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How much does a fly know about its world?

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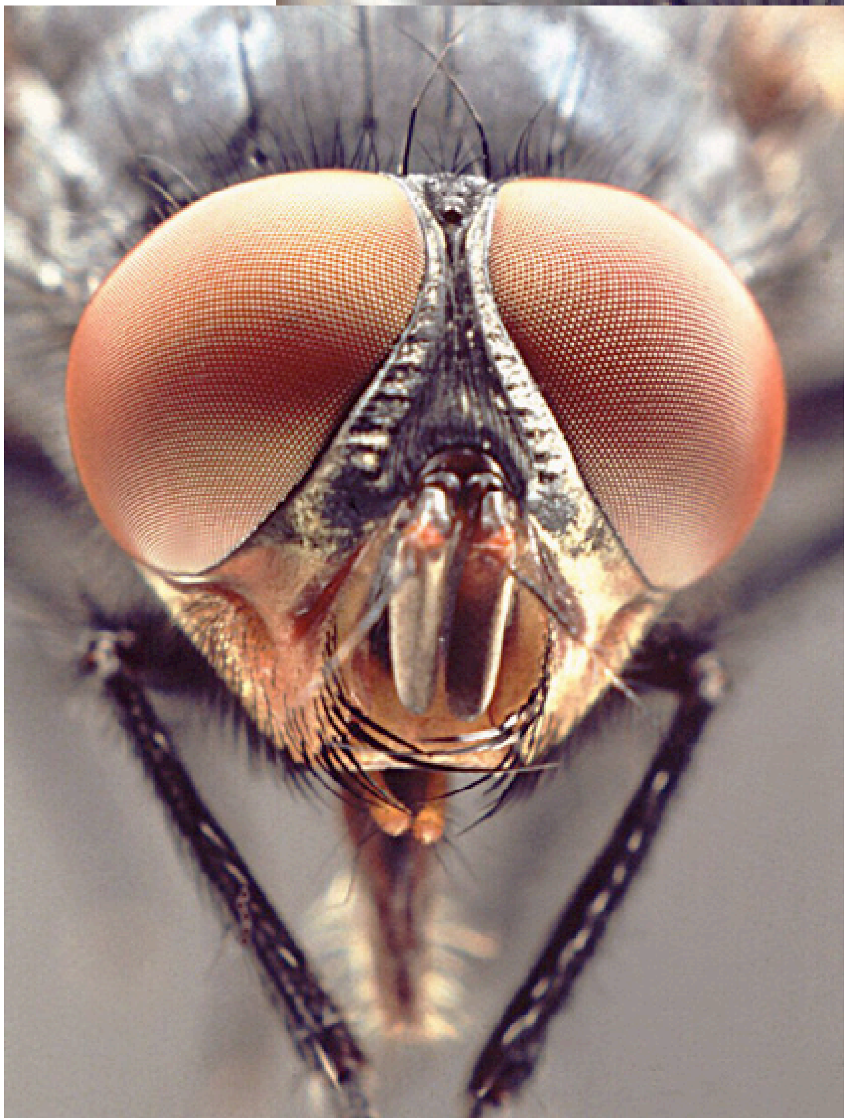
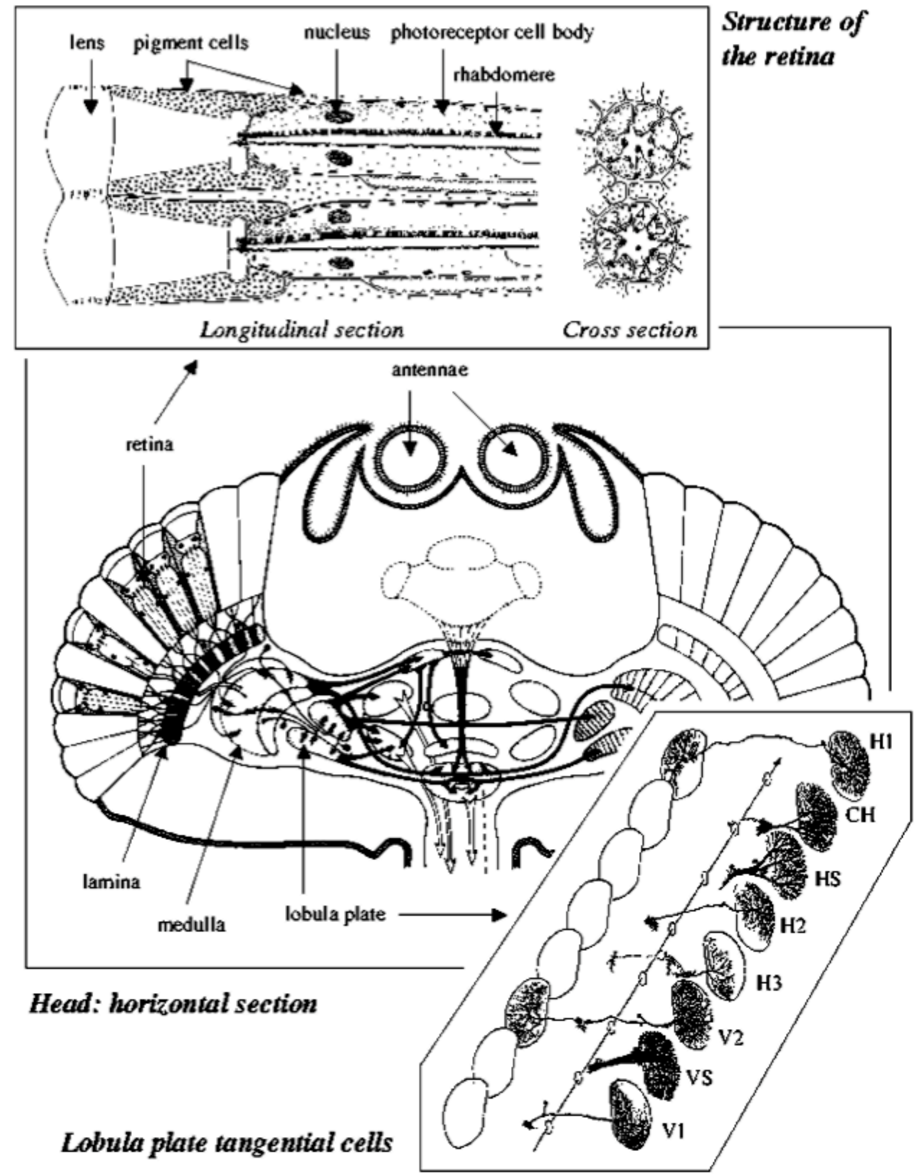
http://sourceforge.net/projects/nsb-entropy





H. L. Leertouwer

De Ruyter and Bialek, 2002

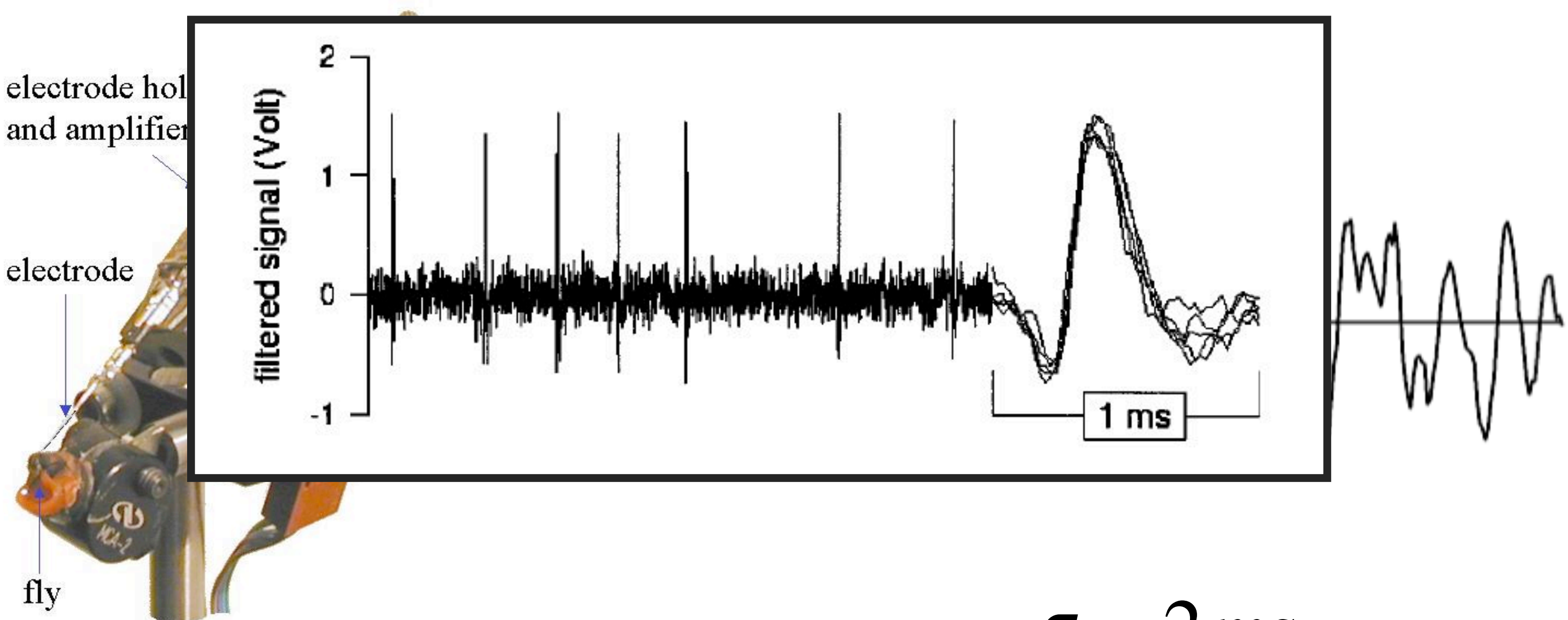
Why fly as a neurocomputing model system?

- Can record for long times
- Named neurons with known functions
- Nontrivial computation (motion estimation)
- Vision (specifically, motion estimation) is behaviorally important
- Possible to generate natural stimuli

Questions

- Can we understand the code?
- Which features of it are important?
  - Is this a rate or a timing code?
  - Synergy between spikes?
- What does the fly code for?
- How much does it know?
- Is there an evidence for optimality?

Motion estimation in fly H1



$$\tau = 2ms$$

(Strong et al., 1998)

Decoding a simple spike train

$$P(t_i \mid s(t)) \sim Poisson[r(s(t_i)]$$

nonlinear

$$P[\{t_i\} \mid s(t)] = \frac{1}{N!} \exp\left[-\int r(s(t))\, dt \right] \prod_{i=1}^{N} r(s(t_i))$$

$$P[s(t)] \propto \exp\left[-\frac{1}{4\tau_c} \int dt \left(\tau_c^2 \dot{s}^2 + s^2 \right) \right]$$

$$s_{est}(t_0) = \int [ds]\ P[s(t) \mid \{t_i\}]\ s(t_0) = \int [ds]\ \frac{\boldsymbol{P[\{t_i\} \mid s]P[s]}}{\boldsymbol{Z}}\ s(t_0)$$

(Bialek, Zee, 1990)

Linear decoding for sparse spikes (cluster expansion)

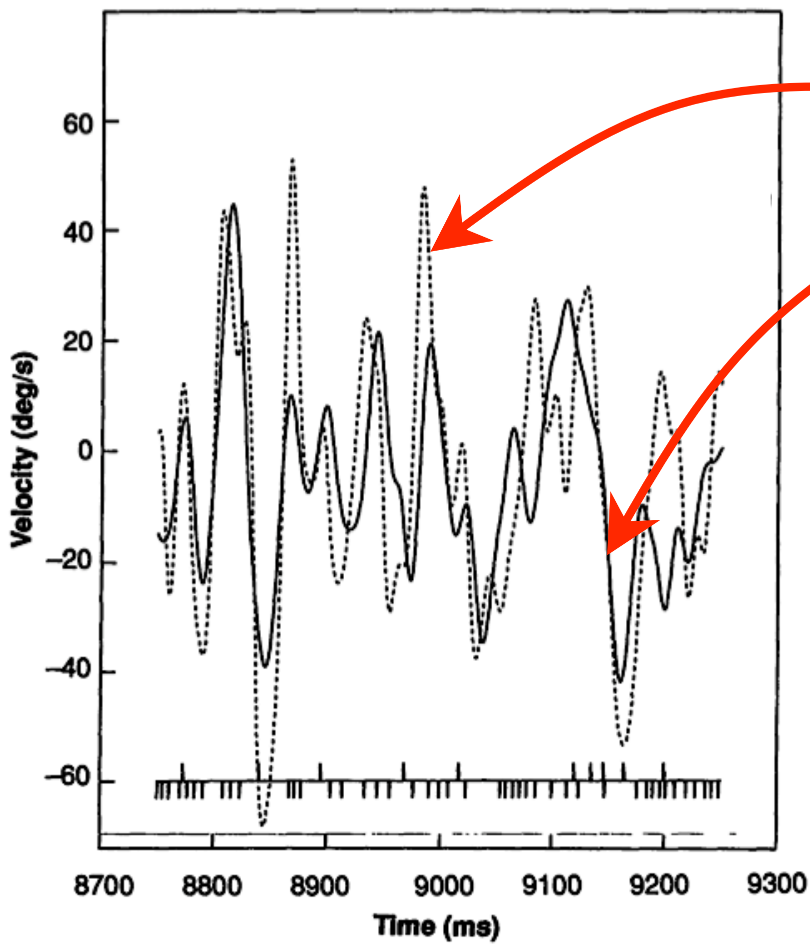
$$s_{est}(t_0) = \frac{\left\langle s(t_0)\prod_{i=1}^{N} r(s(t_i)) \right\rangle_{prior}}{\left\langle \prod_{i=1}^{N} r(s(t_i)) \right\rangle_{prior}}$$

Stimulus couples spikes; but the strength of the coupling drops with $\sim (t_i - t_{i+1})/\tau$ (very fast varying mean field)

$$s_{est}(t) = \sum_i f_1(t-t_i) + \sum_{ij} f_2(t-t_i, t-t_j) + \ldots$$

(Bialek, Zee, 1990)

Linear decoding



stimulus

reconstruction

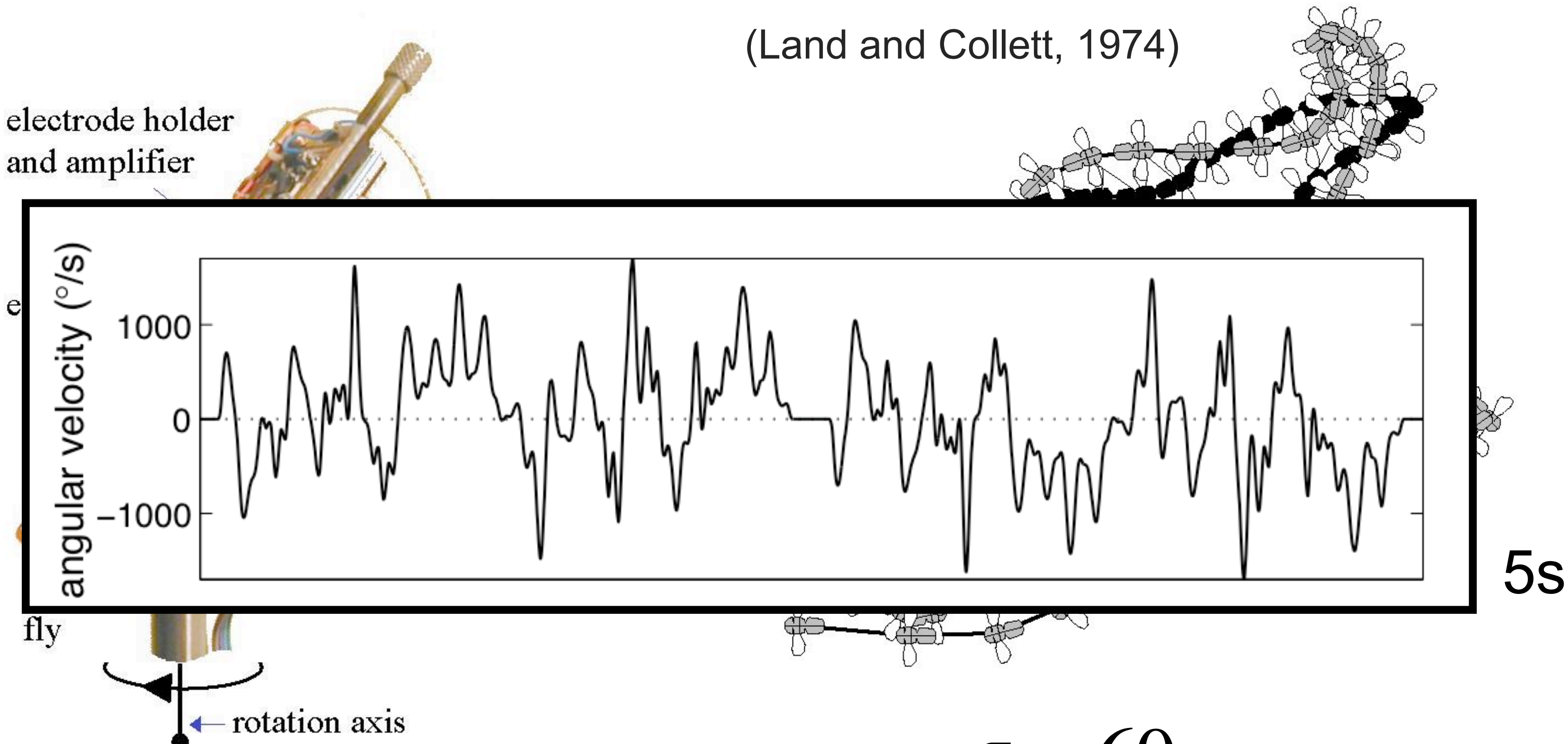
$$\langle t_{i+1} - t_i \rangle = 30ms$$

But what if …

(Bialek et al. 1991)

Natural stimuli

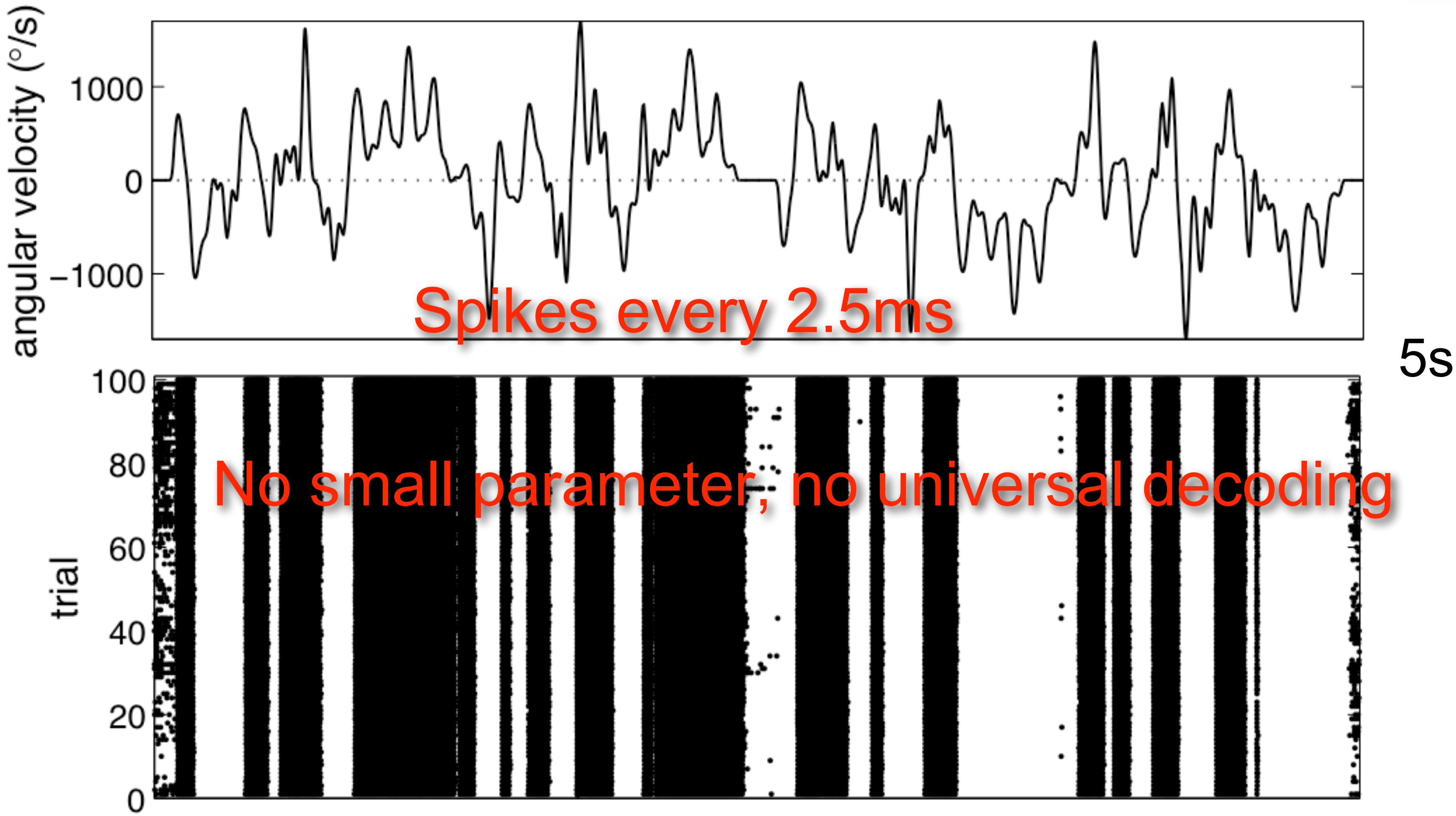
(Land and Collett, 1974)



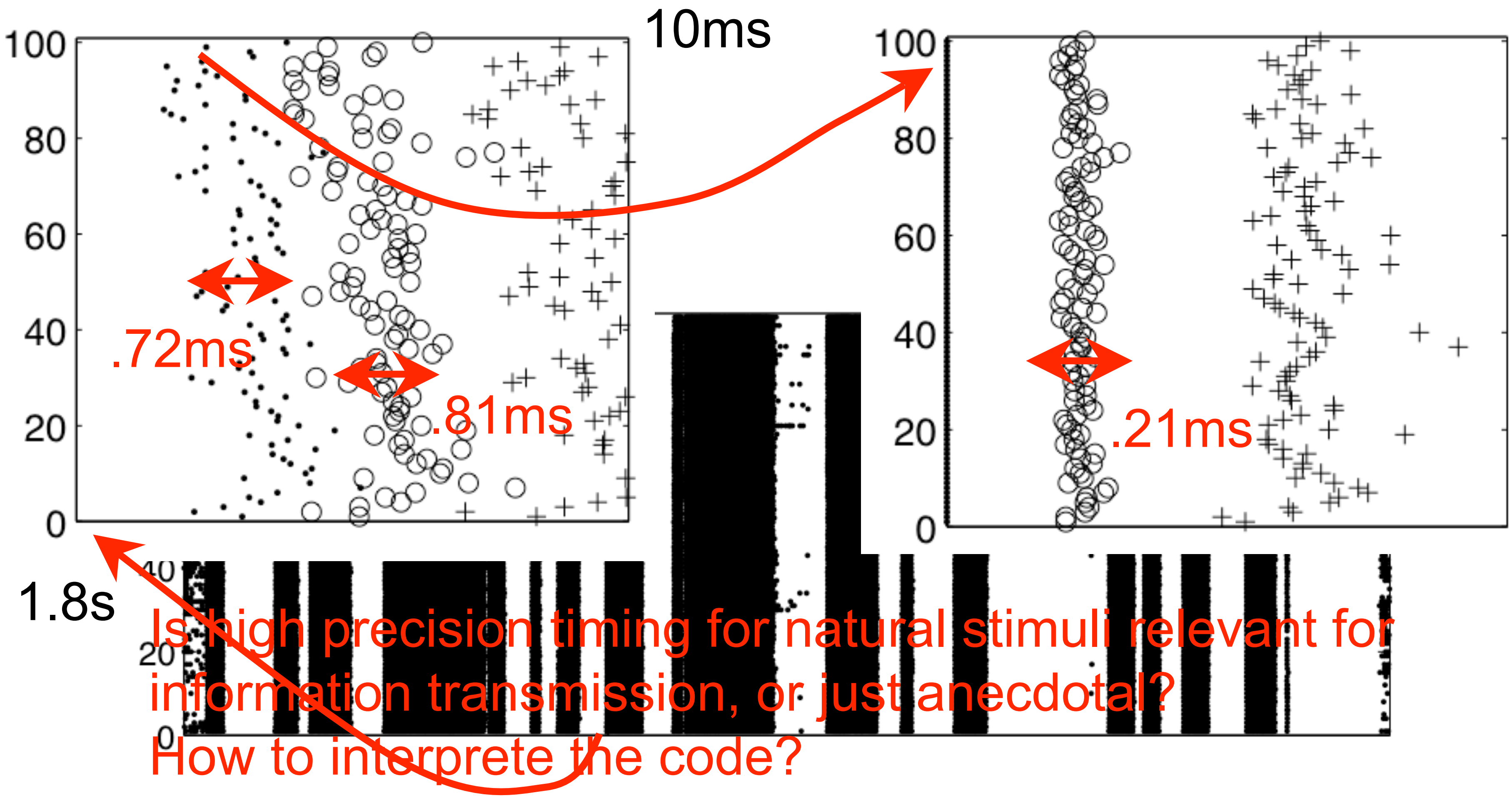
$$\tau = 60ms$$

(Lewen et al, 2001)

Natural stimulus and response



Highly repeatable spikes (not rate coding)



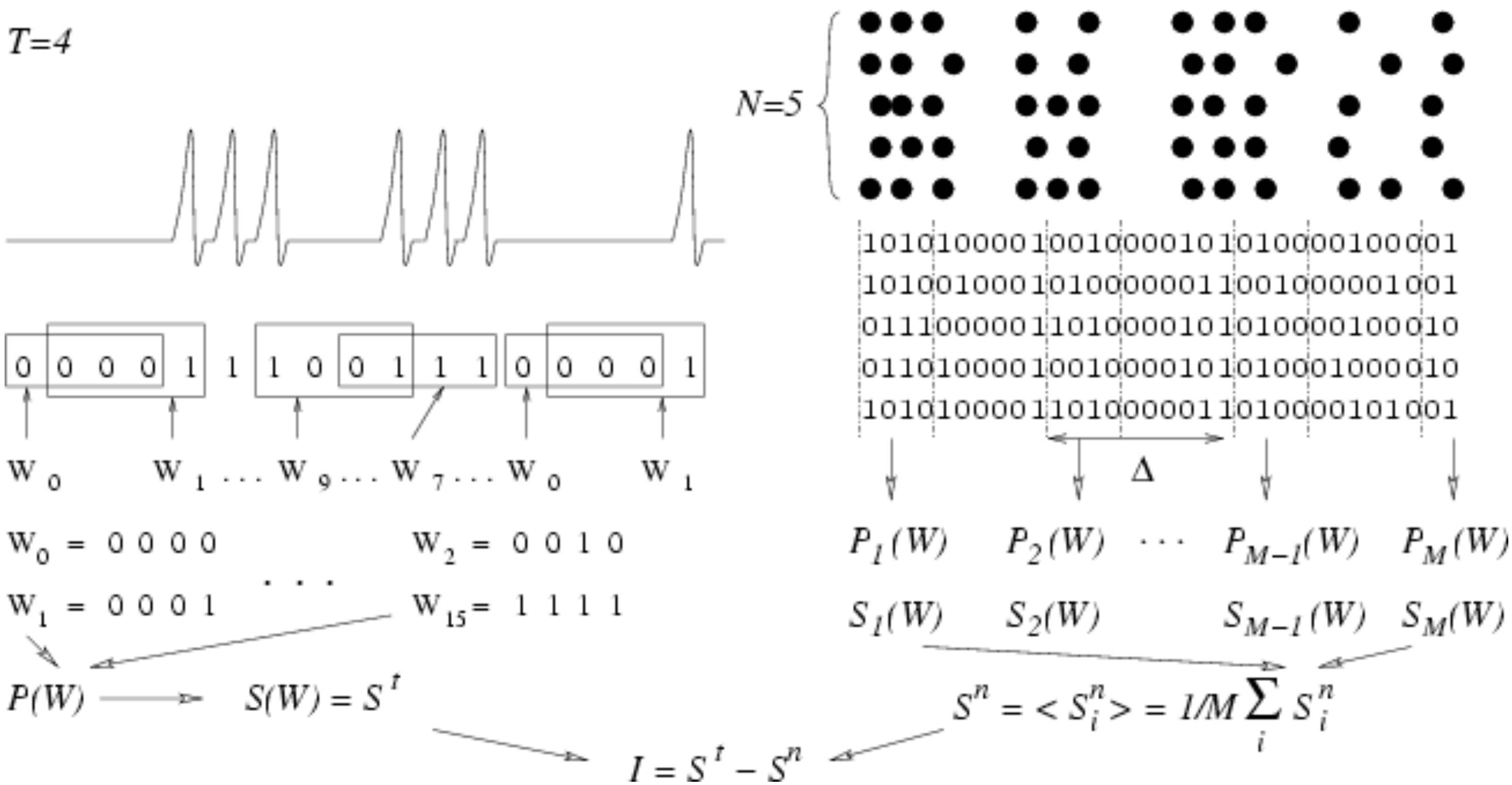
Is high precision timing for natural stimuli relevant for information transmission, or just anecdotal?
How to interprete the code?

How to characterize coding without an explicit decoding ?

$$S[x] = -\sum_{x} p(x) \log p(x), \qquad x = s, \{t_i\}$$

$$I[s,\{t_i\}] = \sum_{s\{t_i\}} p(s,\{t_i\}) \log \frac{p(s,\{t_i\})}{p(s)p(\{t_i\})}$$

Experiment design



(Strong et al., 1998)

Problems

- Total of about 10-15 min of recordings (limited by stationarity of the outside world)
- At most 200 repetitions
- Stimulus correlation of 60ms: only 10000 independent samples (repeated or nonrepeated)
- Need to sample words of length 30 ms (behavioral) to 60 ms (stimulus) at resolution down to 0.2 ms (binary words of length up to 100).

Naively

$$S \ll \log N$$ (negative bias >> variance for reasonable *N*)

13 bits for nonrepeated part
6-7 bits for repeated part

Even refractory Poisson process at this T, τ has over 15-20 bits of entropy!

For estimation of entropy at $K / N \leq 1$ see:
Grassberger 1989, 2003, Antos and Kontoyiannins 2002, Wyner and Foster 2003, Batu et al. 2002, Paninski 2003, Panzeri and Treves 1996, Strong et al. 1998

No universal estimator for $S > \log N$

But there is hope (Ma, 1981):

For uniform K-bin distribution the first coincidence occurs for

$$N_c \sim \sqrt{K} = \sqrt{2^S}$$

$$S \sim 2 \log N_c$$

Can make estimates in the nonasymptotic regime!
Can this be extended to nonuniform cases?

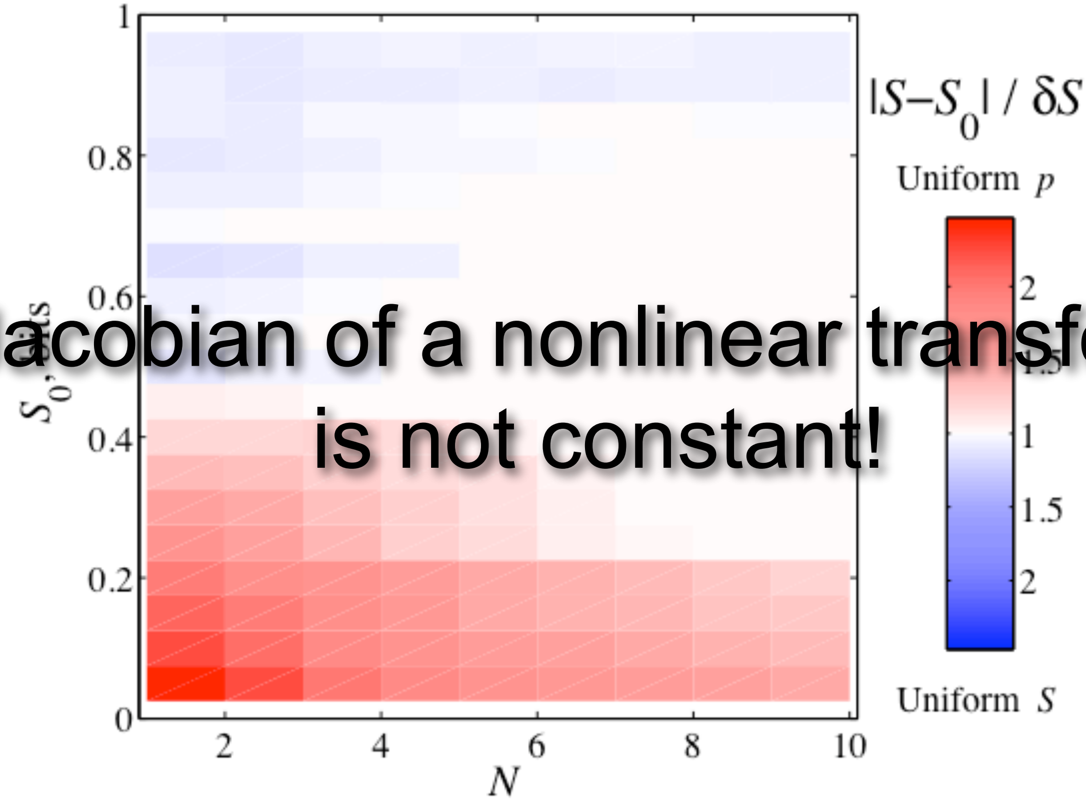
- Assumptions needed
- Estimate entropies without estimating distributions.

Universal problem

- One can use entropy-based measures in bioinformatics (conserved binding sites search, phylogeny, haplotyping) and systems biology (regulatory networks inference)
- They are also used in computational linguistics, mathematical finances, and dynamical systems theory.
- Same problem: severely undersampled data

Unbiased about distribution vs. unbiased about entropy

Binomial distribution with the prior uniform on *p* or *S*:



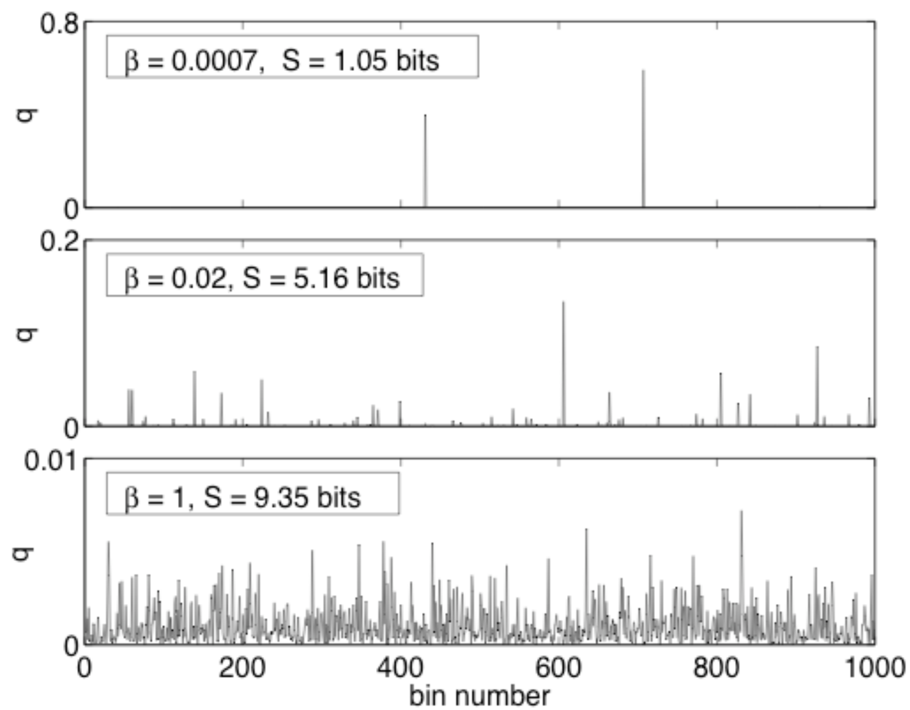
The Jacobian of a nonlinear transformation is not constant!

For large *K* the problem is extreme (*S* known a priori)

$$P_\beta(\{q_i\}) = \frac{1}{Z(\beta)}\,\delta\left(1-\sum_{i=1}^{K} q_i\right)\prod_{i=1}^{K} q_i^{\beta-1}$$

Dirichlet priors, a.k.a., adding pseudocounts (include the uniform prior, the ML prior, and others).

Inference is analytic



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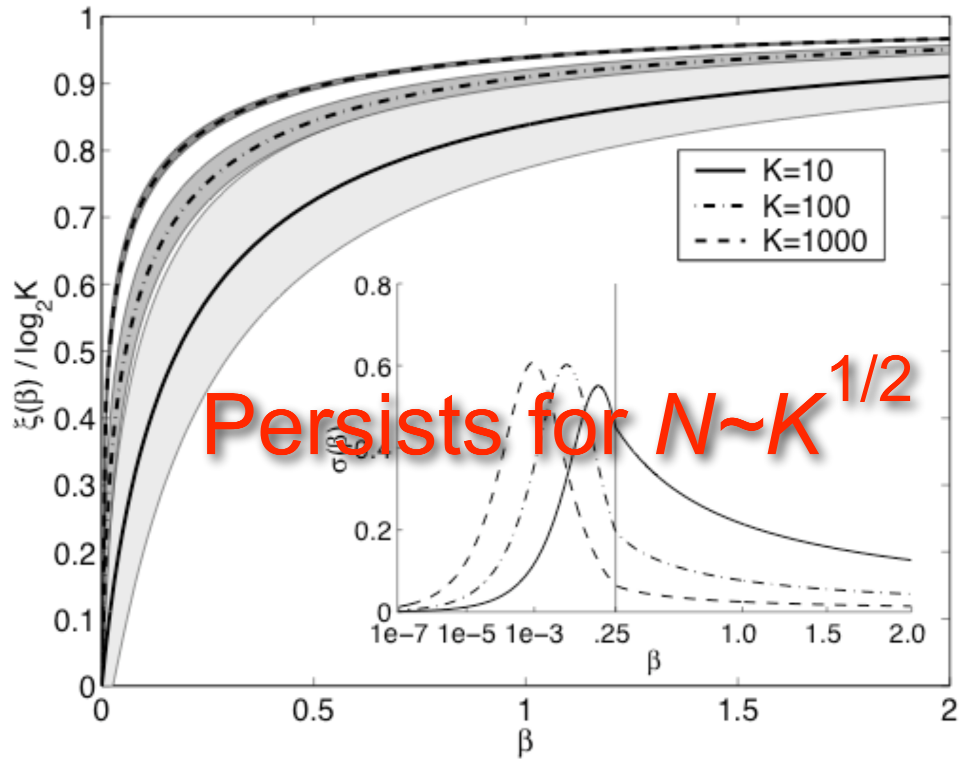


Uniformize on *S*

$$P_\beta(\{q_i\},\beta) = \frac{1}{Z}\,\delta\left(1-\sum_{i=1}^{K} q_i\right)\prod_{i=1}^{K} q_i^{\beta}\,\left.\frac{dS}{d\beta}\right|_{N=0} P(S|_{N=0})$$

- A delta-function sliding along the a priori entropy expectation.
- This is also Bayesian model selection (small β large phase space)
- Have error bars (dominated by posterior variance in β, not at fixed β).

For large *K*

- The problem is more severe.
- Uniformize on *S* (approximately).
- Will work for a certain type of distributions only.

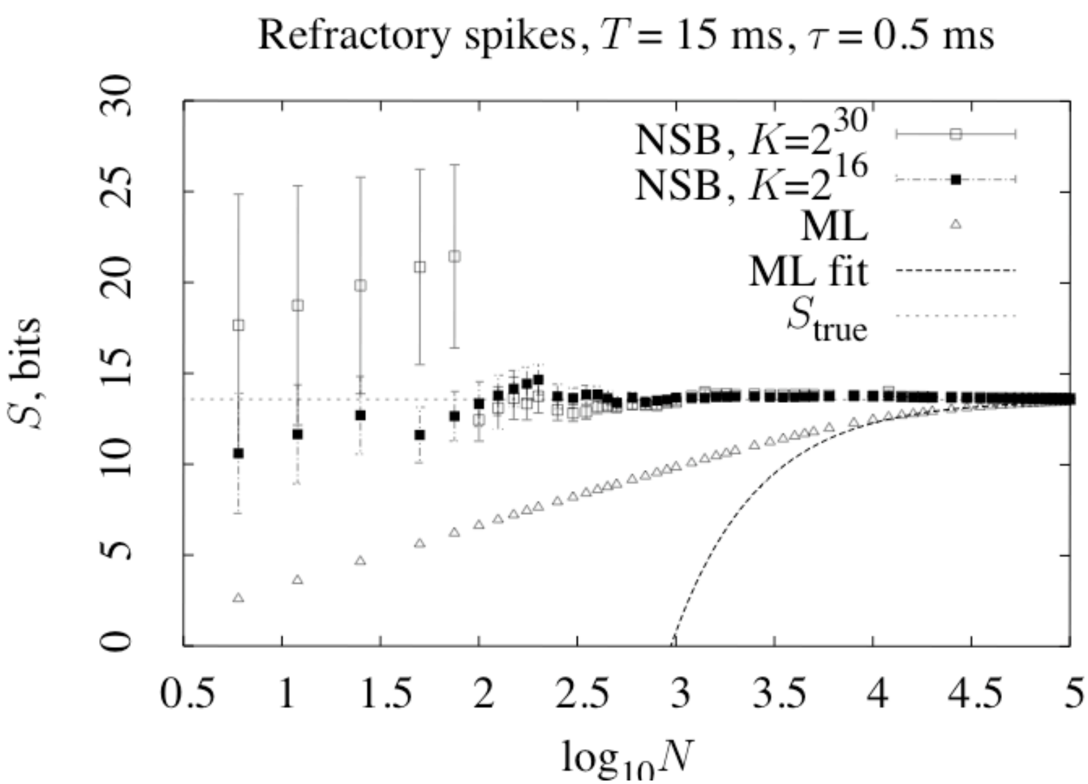
For NSB solution

- Posterior variance scales as $1/\sqrt{N}$
- Little bias, except for distribution with long rank-order tails.
- Counts coincidences and works in Ma regime (if works).
- Is consistent.
- Allows infinite *K*

(Nemenman et al. 2002, Nemenman 2003)

Synthetic test

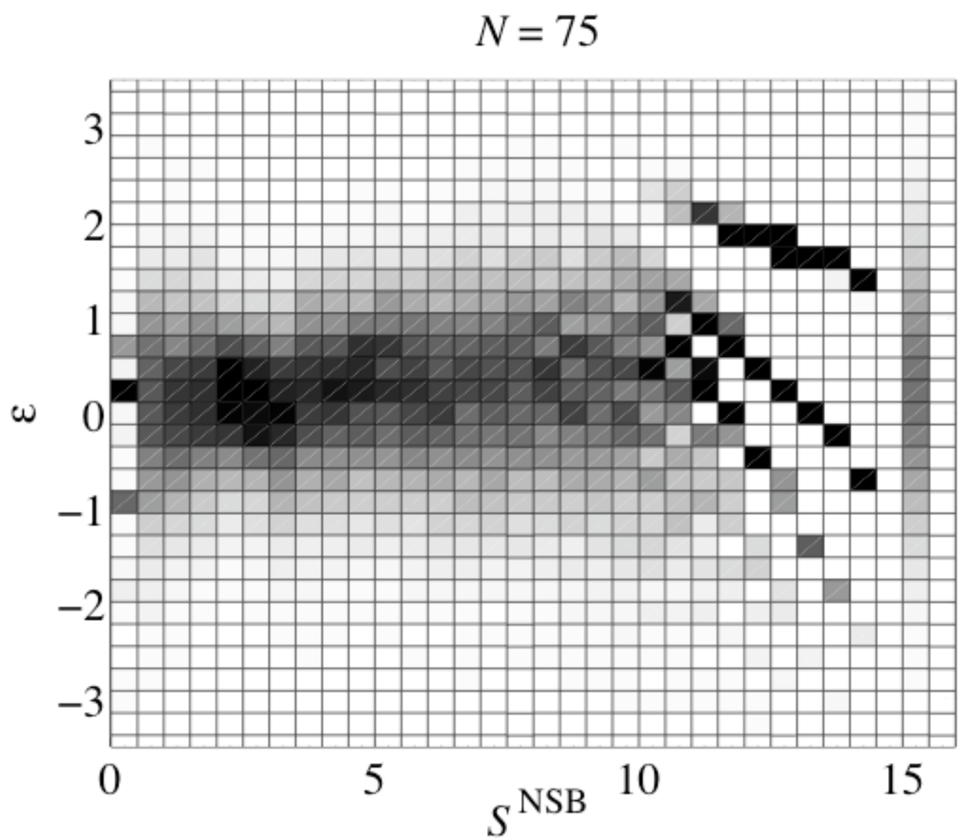
Refractory Poisson, rate 0.26 spikes/ms, refractory period 1.8 ms, *T*=15ms, discretization 0.5ms, true entropy 13.57 bits.



- Estimator is unbiased if consistent and self-consistent.
- Always do this check.

(Nemenman et al. 2004)

Natural data (all S)



$$\varepsilon = \frac{S^{NSB}(N) - S}{\delta S^{NSB}(N)}$$

$$\approx \frac{S^{NSB}(N) - S(N = \max)}{\delta S^{NSB}(N)}$$

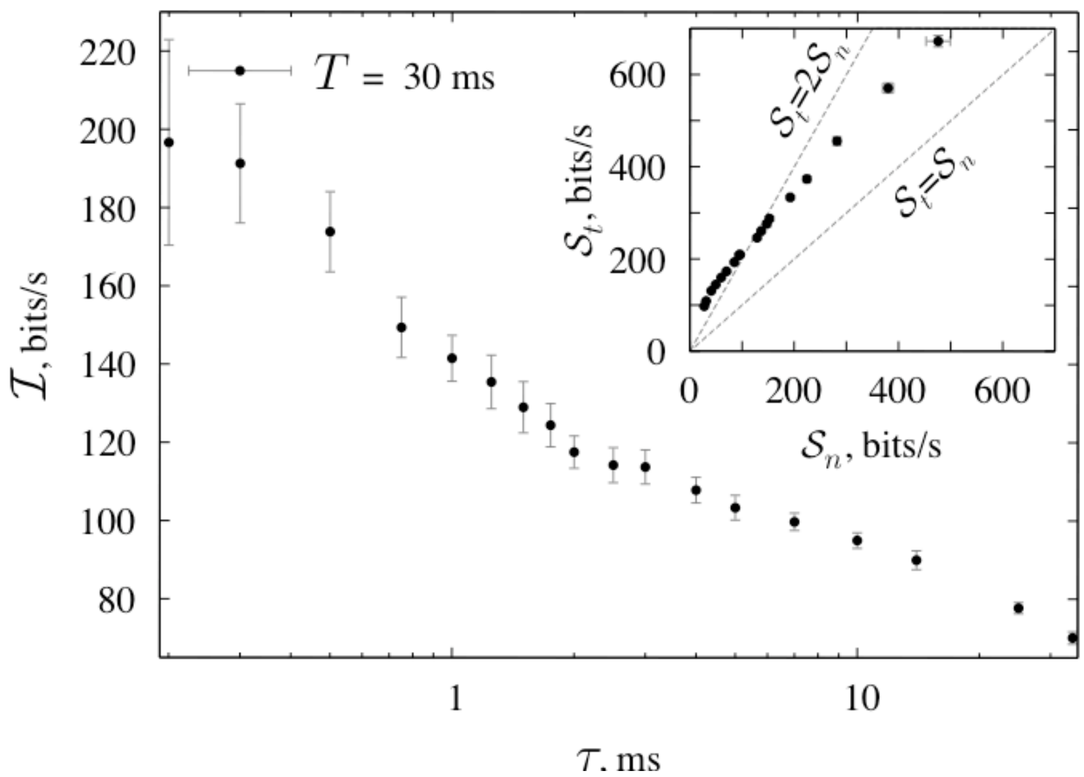
Max=196 repeats

(Nemenman et al. 2004)

Neural code: What remains hidden?

- Given entropy of slices, find the mean noise entropy with error bars (slice entropies are correlated and bimodal).
- Samples for total entropy are also correlated and have long tailed Zipf plots.
- For very fine discretizations and *T*~30ms need extrapolation.

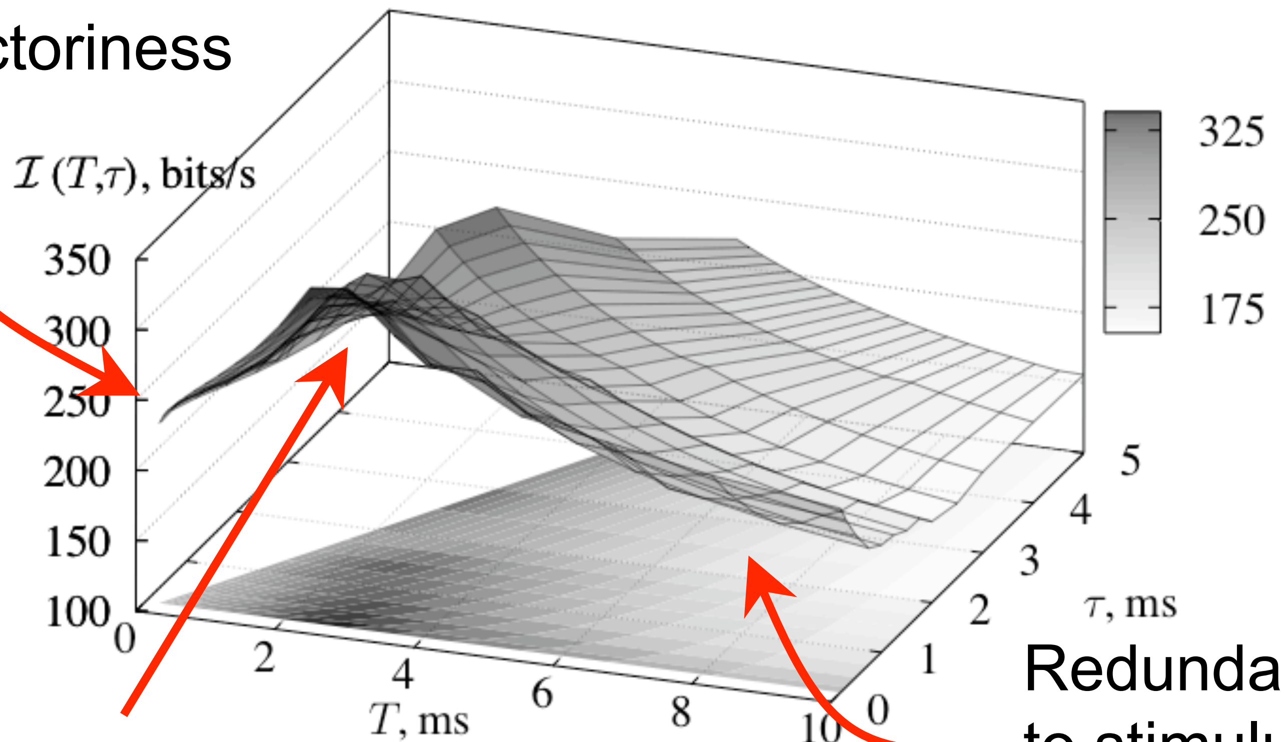
Information rate at T=30ms



- Information present up to τ =0.2-0.3 ms
- 30% more information at τ<1ms. Encoding by refractoriness?
- ~1 bit/spike at 170 spikes/s and low-entropy correlated stimulus. Design principle?
- Efficiency >50% for τ >1ms, and ~80% at 30ms. Optimized for natural statistics?

Synergy from spike combinations

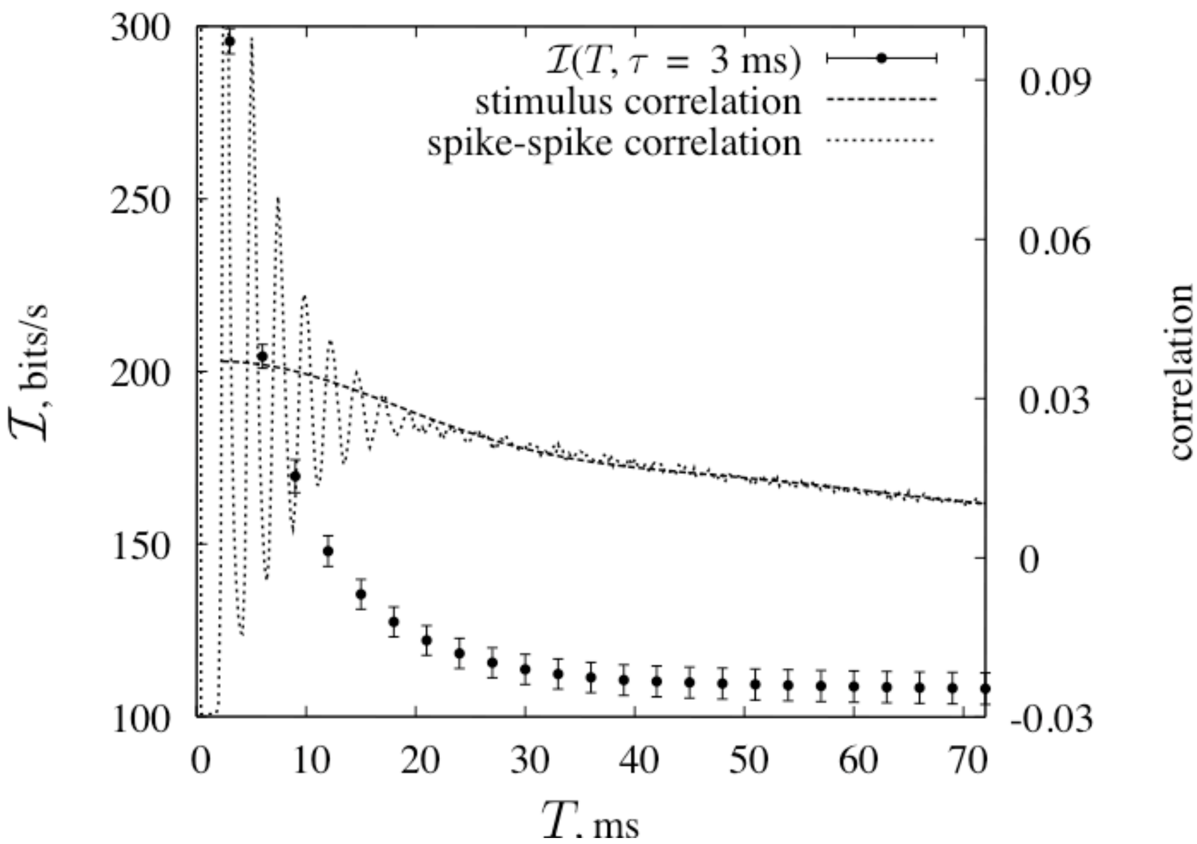
Refractoriness



Spike pairs

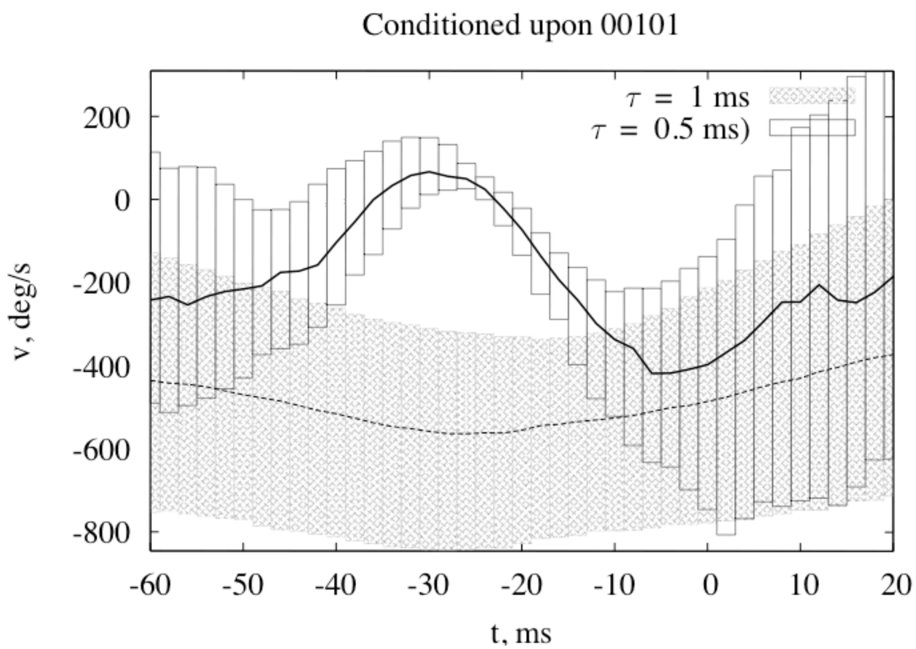
Redundancy due to stimulus

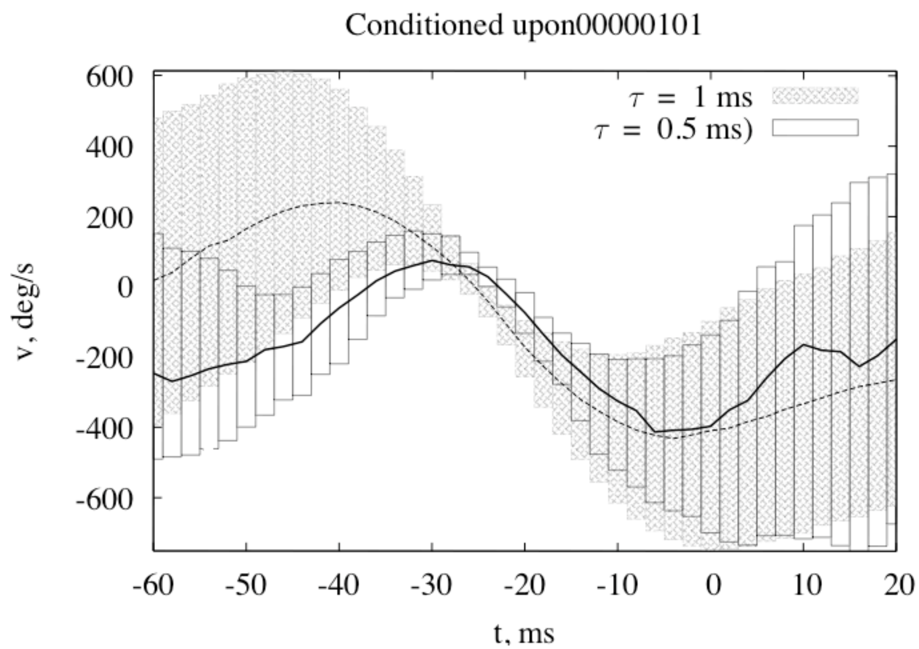
New bits (optimized code)



- Spikes are very regular (15 rings) WKB or liquid decoder? Interspike potential?
- CF at half its value, but fly gets new bits every 30 ms
- Independent info (even though entropies are T dependent).

Information about…



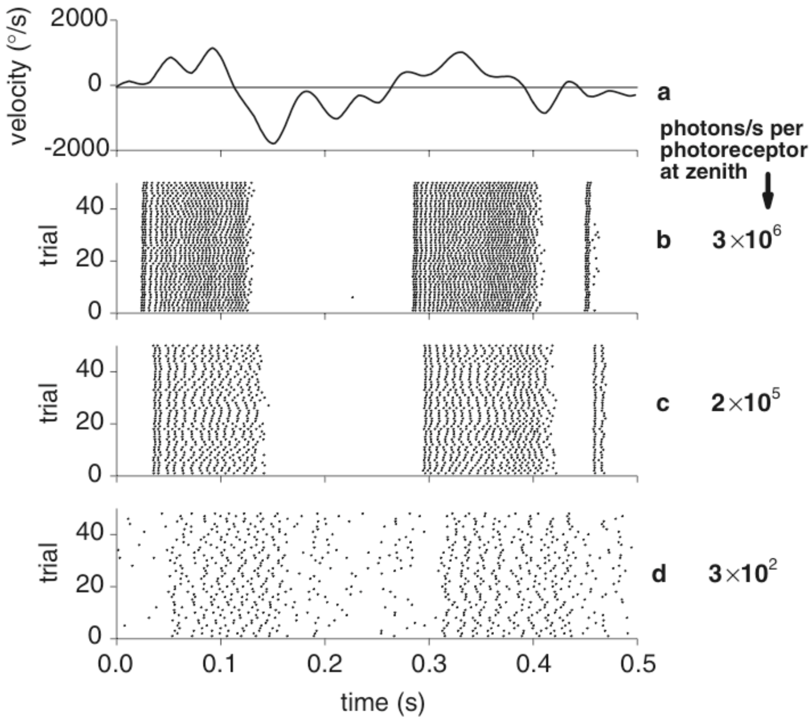


Signal shape

Zero-crossings time

Best estimation at 25ms delay. Little time for reaction.

Precision is limited by physical noise sources



(Lewen, et al 2001)

We see evidence for lowering of the information rate with the light intensity dropping 0.3 log unit from its midday value.

Motion prediction by fly

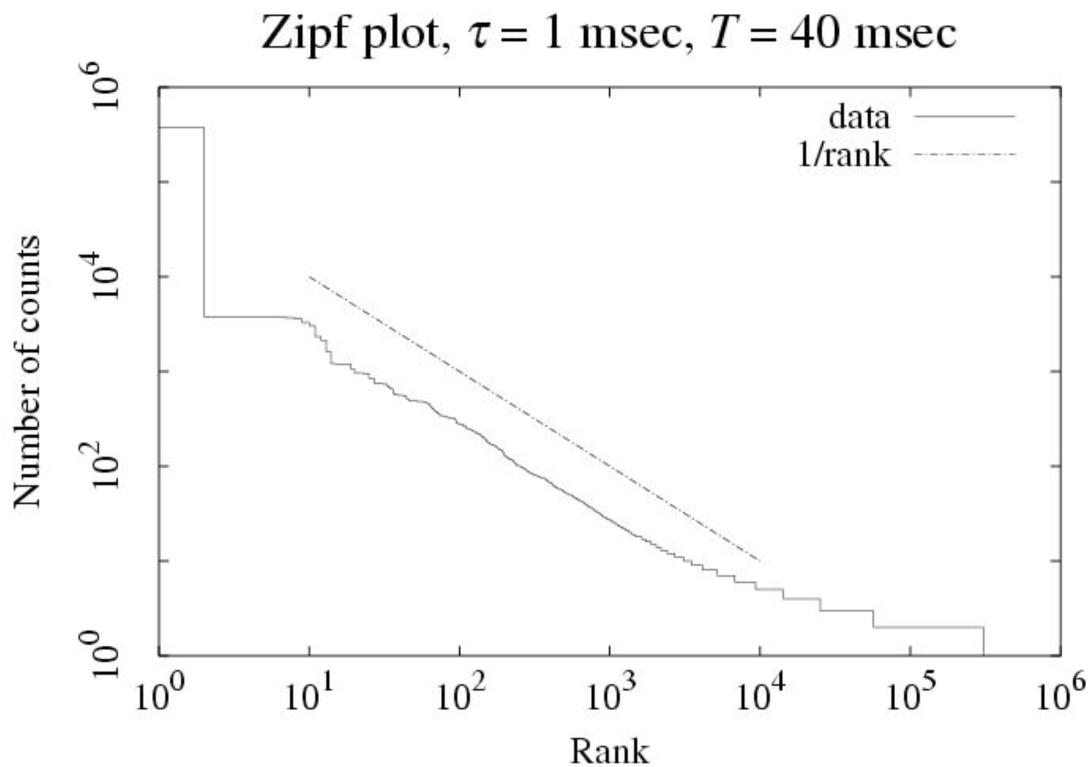
- Receptor delay (sampling) ~8ms
- Correlation time 60ms
- Efficient estimation possible at delays of

$$\sim \sqrt{\lambda\tau} \sim 20 - 25ms$$

- Nicely matches behavioral times
- For 30ms windows, coding at <1ms may be needed.

A very intelligent fly

- One often considers a 1/f rank-order plot as a sign of intelligence.
- But…



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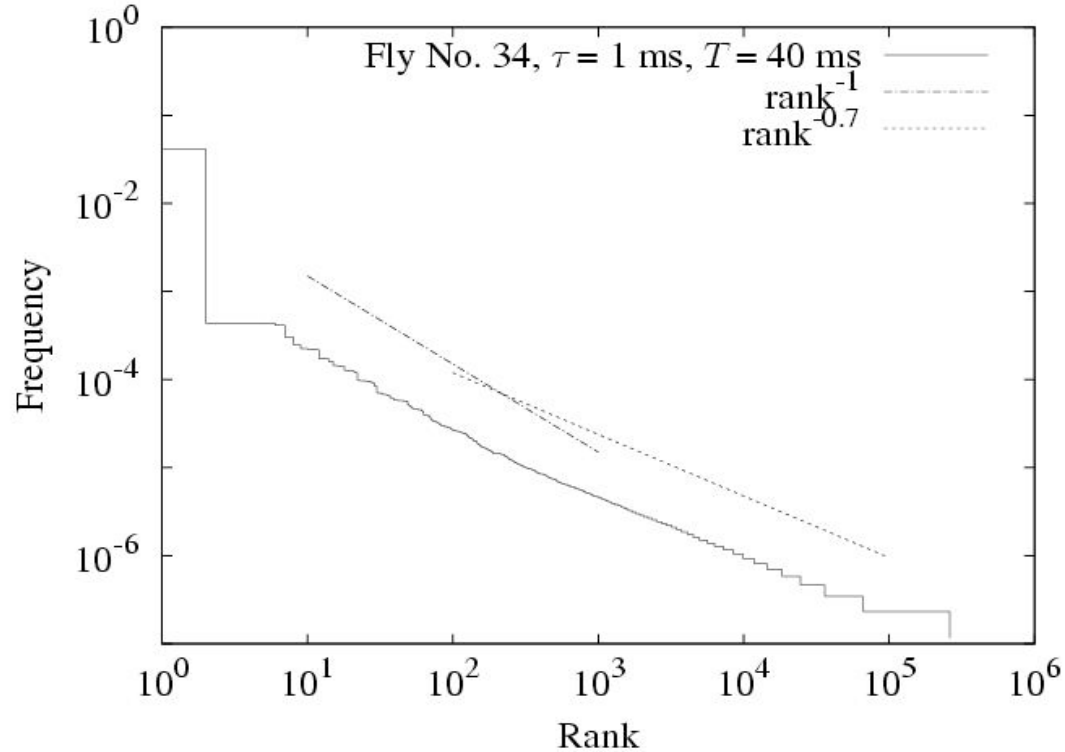

Zipf law may be a result of complexity of the world, not the language.