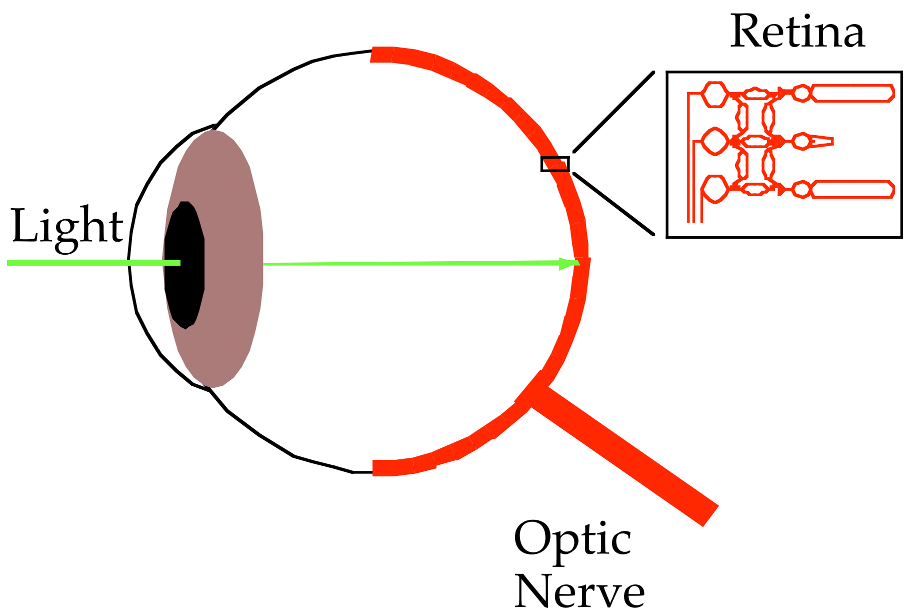
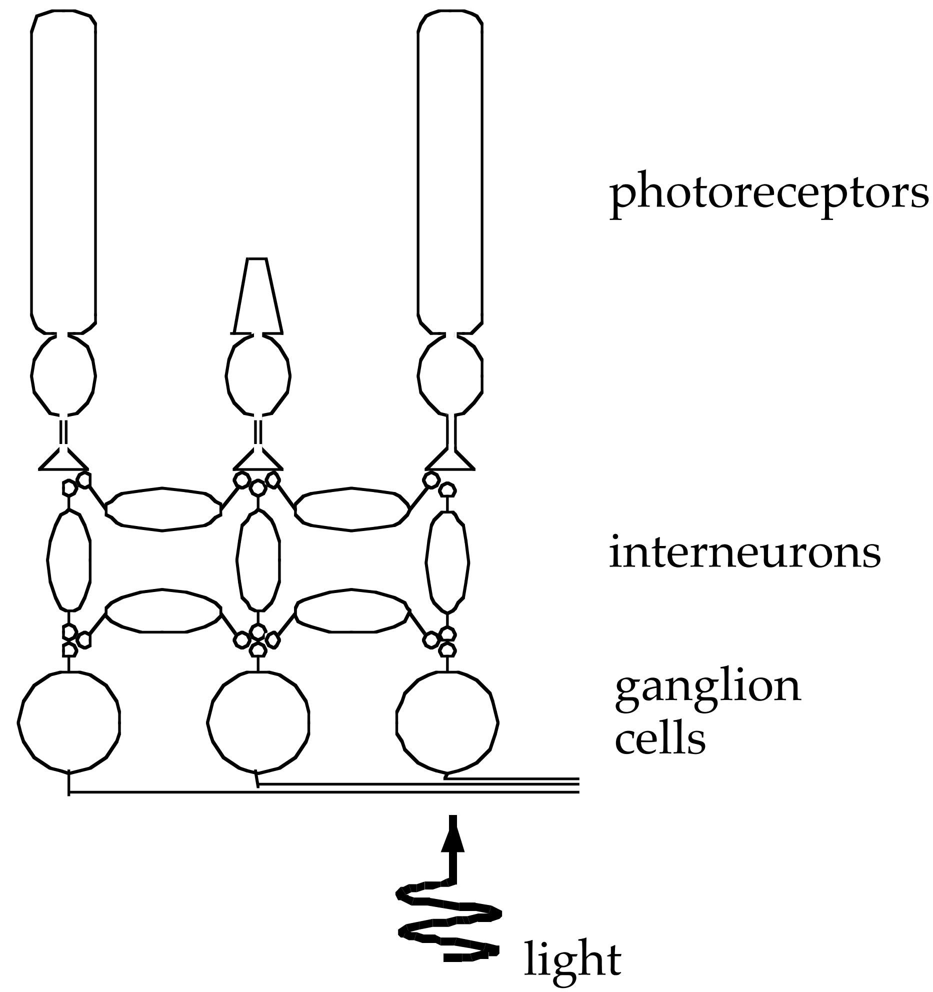
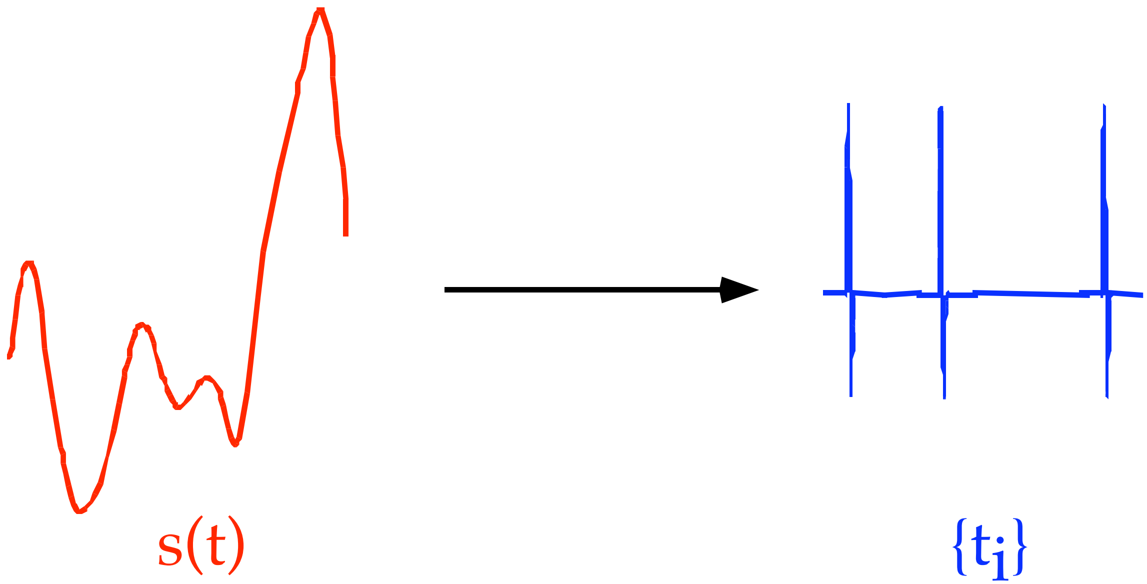




- encoding and estimation
- bottleneck and limits to visual fidelity

The Neural Coding Problem

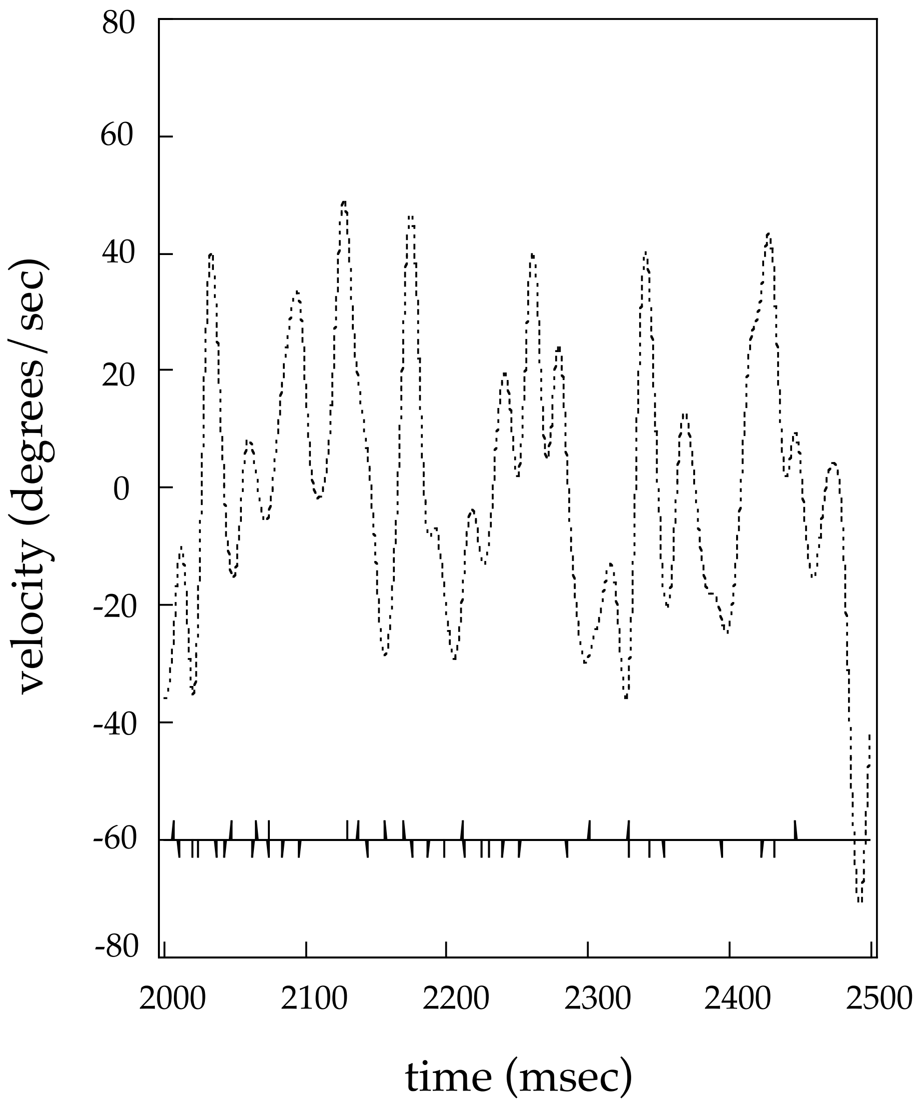


Central goals for today:

- important properties of coding process
    - to be complete must deal with spikes (not rate)

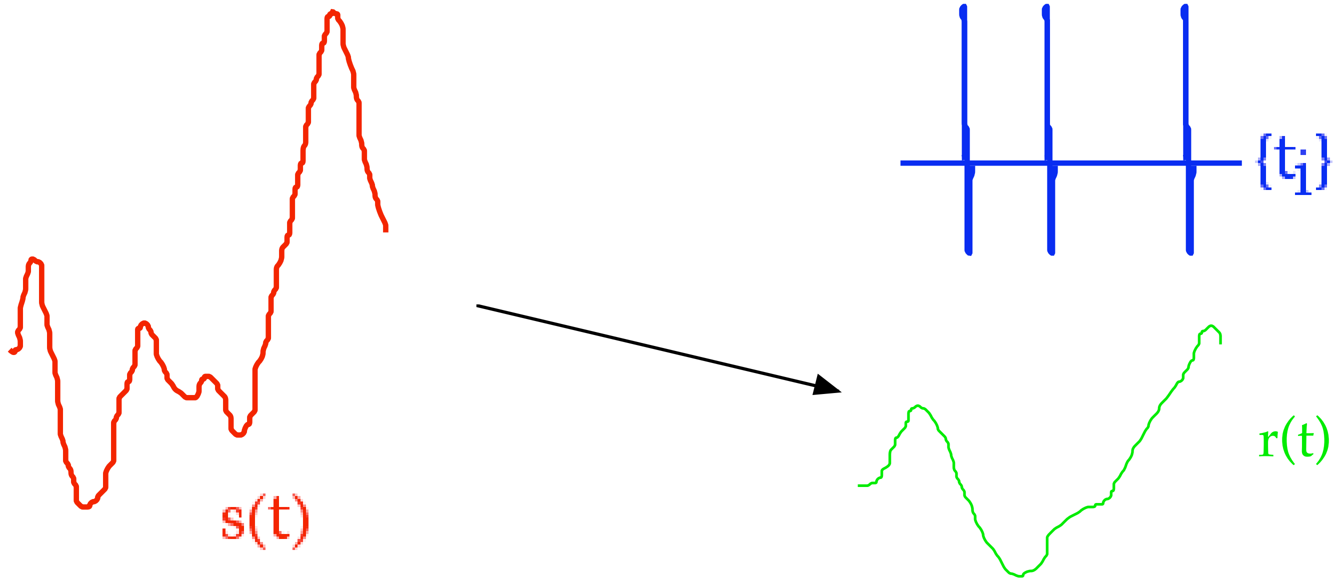
- desiderata and comparison of different approaches
    - how do we know when we are done?
    - would like 'answer' to provide functional and mechanistic insights

- reliability and coding efficiency
  (approaches fundamental limits ...)



stimuli of interest change on time scale comparable to interval between spikes

WHY DO WE NEED MORE THAN RATE CODING?

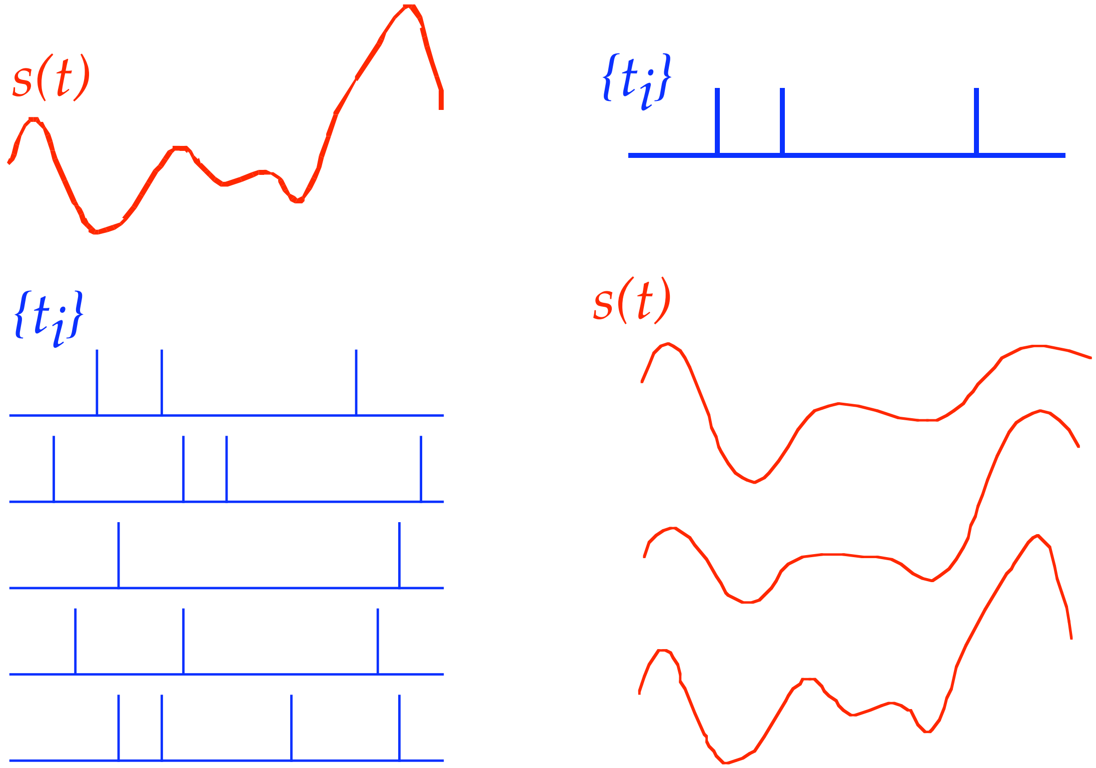


- Most of what we know about how sensory signals are represented comes from measuring dependence of mean firing rate on some parameter of stimulus (receptive fields, tuning curves, …)

- While this has clearly been fruitful, for some quantitative issues need to be sure we have complete understanding of code
  - relation between neural activity and behavior
  - comparison of fidelity at different stages of system

- In some systems clear that behavior influenced by small # of spikes, making rate not a particularly useful quantity. In many systems time scale of behavioral decision similar to interval between spikes -- hence cannot average over time to get rate.

CODING IS PROBABILISTIC



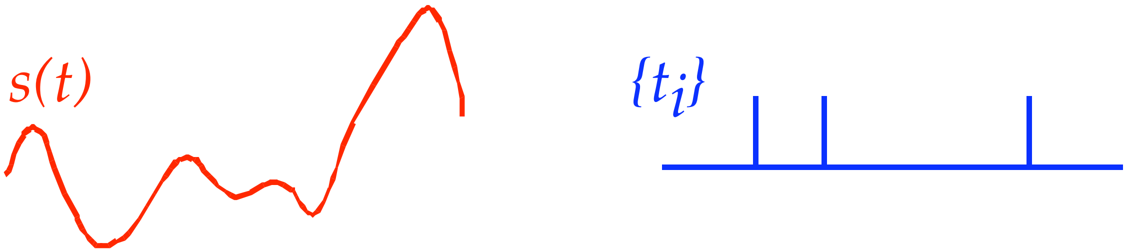
encoding $P[\{t_i\} \mid s(t)]$ decoding $P[s(t) \mid \{t_i\}]$

Bayes' Rule

$$P[\{t_i\} \mid s(t)]\, P[s(t)] = P[s(t) \mid \{t_i\}]\, P[\{t_i\}]$$

Any approach to coding must deal with its probabilistic nature!

PRACTICAL CONSIDERATIONS



- $P[\{t_i\} | s(t)]$ and $P[s(t) | \{t_i\}]$ are high dimensional

  $\{t_i\}$ ~ 100 msec window, 1 msec bins

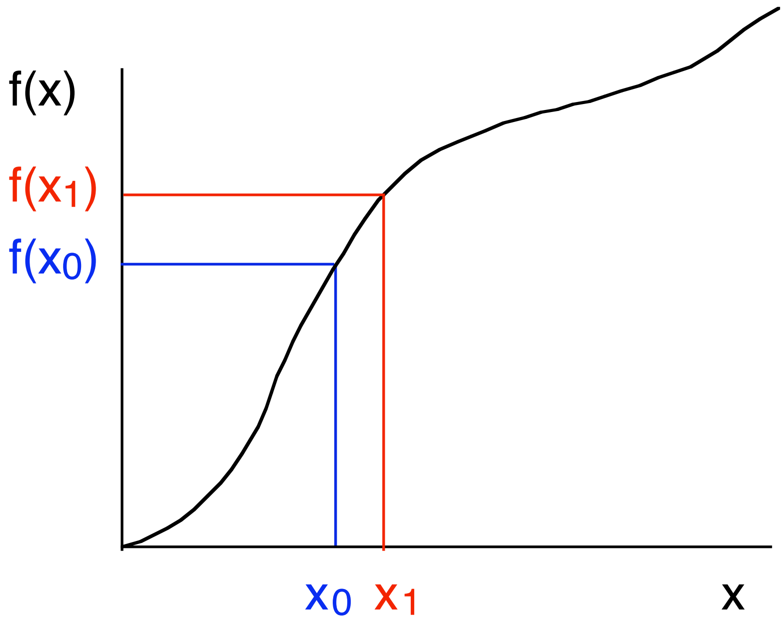
  $s(t)$ ~ time dimensions + others (space, color, ...)

- collect ~ 10,000 spikes in typical experiment

- impossible in practice to get entire distribution

- try to capture structure of $P[\{t_i\} | s(t)]$ or $P[s(t) | \{t_i\}]$ with finite data

TAYLOR SERIES APPROXIMATION



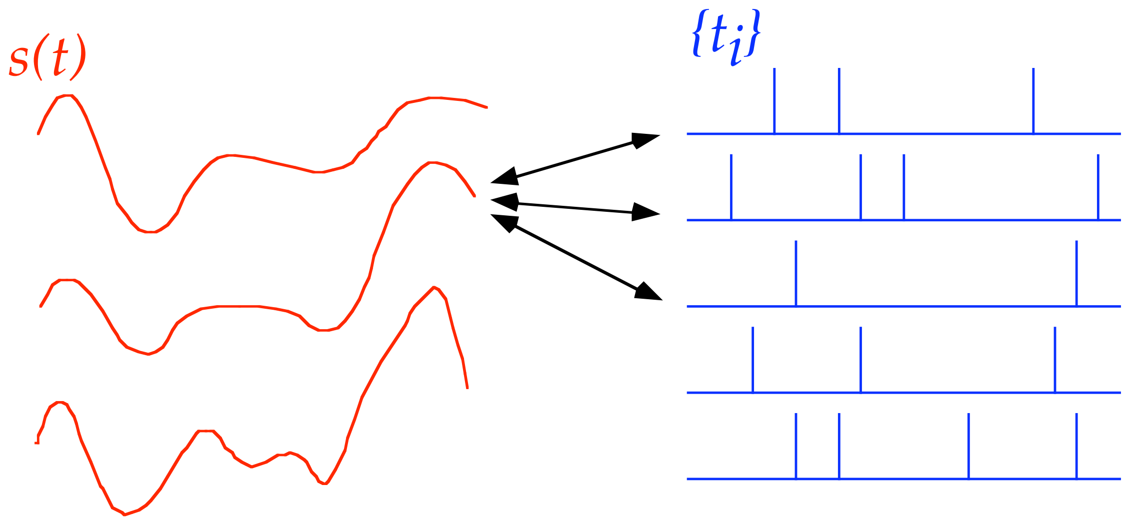
$$f(x_1) = f(x_0) + (x_1 - x_0)\left.\frac{df}{dx}\right|_{x_0} + \frac{1}{2}(x_1 - x_0)^2 \left.\frac{d^2f}{dx^2}\right|_{x_0} + \ldots$$

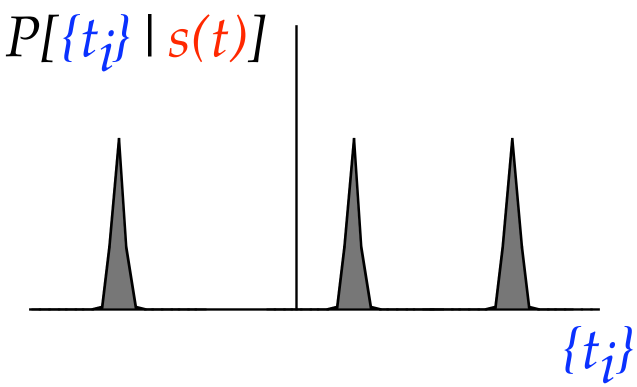
KEY:

$$f(x_0) >> (x_1 - x_0)\left.\frac{df}{dx}\right|_{x_0}$$

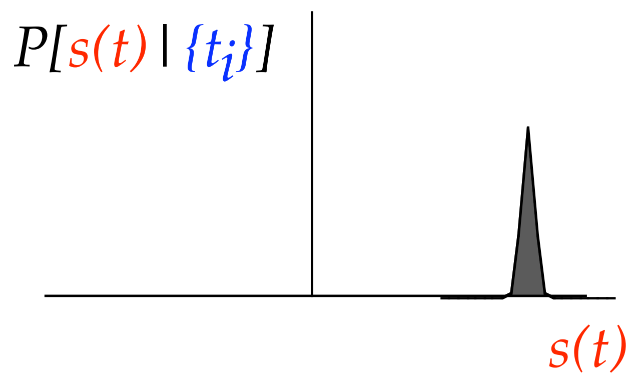
i.e. expand about small parameter

STRUCTURE OF CONDITIONAL DISTRIBUTIONS





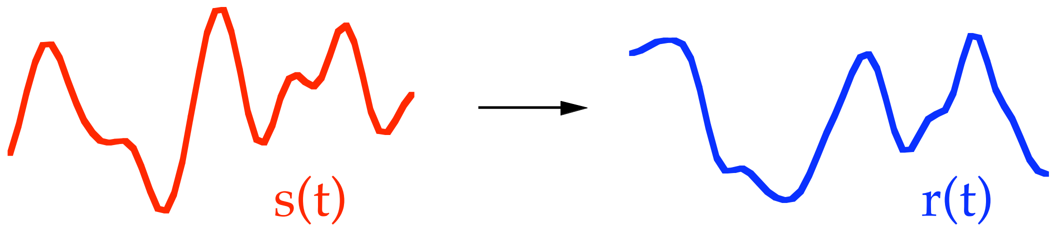
encoding ambiguous



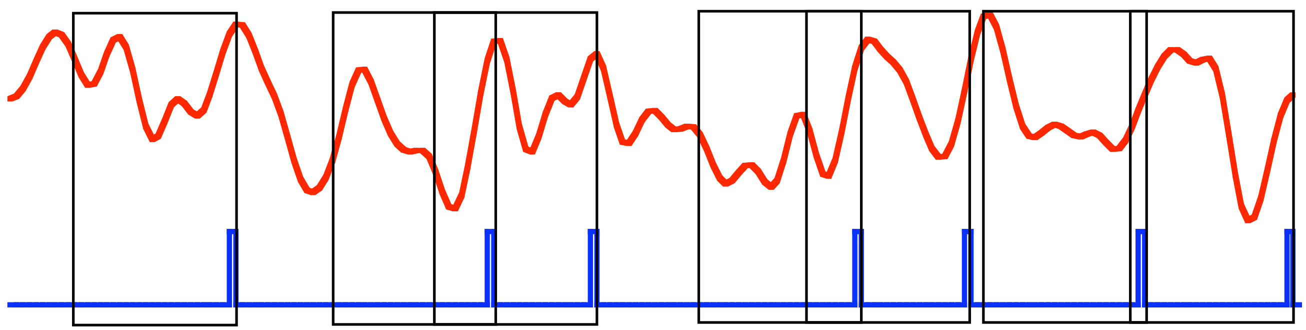
decoding single-valued

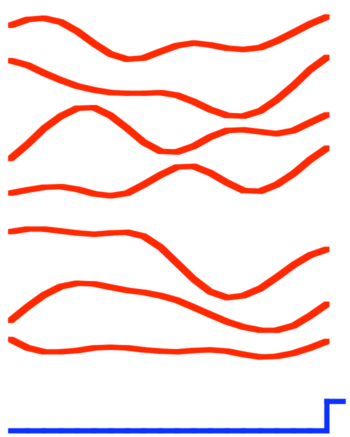
Although encoding and decoding in principle equivalent (Bayes' Rule), in practice may not be

ENCODING: WIENER AND VOLTERRA APPROACHES



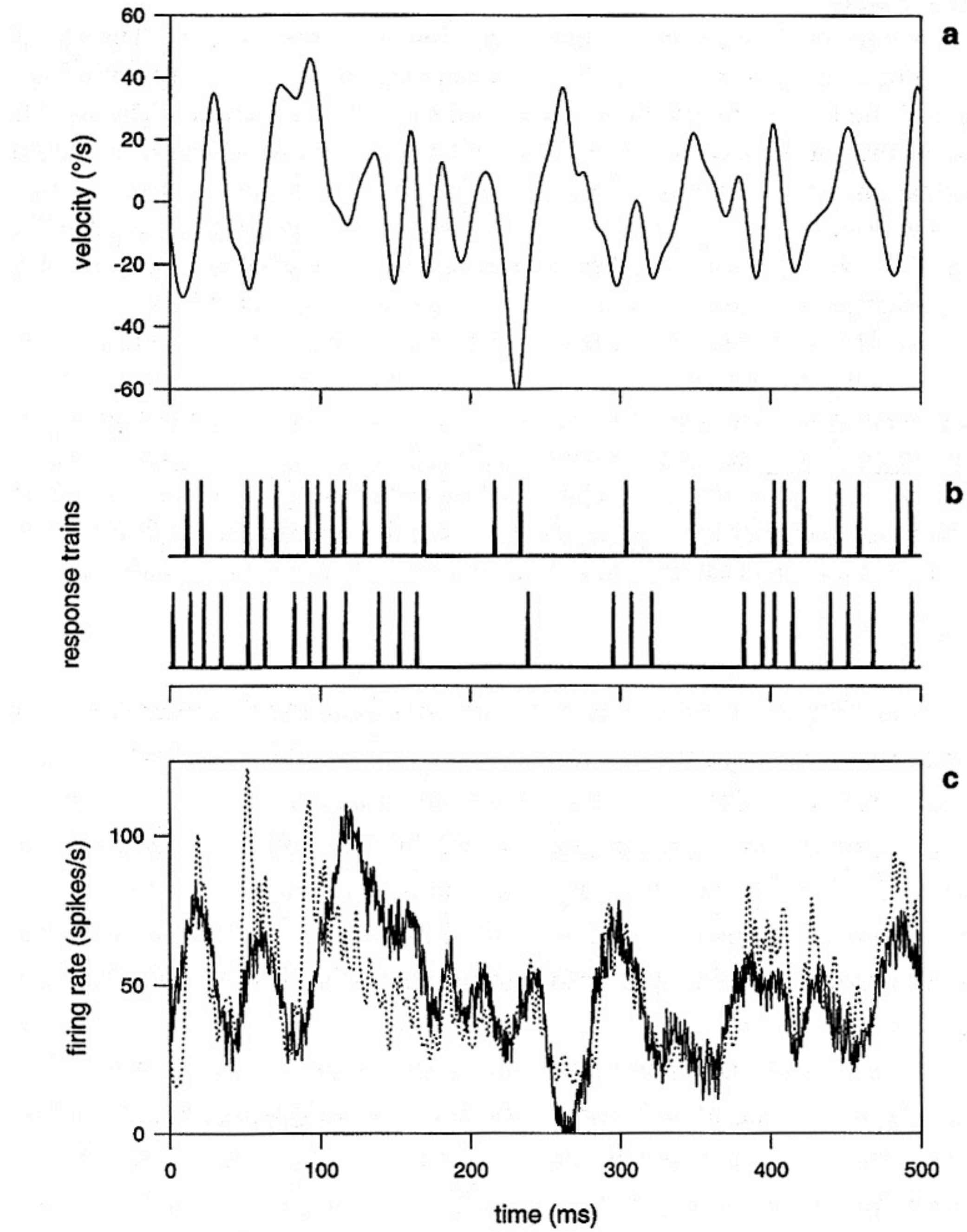
• What are statistical properties of stimulus leading to spike?





(1) Collect stimuli preceding spike
(2) Measure mean, covariance, ...

FIRST-ORDER FIRING RATE ESTIMATE



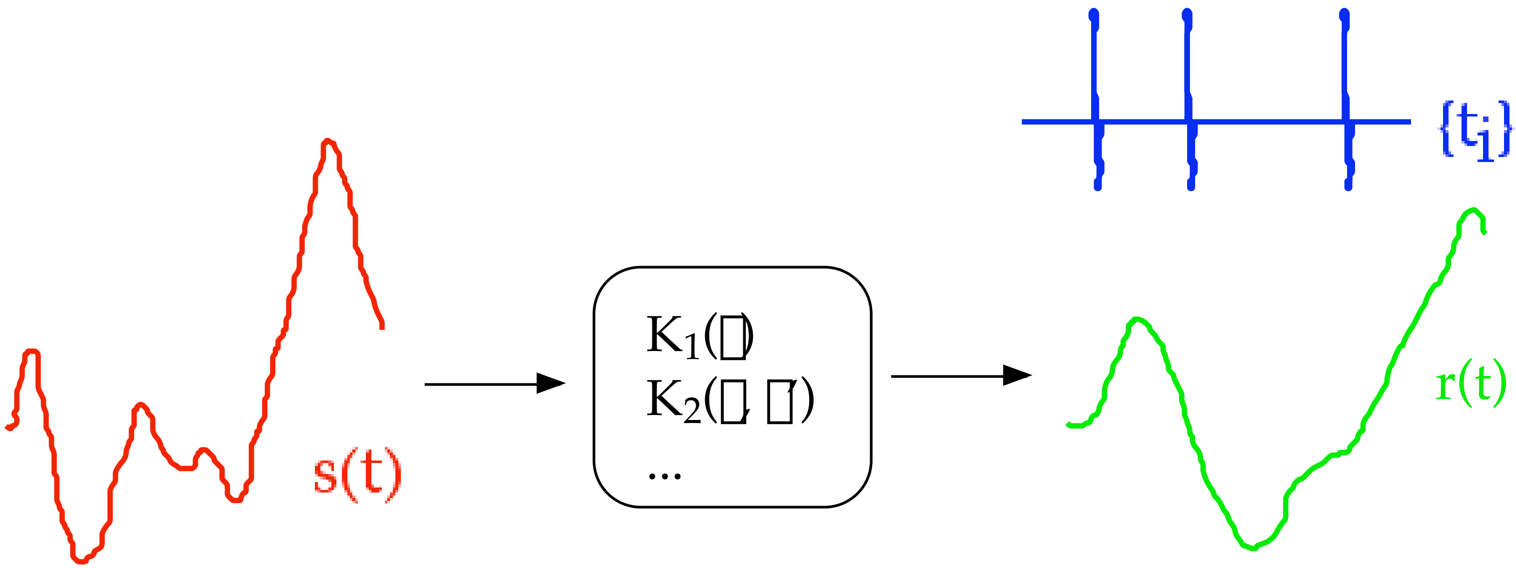
$s(t)$

$\{t_i\}$

Dashed: $r(t)$

Solid: $r_{est}(t) = \int d\tau\, K_1(\tau)\, s(t-\tau)$

ENCODING: WIENER AND VOLTERRA APPROACHES

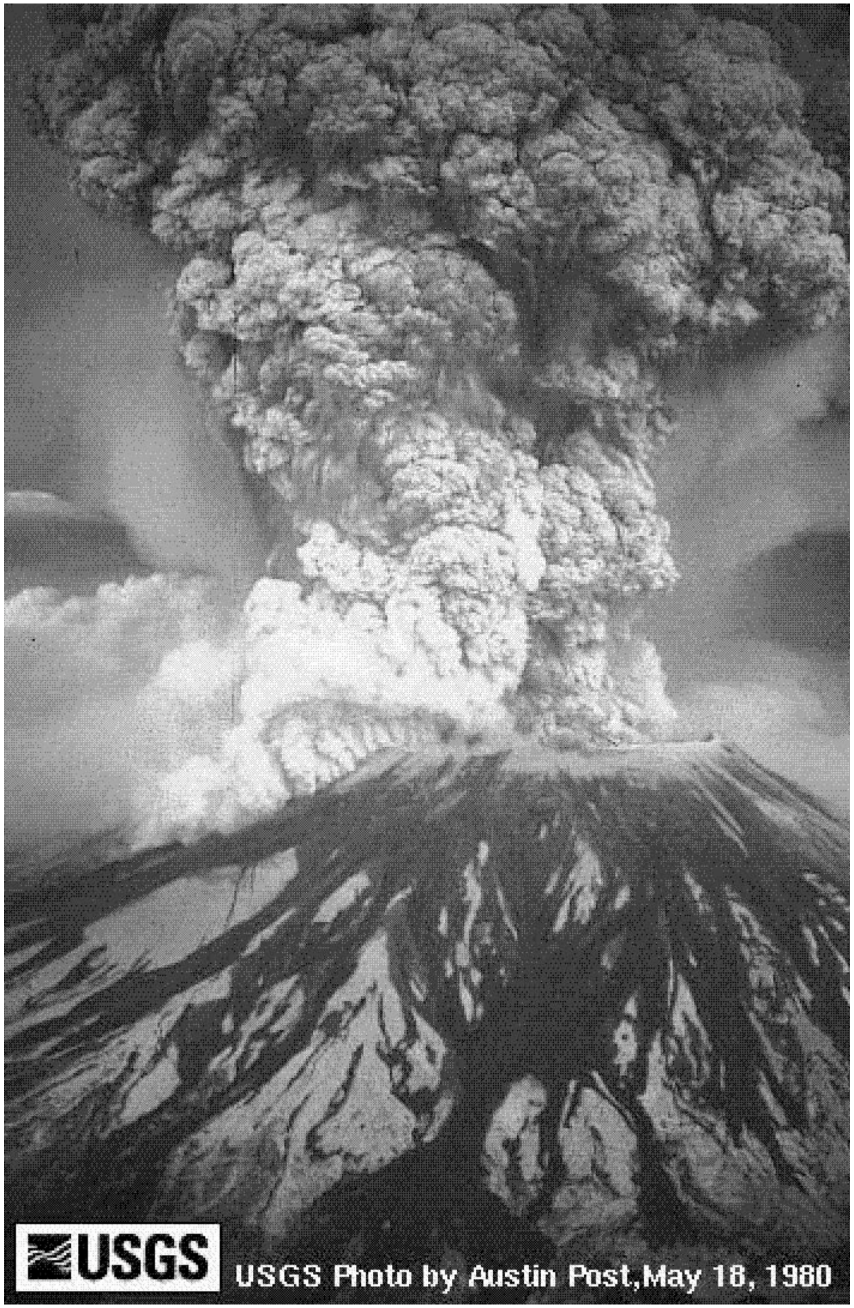


PROS:

- systematic
- often easily interpreted

CONS:

- typically does not converge quickly
  - no ‘small parameter’
  - usually run out of data before terms stop contributing
- estimates rate, not spike train
  - hard to say how well it works
  - effectively assumes spikes are independent

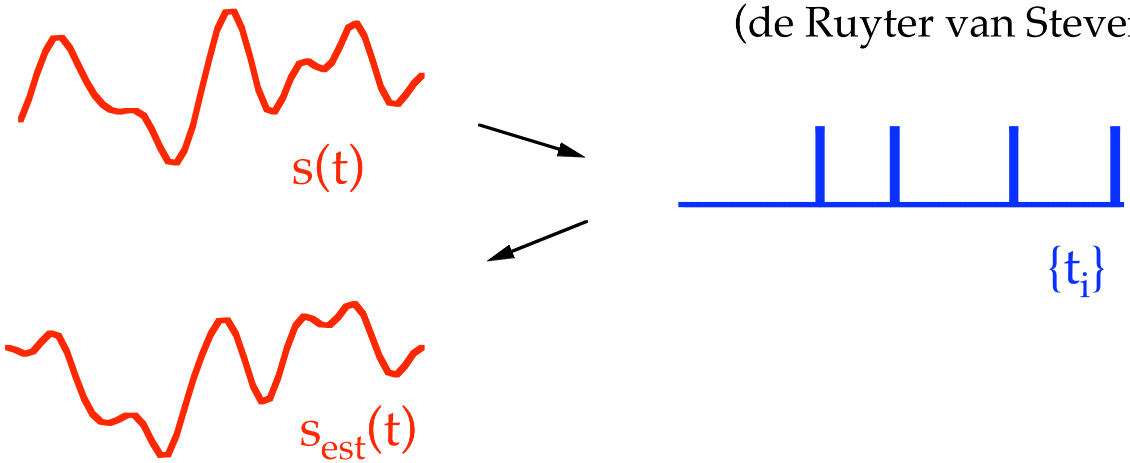


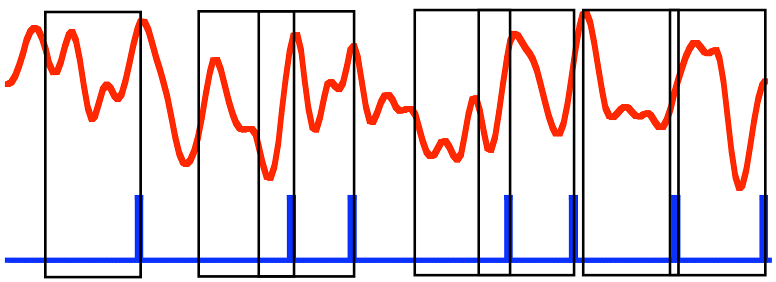
Is explosion due to assumption of independent spikes?
- deal with spike interactions directly

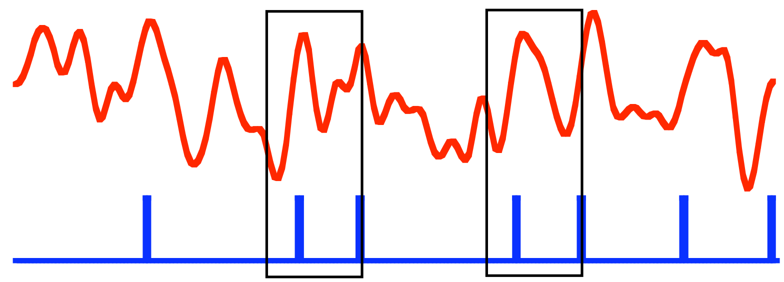
EJC (2000): “We are all losing, the only question is how badly”

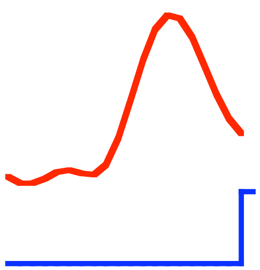
DECODING: THE LOOK-UP-TABLE APPROACH

(de Ruyter van Steveninck and Bialek, 1987)

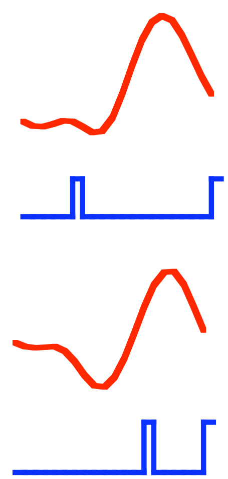








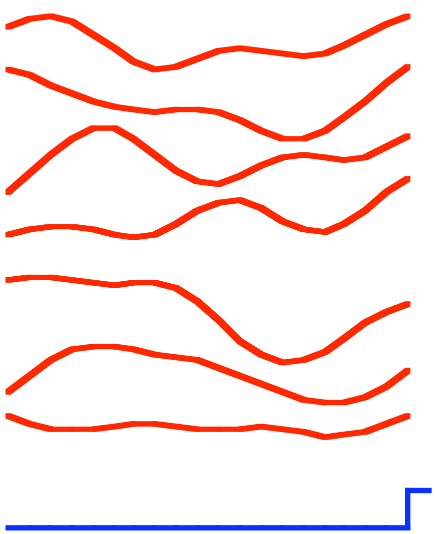
- Estimate stimulus by replacing each spike with spike triggered average



- Estimate stimulus by replacing each interval with appropriate interval triggered average

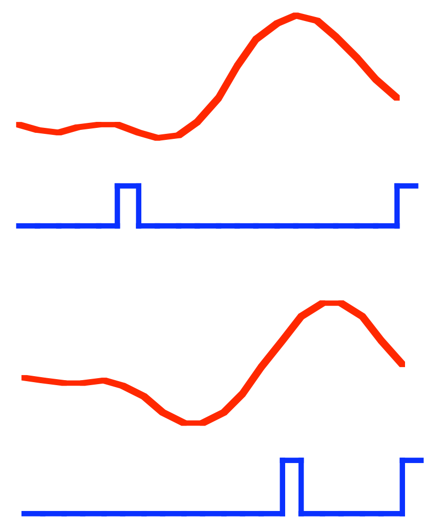
ENCODING:

- determine what stimulus features trigger a spike
- use to estimate firing rate
- expansion is in statistical aspect of stimulus (mean, covariance, ...) prior to spike



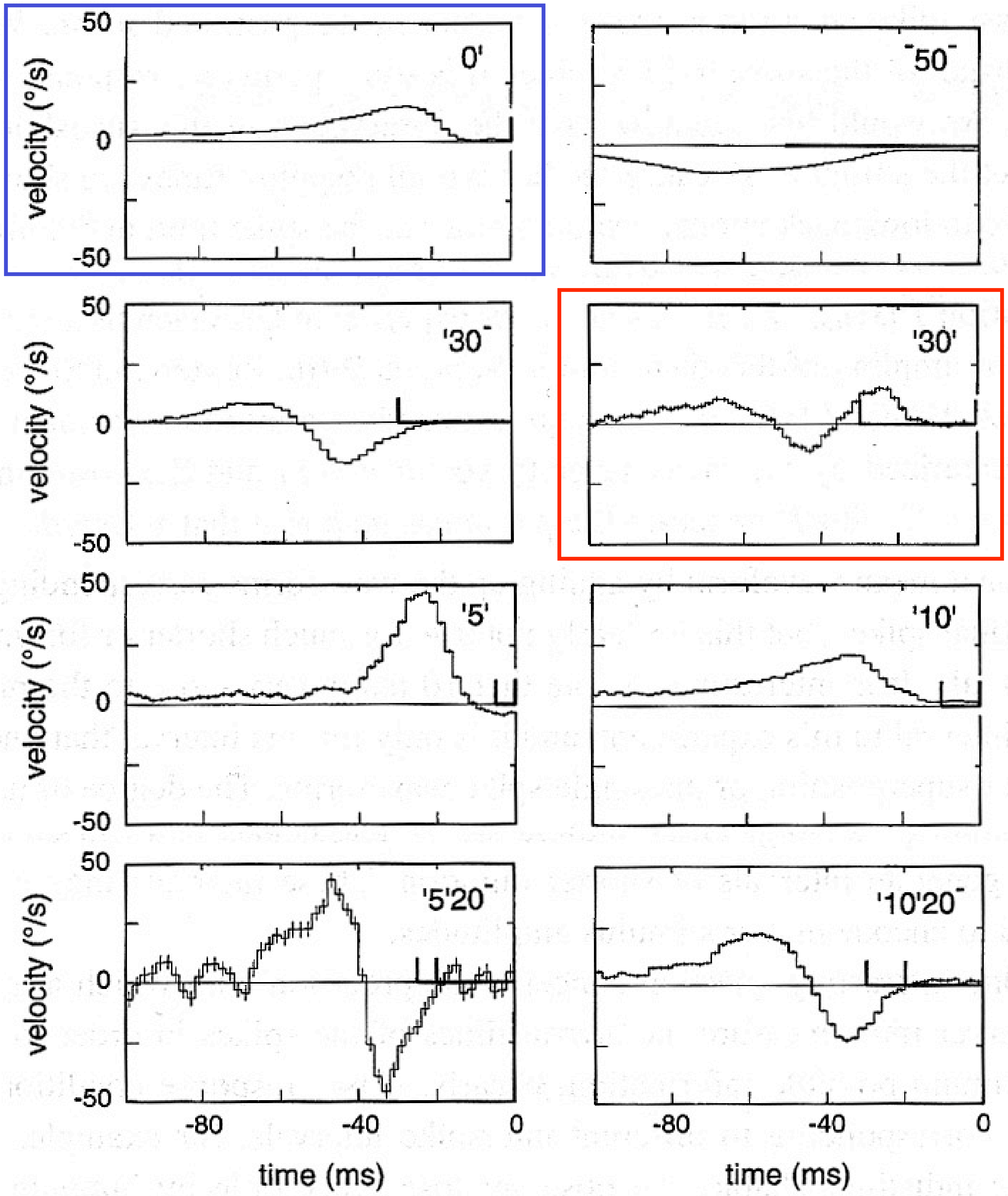
DECODING: Look-up-table approach

- determine what each spike sequence 'stands for'
- consider only linear relation between stimulus and each spike sequence
- expansion is in spike sequences



ENTRIES IN THE LOOK-UP TABLE

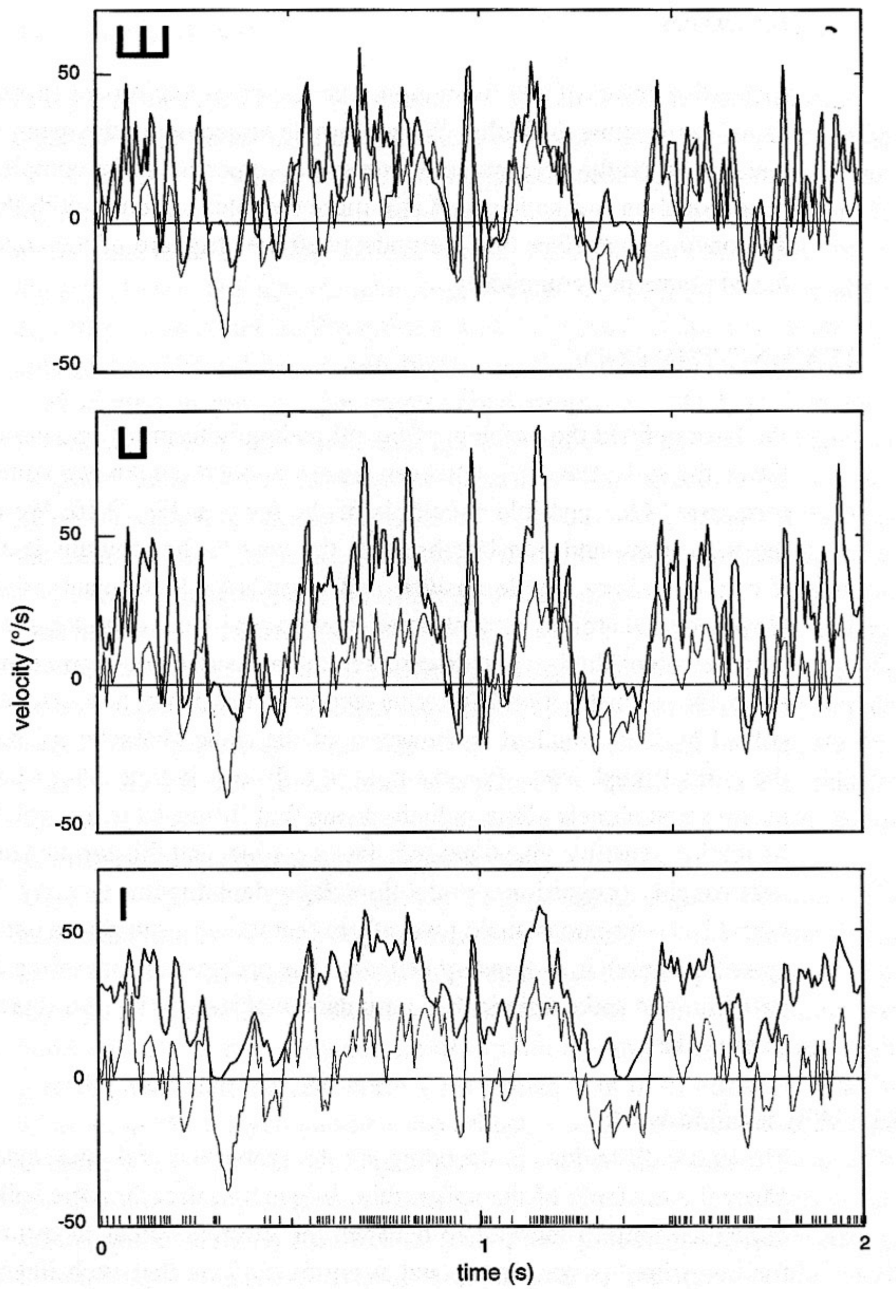
spike-triggered average



structure of interval-triggered averages not simply predicted from STA

(de Ruyter van Steveninck and Bialek, 1987)

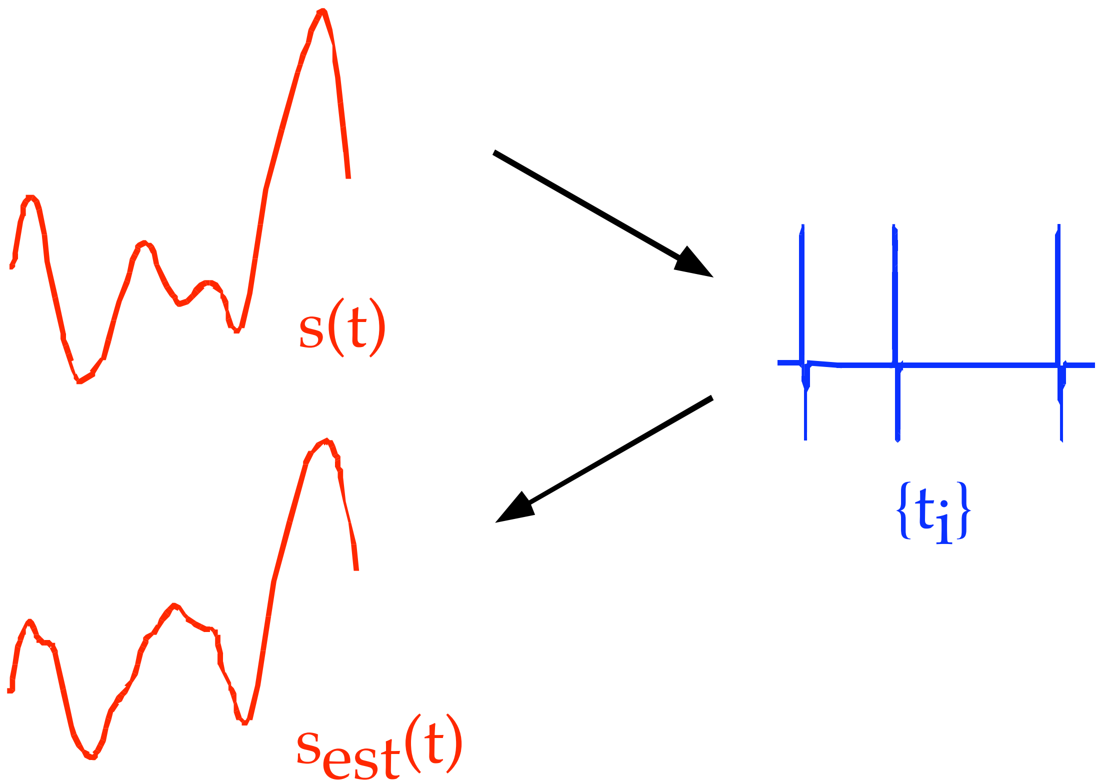
STIMULUS ESTIMATES USING LOOK-UP TABLE



- complex patterns (at least up to 3 spikes) continue to help
- not enough data to go to 4 spike patterns (despite 1e6 spikes in this experiment!)

(de Ruyter van Steveninck and Bialek, 1987)

LOOK UP TABLE APPROACH

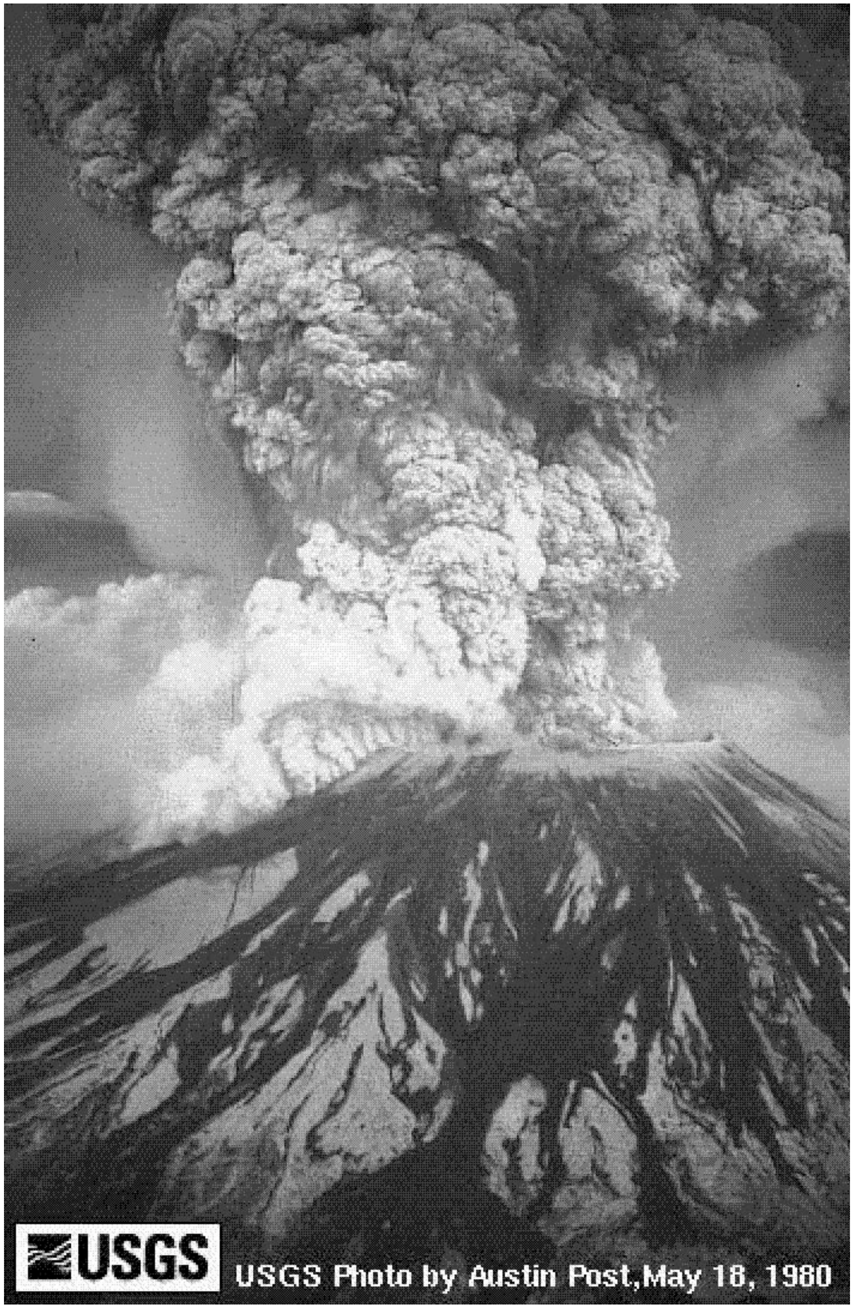


PROS:

- systematic
- easy to compare stimulus and estimate
- simple to evaluate accuracy
- deals with non-independence of spikes directly

CONS:

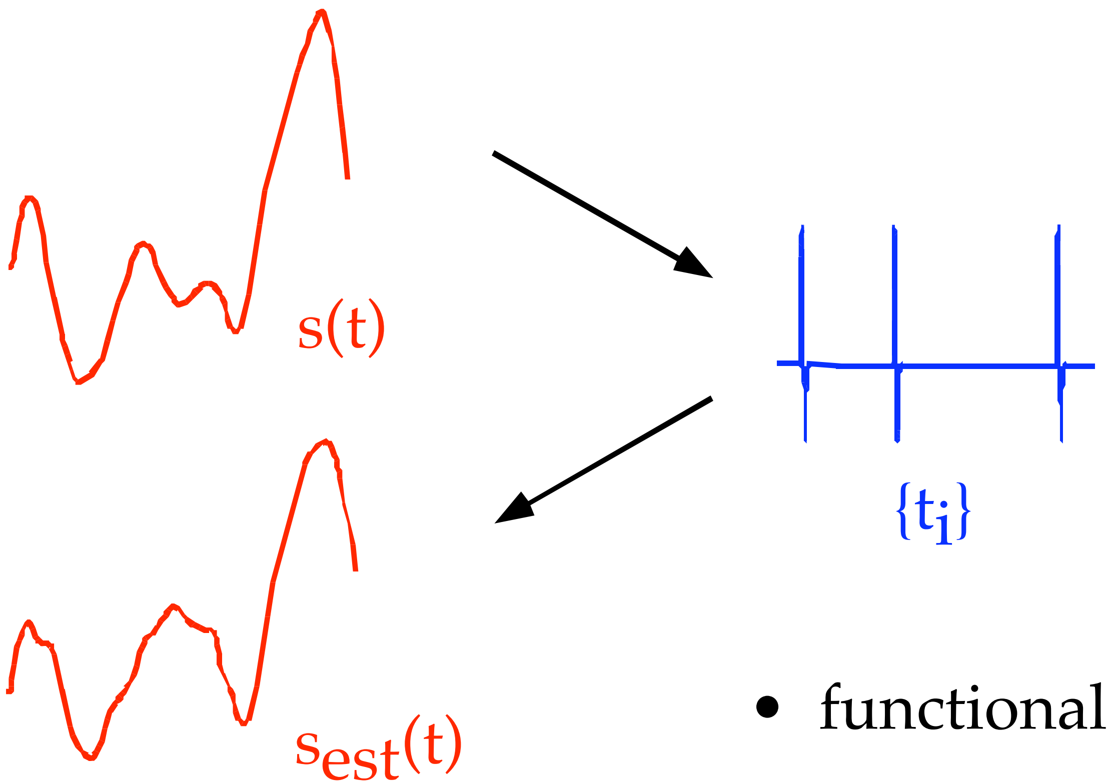
- typically does not converge quickly
  - again no ‘small parameter’
  - run out of data before clearly done
- implementation?
- resolution of overlap difficult



Possible reasons for continued incineration:

- each spike sequence stands for something special
- refractoriness introduces another time scale and we get this only slowly by considering each spike sequence

DECODING AS FILTERING



- functional approach

$$s_{est}(t) = \sum F_1(t-t_i) + \sum F_2(t-t_i, t-t_j) + \ldots$$

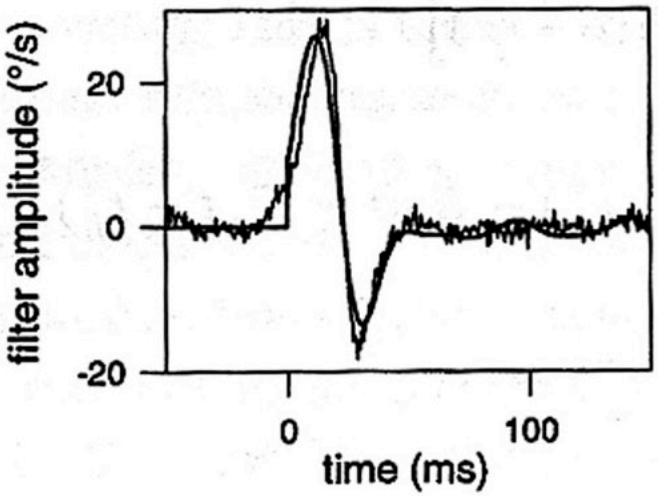
- choose F's to minimize ϵ^2

$$\epsilon^2 = < | s(t) - s_{est}(t) |^2 >$$

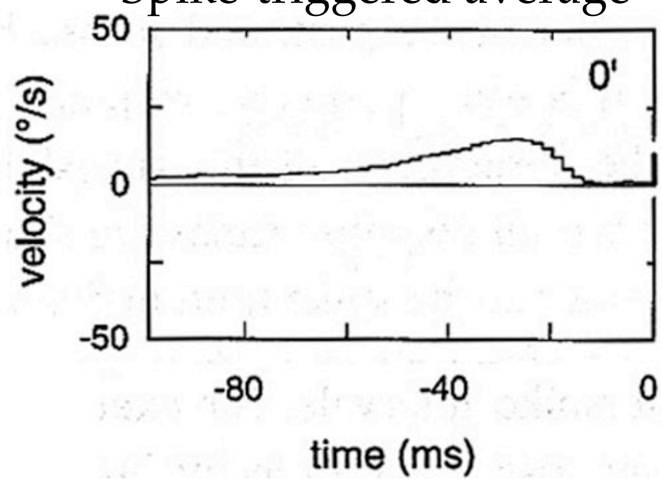
DIRECT DECODING IN FLY MOTION-SENSITIVE NEURON

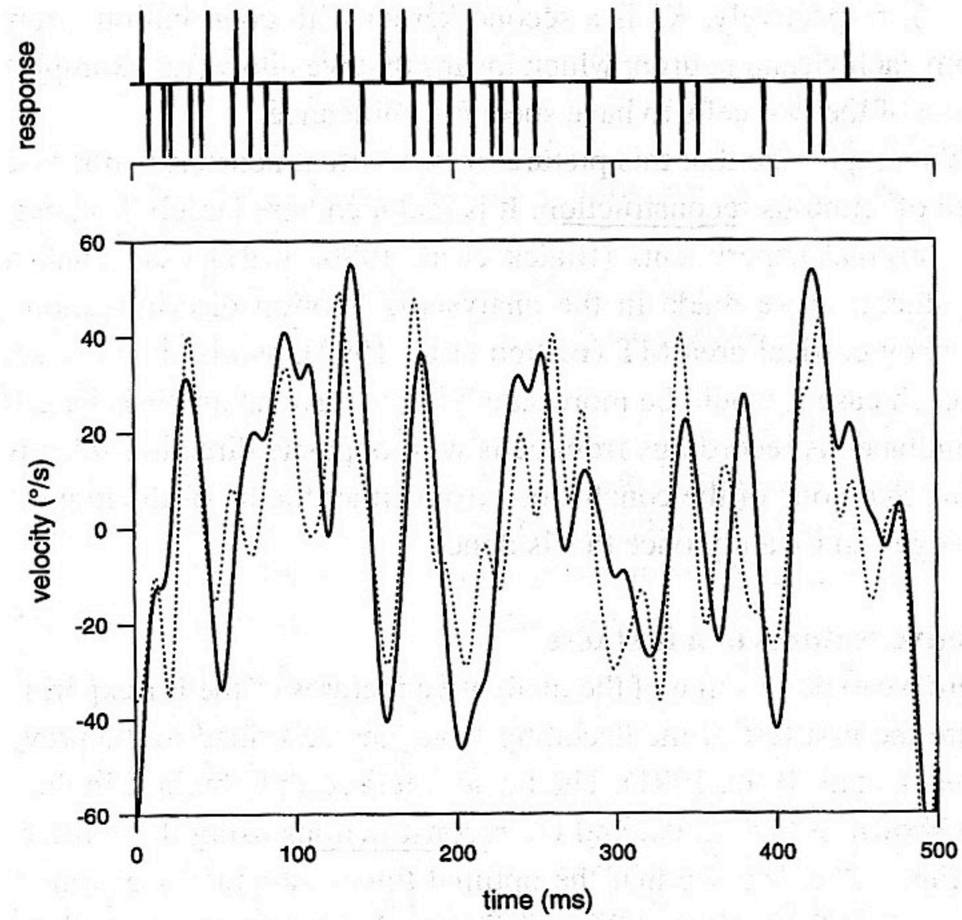
(Bialek et al., 1991)

Linear estimation filter



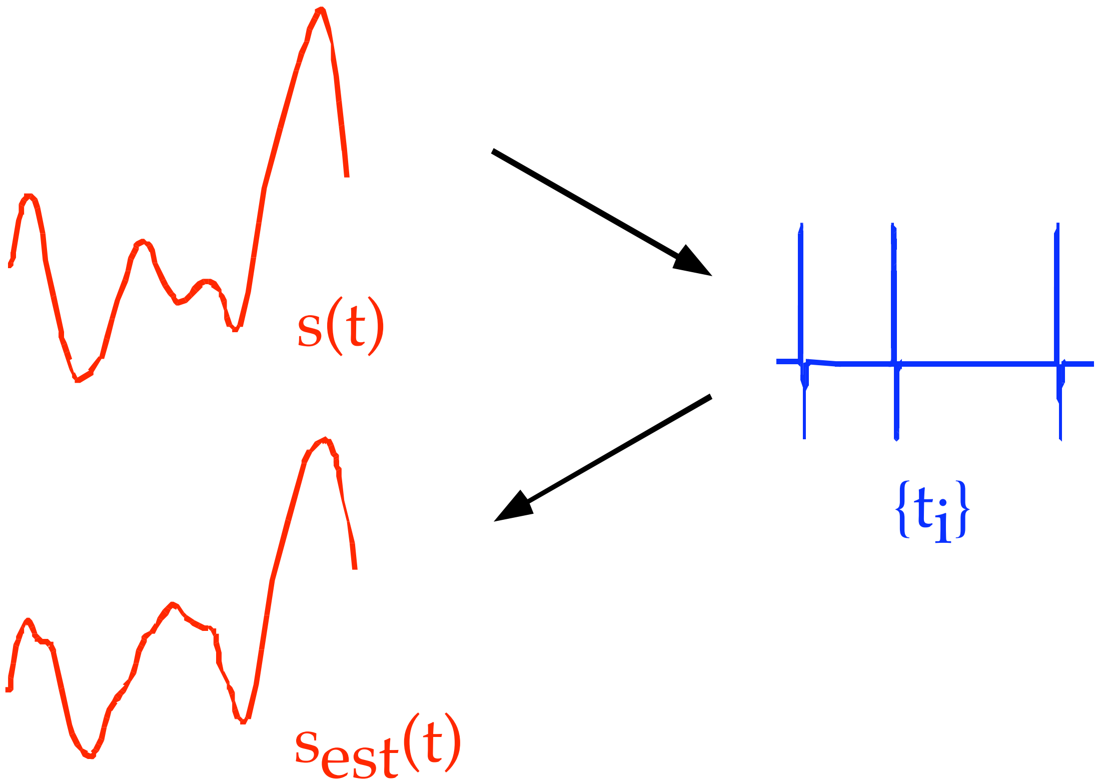
Spike-triggered average





quality of estimate with linear term similar to that of 3-spike patterns in look-up table approach - i.e. seems to be converging

DIRECT DECODING SUMMARY

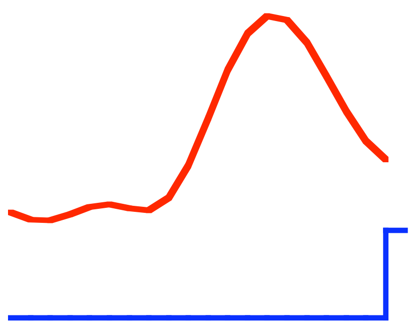


PROS:
- systematic
- easily interpreted
- seems to converge
- easy to evaluate accuracy

CONS:
- still no 'small parameter'
- mechanistic interpretation?

ENCODING:

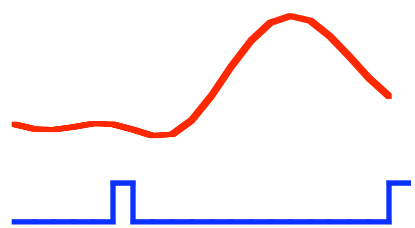
- determine what stimulus features trigger a spike

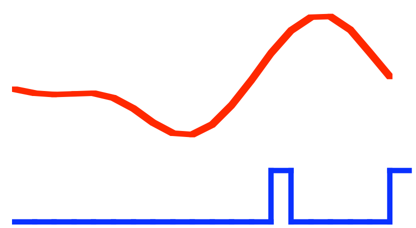


DECODING:

Look-up-table approach

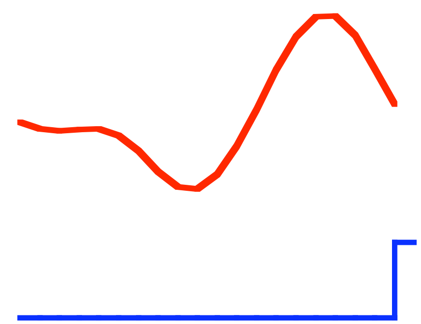
- determine what each spike sequence 'stands for'



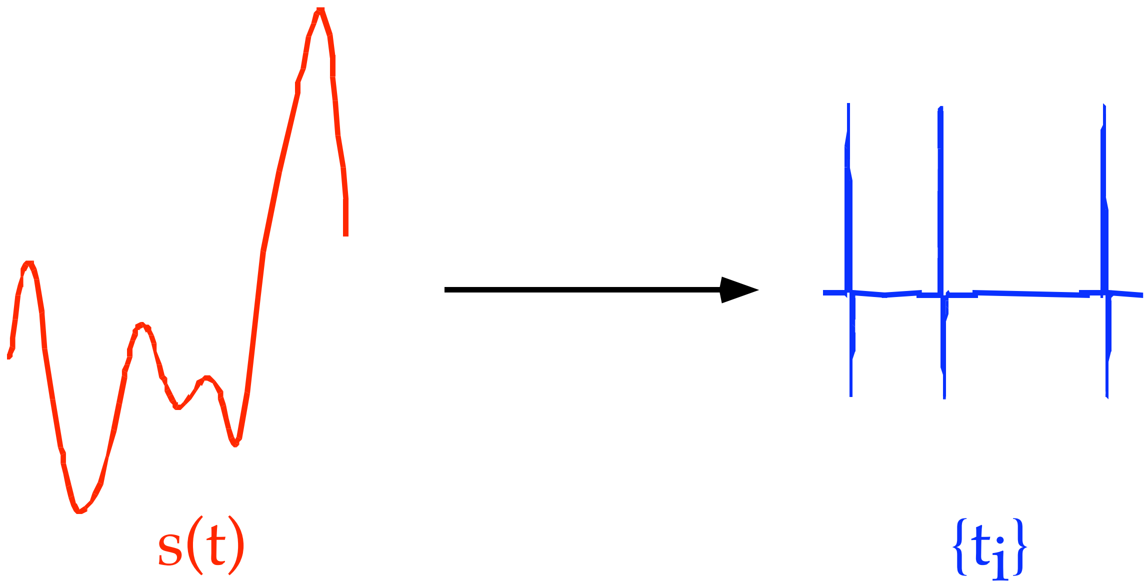


Direct approach

- determine what each spike 'stands for' - correct for bias of spiking dynamics



The Neural Coding Problem



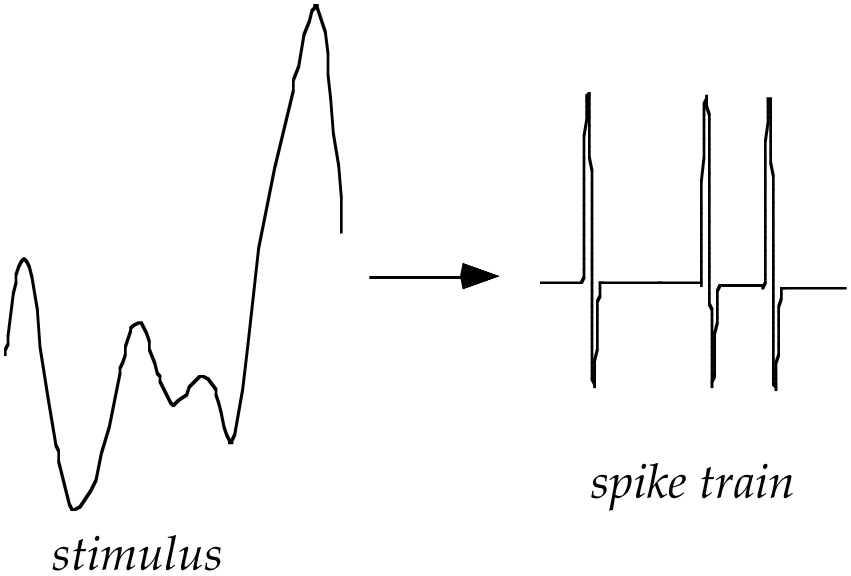
Central goals for today:

- important properties of coding process
  - to be complete must deal with spikes (not rate)

- desiderata and comparison of different approaches
  - how do we know when we are done?
  - would like 'answer' to provide functional and mechanistic insights

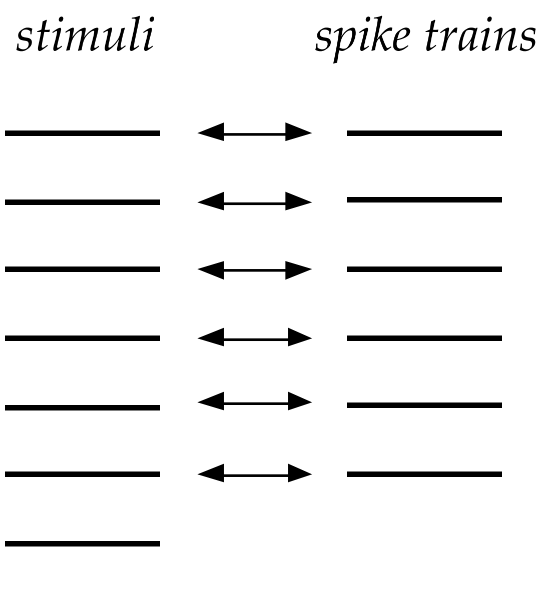
- reliability and coding efficiency
  (approaches fundamental limits ...)

CODING EFFICIENCY: HOW DO YOU KNOW WHEN YOU ARE DONE?

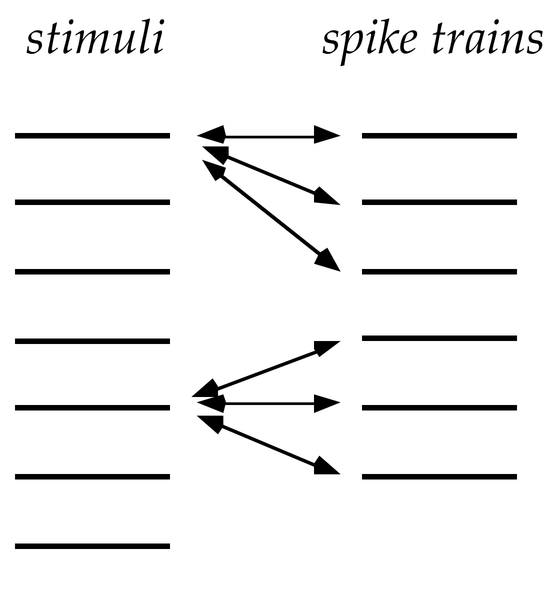


$$\text{coding efficiency} = \frac{\text{information provided by spikes about stimulus}}{\text{spike train entropy}}$$

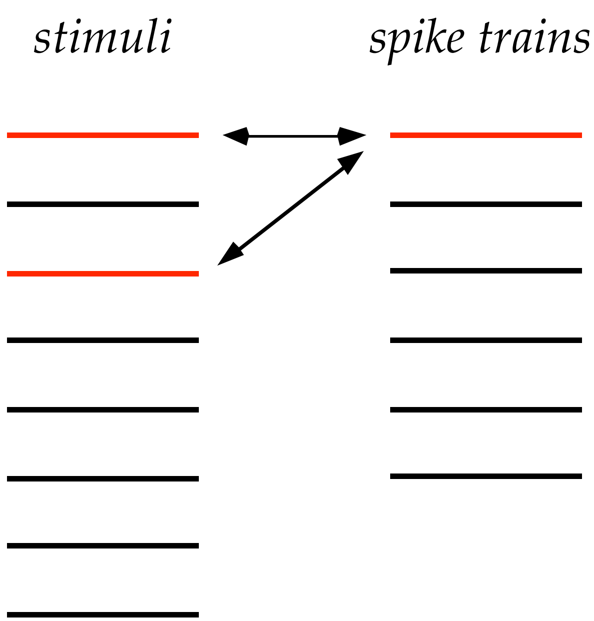
High Efficiency



Low Efficiency



$$\text{coding efficiency} = \frac{\text{information provided by spikes about stimulus}}{\text{spike train entropy}}$$



How much does observation of the spike train reduce uncertainty about the stimulus?

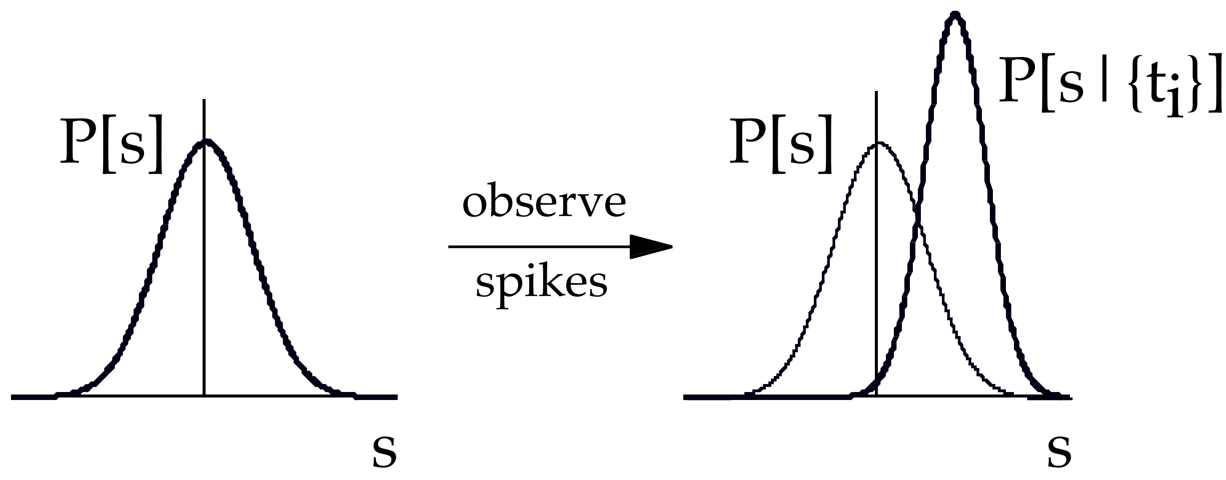
Prior: P[*stimulus*]

Conditional distribution: P[*stimulus* | *spike train*]

Measure reduction in uncertainty on logarithmic scale (entropy)

- additivity
  - information from two independent measurements should add
- relative measure
  - compare information about different aspect of stimulus (e.g. color and orientation)

Information theory (Shannon)

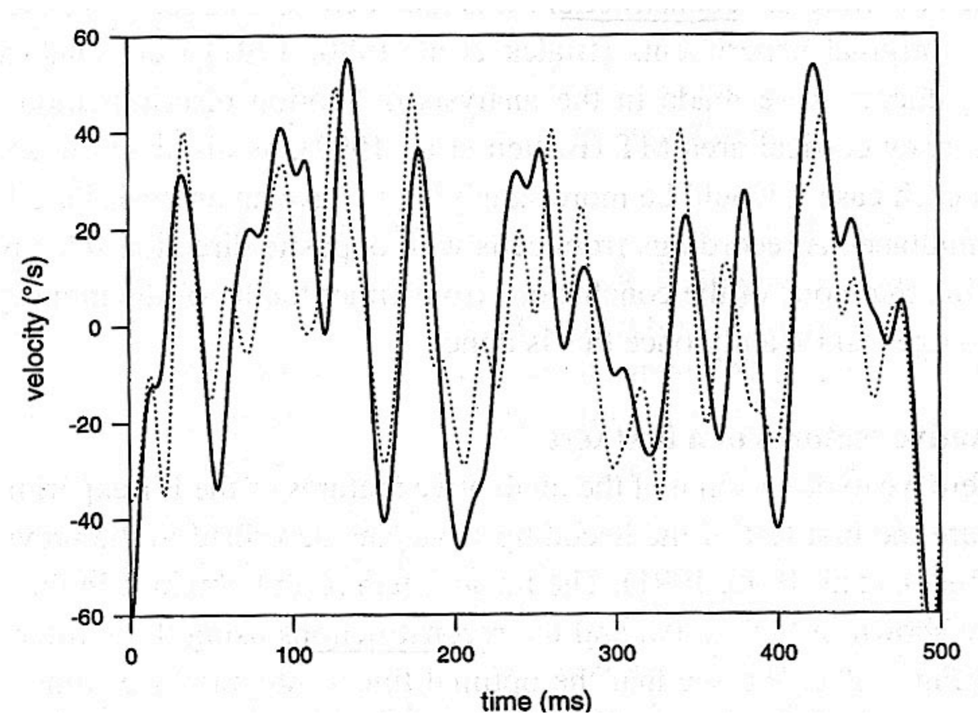


$$\text{Info} = -\int Ds\, P[s] \log_2 P[s] + \int Ds\, Dt_i\, P[s \mid \{t_i\}] \log_2 P[s \mid \{t_i\}]$$

For Gaussian signal and noise

$$R_{info} = \int df \log_2[1 + SNR(f)]$$

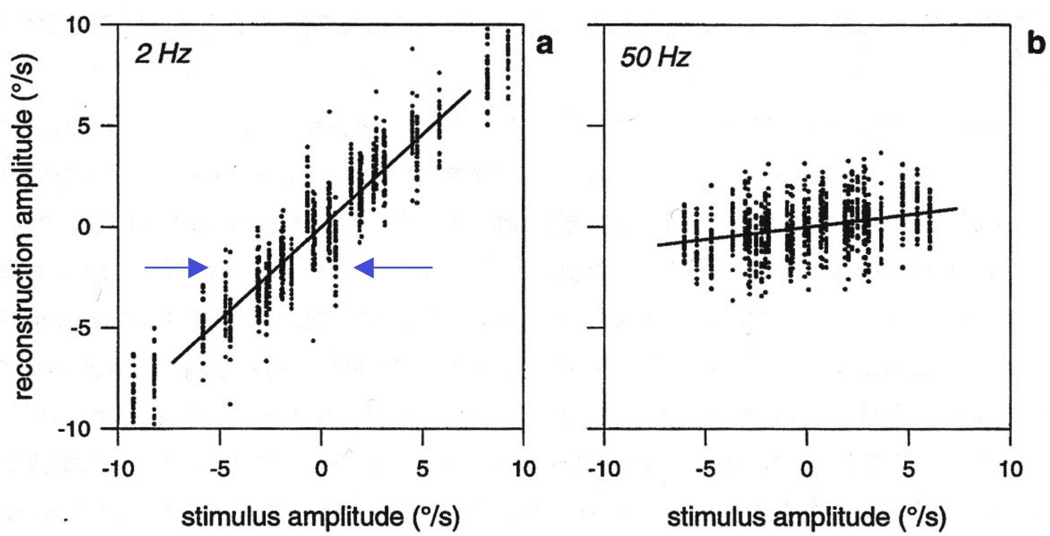
NOISE IN THE ESTIMATED STIMULUS



- difference between stimulus and estimate contains both random and systematic errors

- separate by measuring correlation at each temporal frequency

$$s_{est}(f) = g(f) * [\ s(f) + n(f)\ ]$$

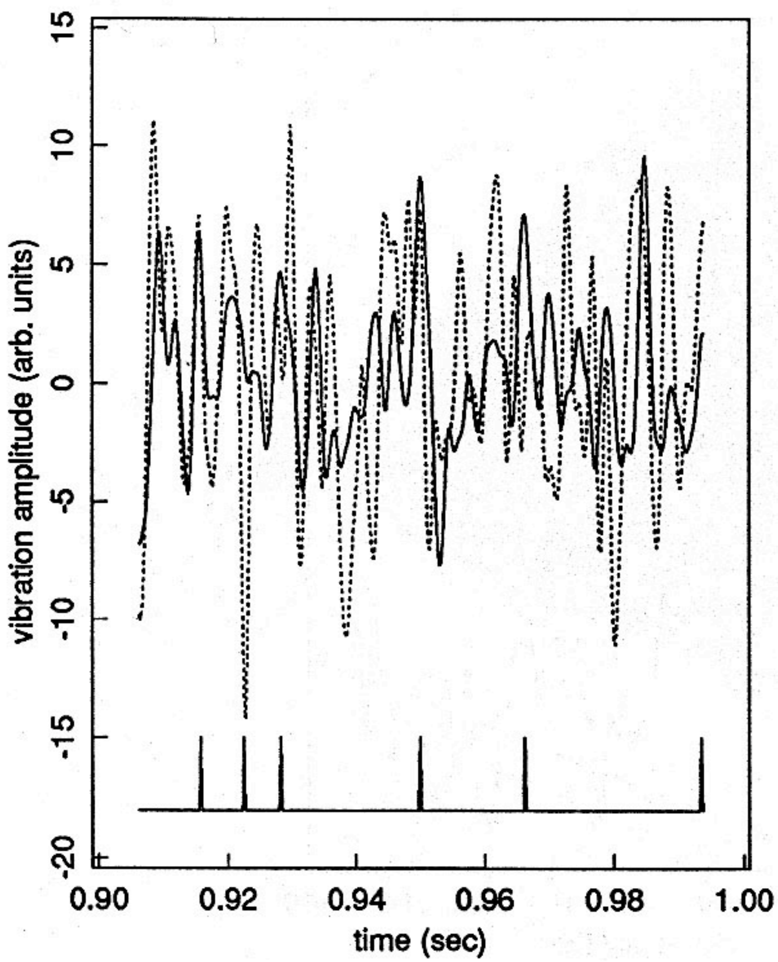


slope g(f): systematic bias

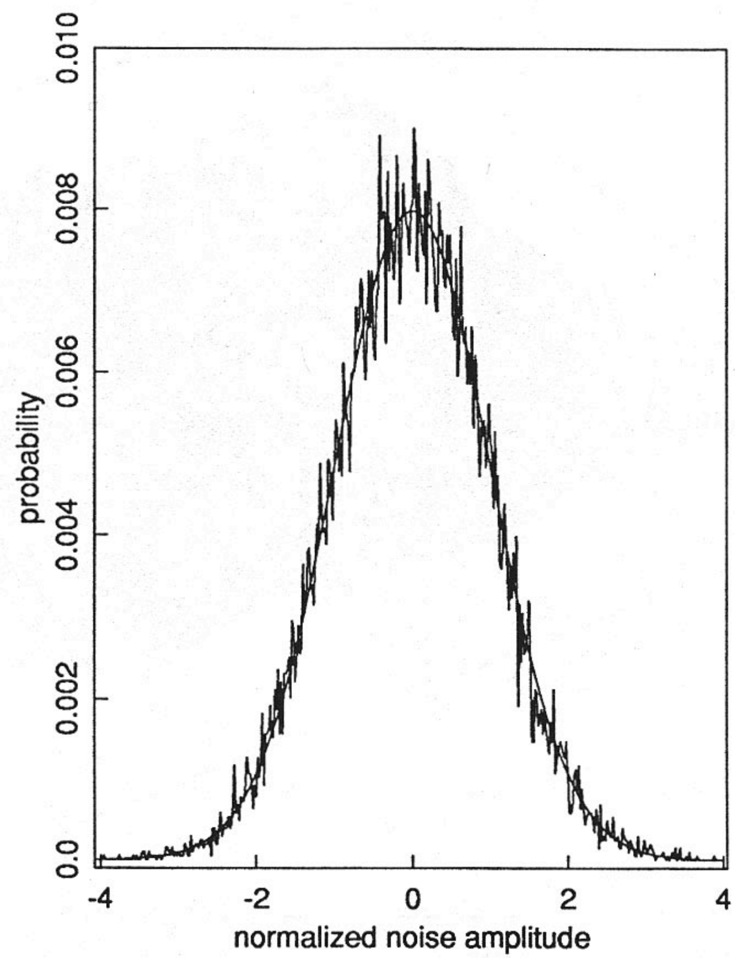
scatter n(f): effective input noise

NOISE IS APPROXIMATELY GAUSSIAN

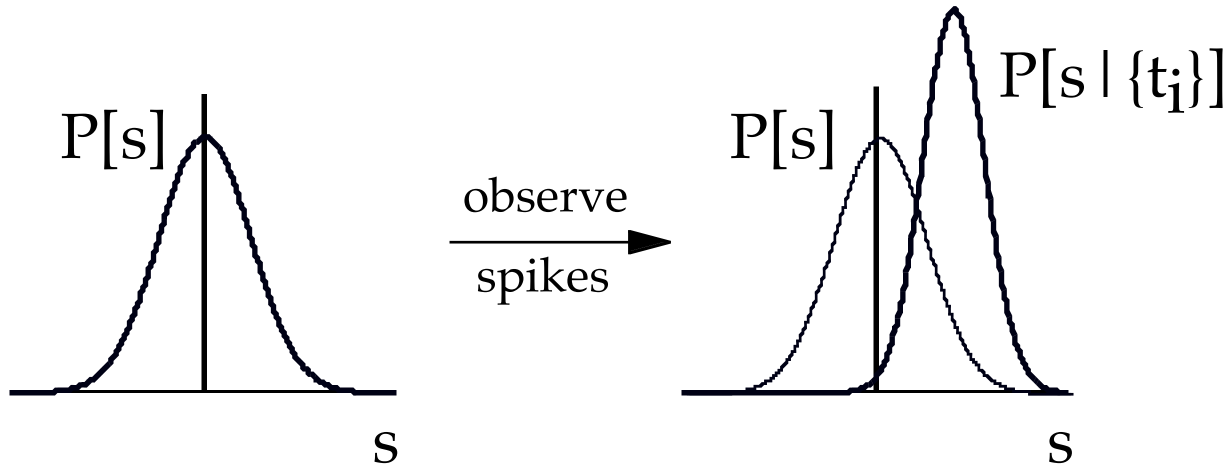
reconstruction of vibration amplitude using afferent from frog sacculus



distribution of random errors in estimate



Information theory (Shannon)



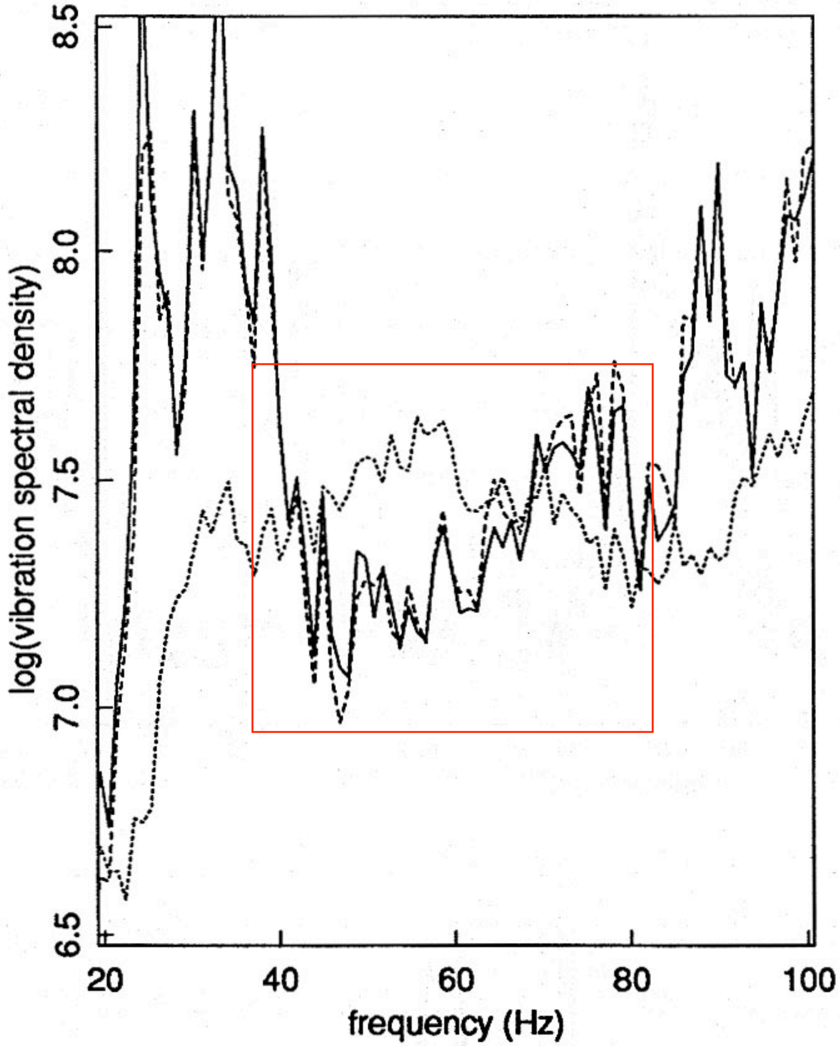
$$R_{info} = -\int Ds\, P[s] \log_2 P[s] +$$

$$\int Ds\, Dt_i\, P[s \mid \{t_i\}] \log_2 P[s \mid \{t_i\}]$$

For Gaussian signal and noise

$$R_{info} = \int df \log_2[1 + SNR(f)]$$

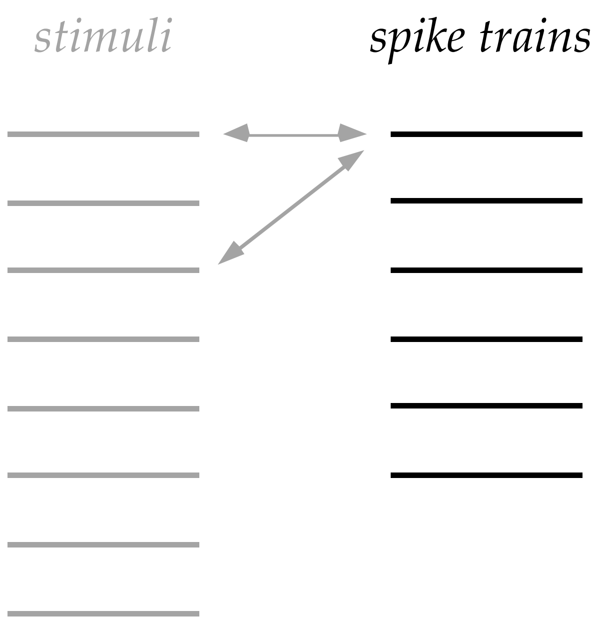
SIGNAL-TO-NOISE IN SACCULUS AFFERENT



$$R_{info} = \int df \log_2[1 + SNR(f)]$$

$$= 150 \text{ bits/sec}$$

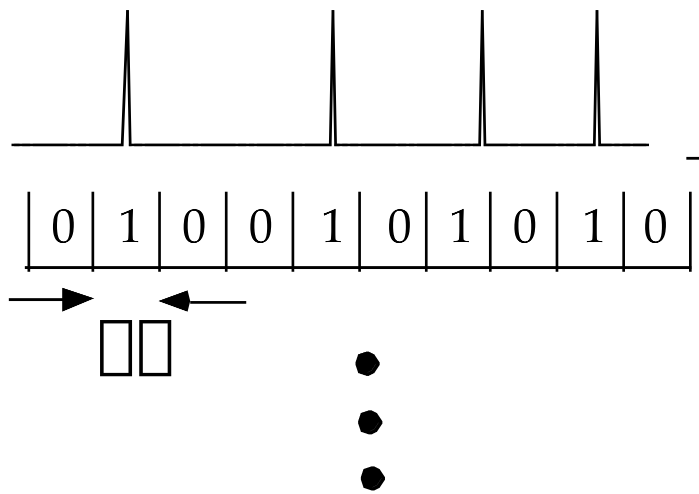
$$\text{coding efficiency} = \frac{\text{information provided by spikes about stimulus}}{\text{spike train entropy}}$$



How many distinguishable spike trains can the cell generate?

P[*spikes*]

Spike train entropy (MacKay and McCulloch)



$$S(\square\square) = -\frac{1}{\square\square}\left[p \log_2 p + (1-p)\log_2(1-p)\right]$$

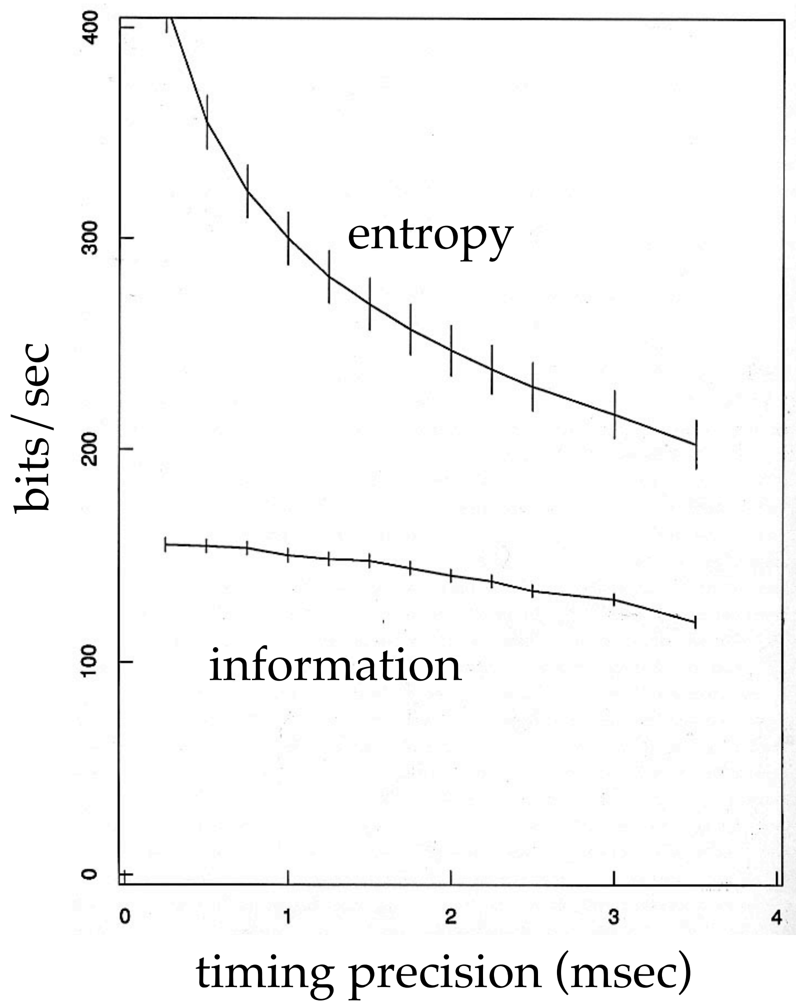
Coding efficiency

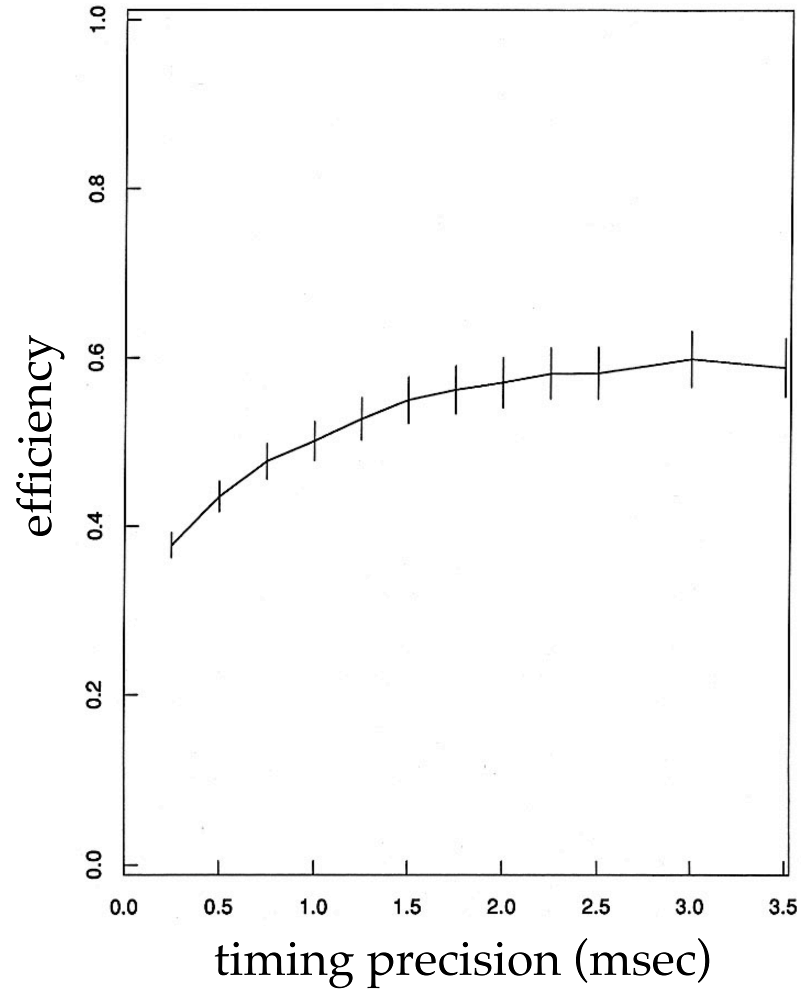
(1) measure $R_{info}(\square\square)$

(2) measure $S(\square\square)$

→ $\square(\square\square)$

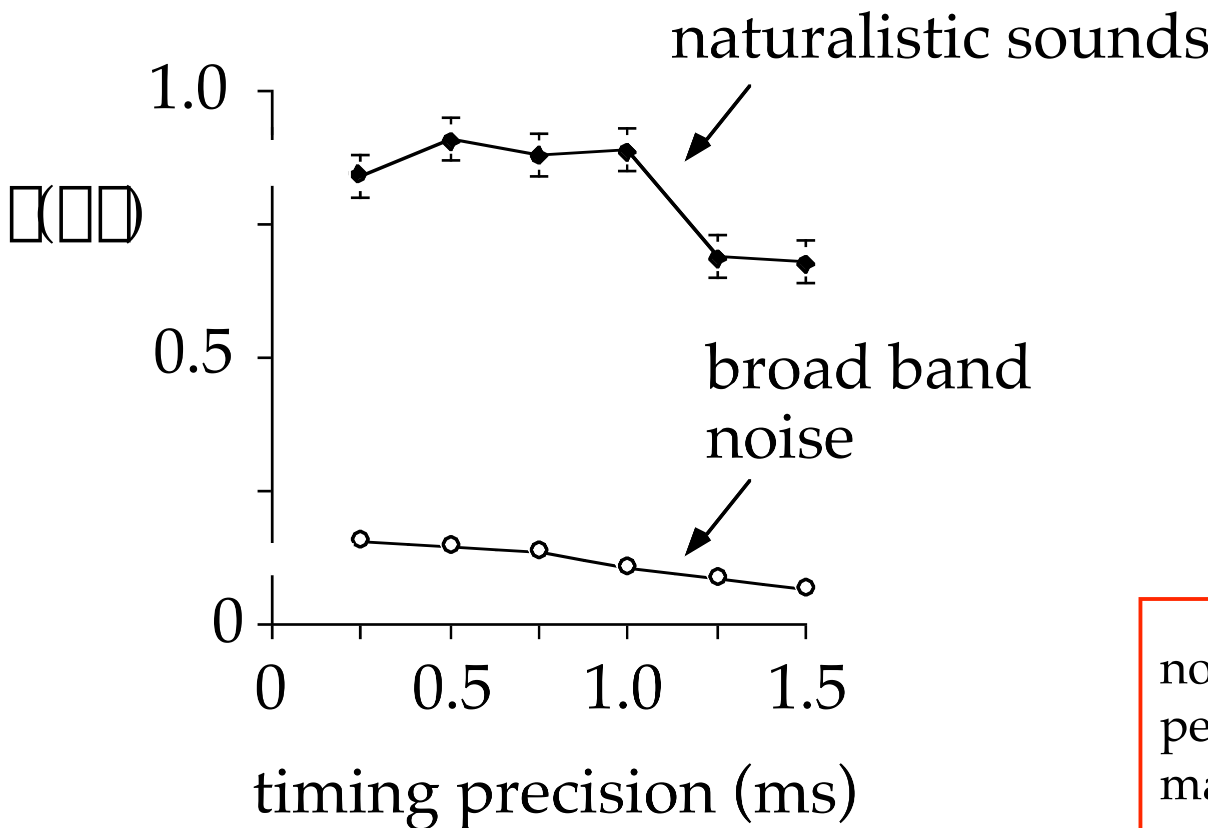
$$\text{coding efficiency} = \frac{\text{information provided by spikes about stimulus}}{\text{spike train entropy}}$$





CODING EFFICIENCY HIGHER FOR 'NATURAL' SIGNALS

(Rieke, Bodnar and Bialek, 1995)



nonlinearities in
peripheral auditory system
matched to statistical
properties of signals

Summary of Coding Efficiency Measurements

system	*efficiency*
cricket mechanoreceptors	>50%
frog mechanoreceptors	>50%
frog auditory afferents	10-30% for broad band noise 50-90% for naturalistic sounds
- -	
retinal ganglion cells	~20% for white noise inputs (Warland Reinagel and Meister, 1997)

EJC (2000): “We are all losing, the only question is how badly”

SOME OPEN QUESTIONS

• Coding in cell populations
- distributed coding (e.g. correlations)

• Adaptive codes
- how maintain efficient coding when properties of input signals change?

• Statistics of natural images
- efficiency of coding in ganglion cells

• Optimal coding?
- coding is efficient -> predict dynamics?