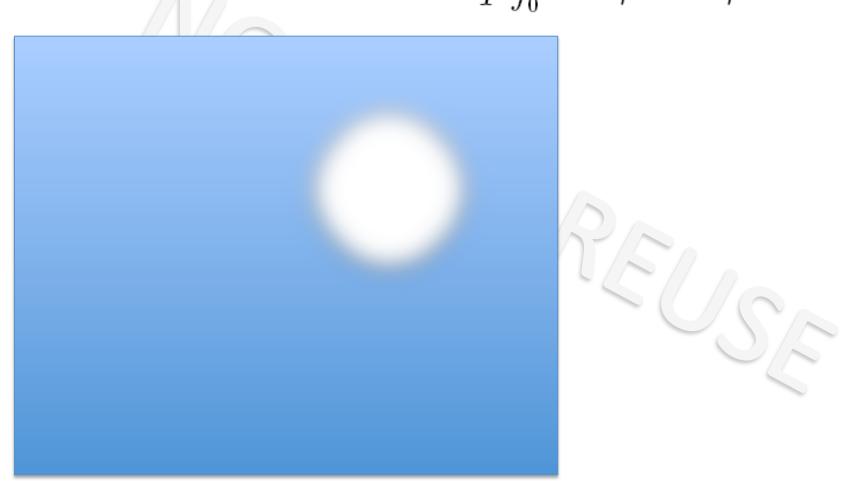
- No explicit stimulus dependence (no coding/decoding model)
- The rate *r* does not have to mean rate of spikes; rate of any event.

What limits information?

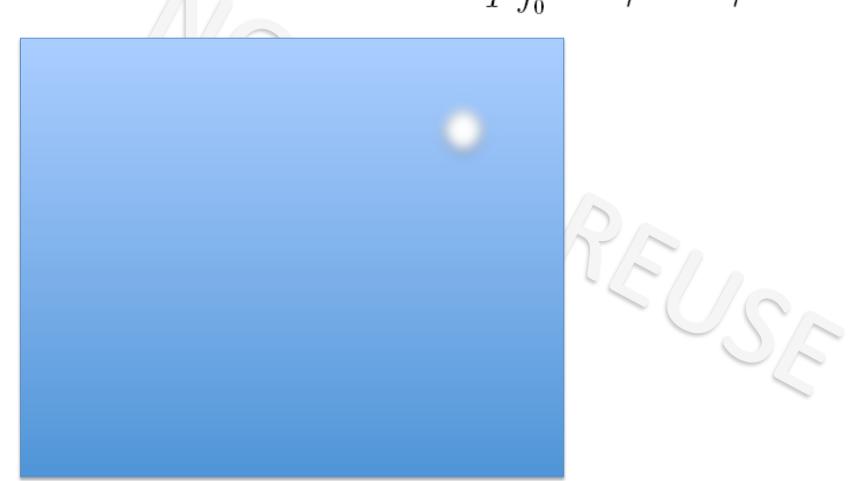
- > spike precision, which blurs r(t)
- > the mean spike rate.



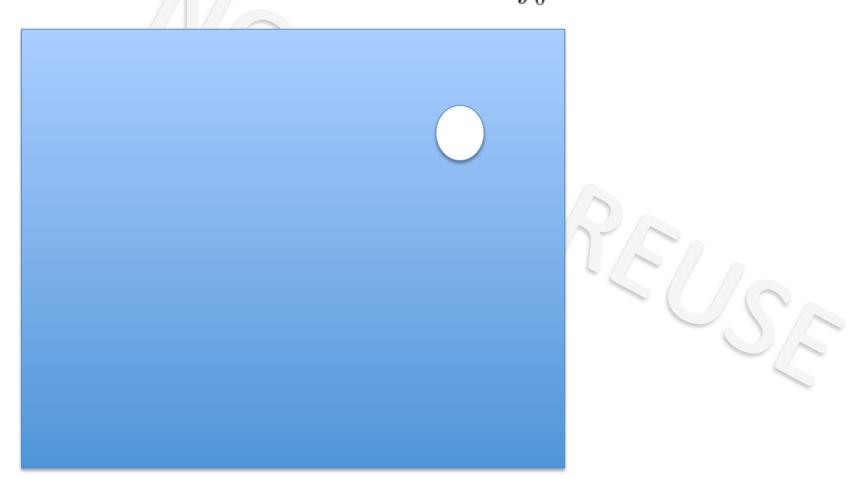
Information per spike:  $I(r,s) = \frac{1}{T} \int_0^T dt \, \frac{r(t)}{\bar{r}} \log \frac{r(t)}{\bar{r}}$ 



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# Next up: information and coding efficiency

- What are the challenges posed by natural stimuli?
- What do information theoretic concepts suggest that neural systems should do?
- What principles seem to be at work in shaping the neural code?