Estimating information quantities from biological data

Ilya Nemenman

Thanks to: William Bialek, Rob de Ruyter van Steveninck, Fariel Shafee

(UCSB, Princeton University, Indiana University)

http://arxiv.org/abs/physics/0306063
http://arxiv.org/abs/physics/0207009
http://arxiv.org/abs/physics/0108025
http://arxiv.org/abs/physics/0103088

Talk outline

Problem setup Why bother?

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Developing intuition Why hard?

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The method An idea, analysis, asymptotics.

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The method An idea, analysis, asymptotics.
Applications Synthetic and natural neural data.

Entropy and information

Assumptions-free measures of randomness and dependence.

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$$I[x,y,z] = \sum_{x,y,z} q(x,y,z)\,\log\frac{q(x,y,z)}{q(x)q(y)q(z)}\;\ldots$$

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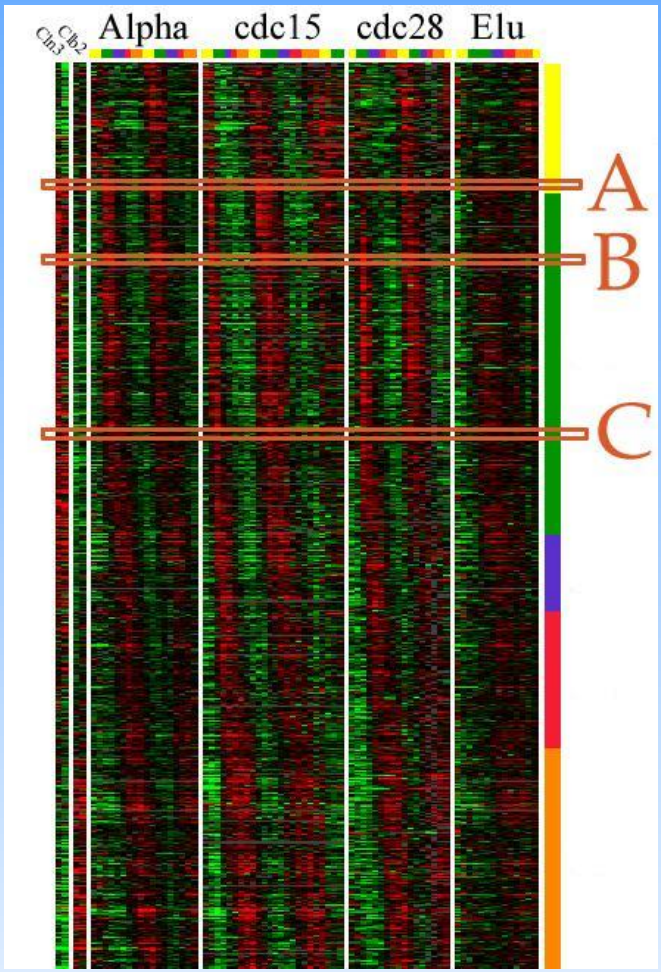
How can we estimate entropy (with error bars) from undersampled data?

A use: Inferring regulatory networks



(Spellman et al., 1998)

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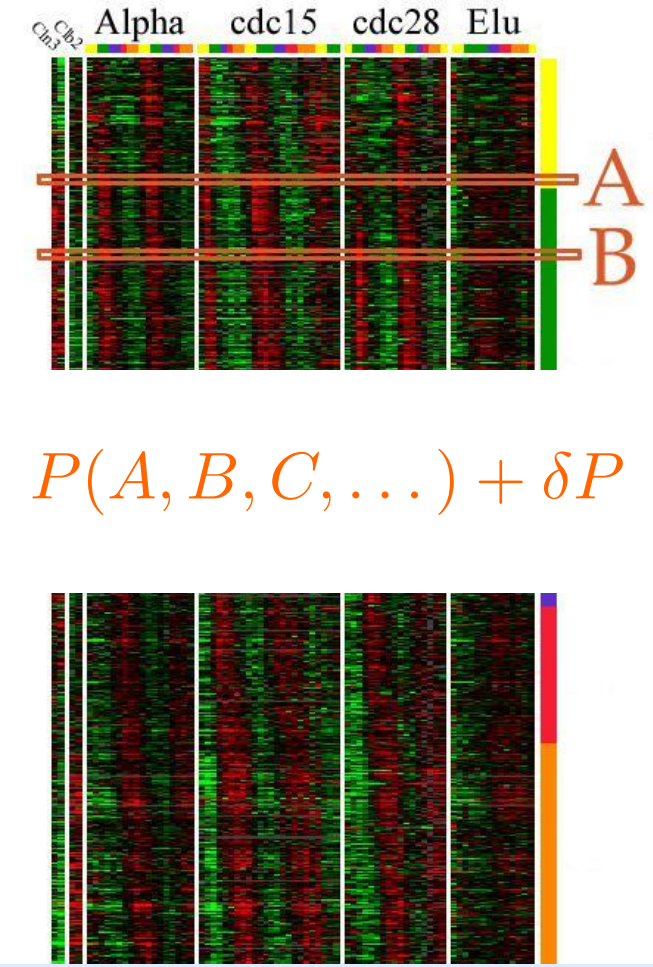

$$P(A, B, C, \ldots) + \delta P$$

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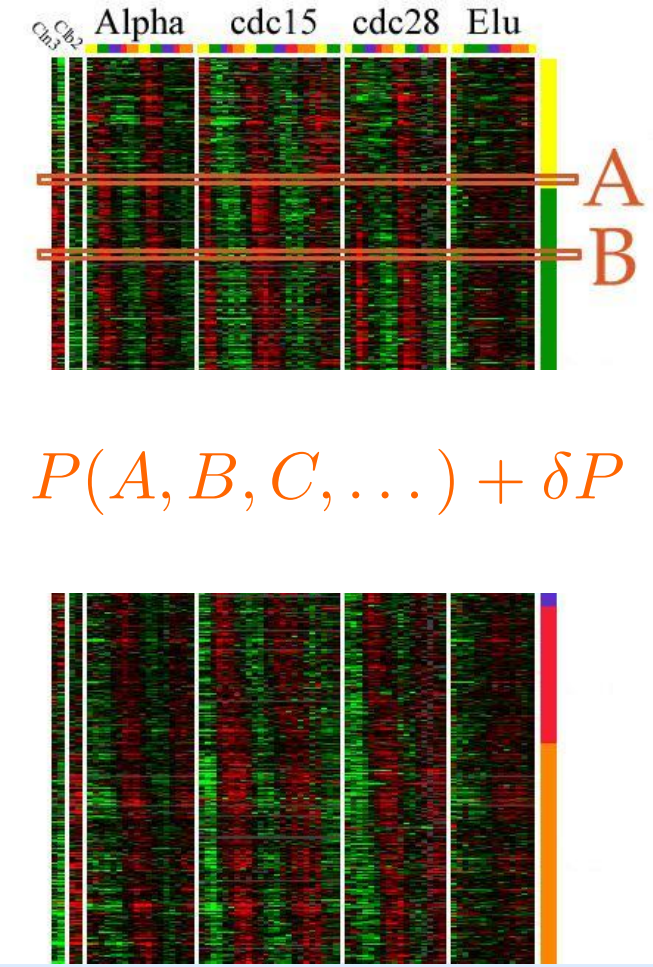

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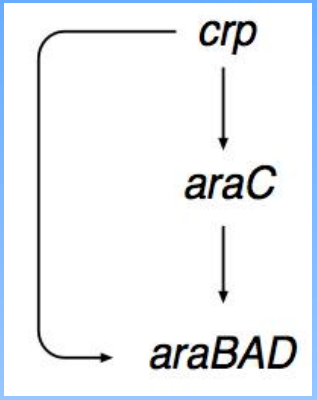
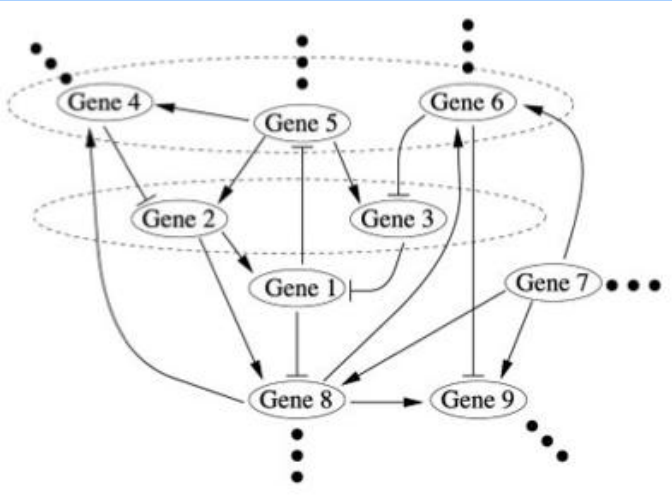
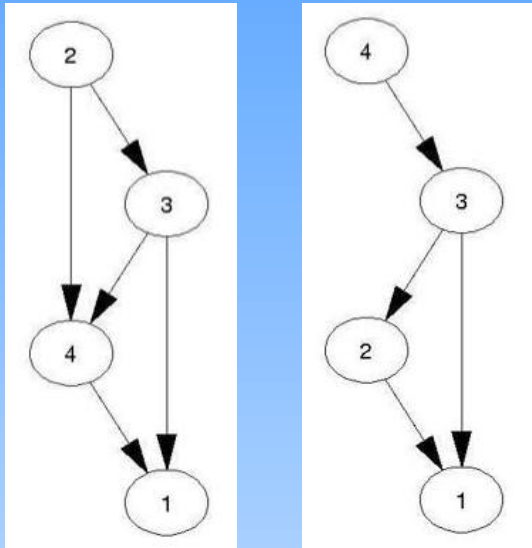


(Shen–Orr et al., 2002)



(Yeung et al., 2002)

. . . but



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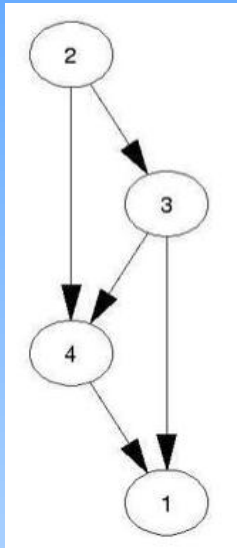

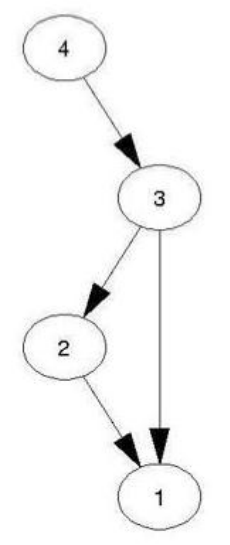

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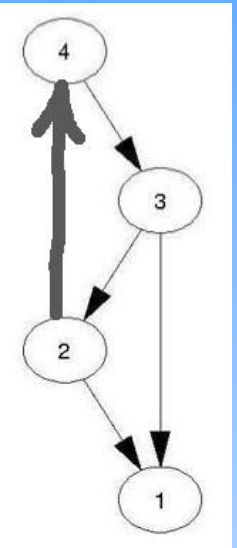

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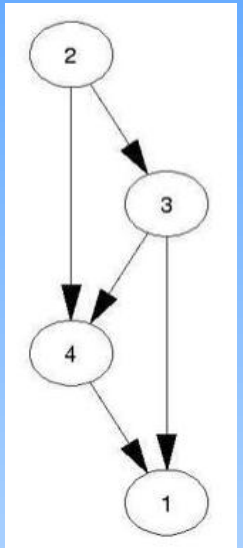

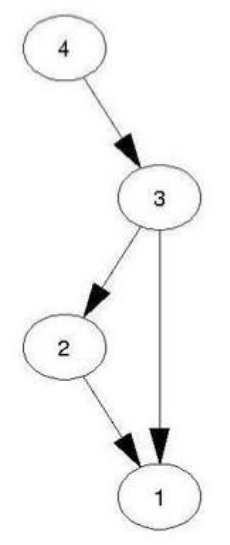

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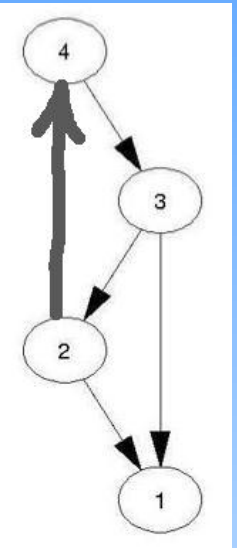

Does the data support the dependence between 2 and 4?

Solved by estimating various multiinformations (Nemenman, 2004).

A use: conserved elements search

$$\cdots x_{-1}x_0 \boxed{x_1 x_2 \cdots x_N} \underbrace{\cdots}_{D} \boxed{x_{N+D+1} x_{N+D+2} \cdots x_{N+D+M}} \cdots$$

x — aminoacid, nucleic acid, angles in the protein structure

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Study predictability $S_D(M|N)$.

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Study predictability $S_D(M|N)$.

- change in S indicates new region (coding–noncoding, helix–sheet,. . .)
- search for conserved sequences (motifs, new structural elements,. . .)
- protein length ~ 100, $N, M, D \sim 10$ — severe undersampling

A use: phylogeny and haplotyping

$$\begin{array}{ccc} & \overbrace{}^{N} & \\ \text{gccta} & \boxed{\text{accGt}} & \text{ggtccatatataaggaa} \\ \text{gccta} & \boxed{\text{accAt}} & \text{ggtccatatatatggac} \\ \text{accta} & \boxed{\text{accAt}} & \text{ggtcgatatataaggac} \end{array}$$

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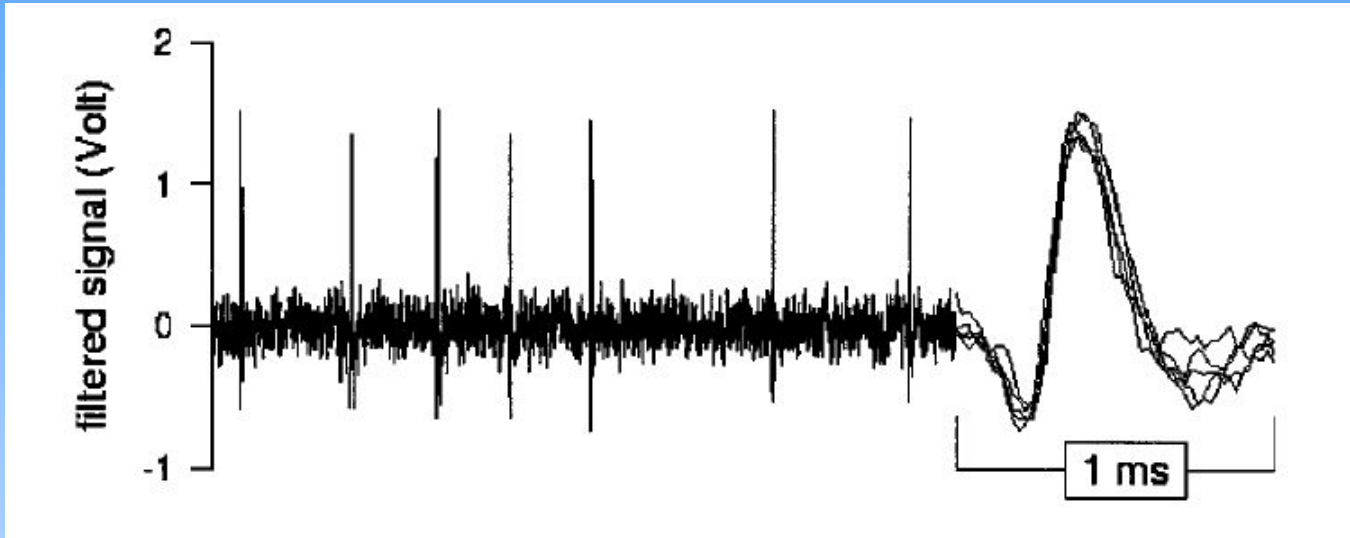
- length $10^6 \ldots 10^9$
- N up to 20
- < 100 repeats

Severe undersampling.

Other uses

- information transmission in molecular cell signals
- cross–compression: comparative texts analysis (authorship of texts, similarity between languages,. . .)
- financial data and other prediction games
- dimensions of attractors in dynamical systems

Neurophysiological applications



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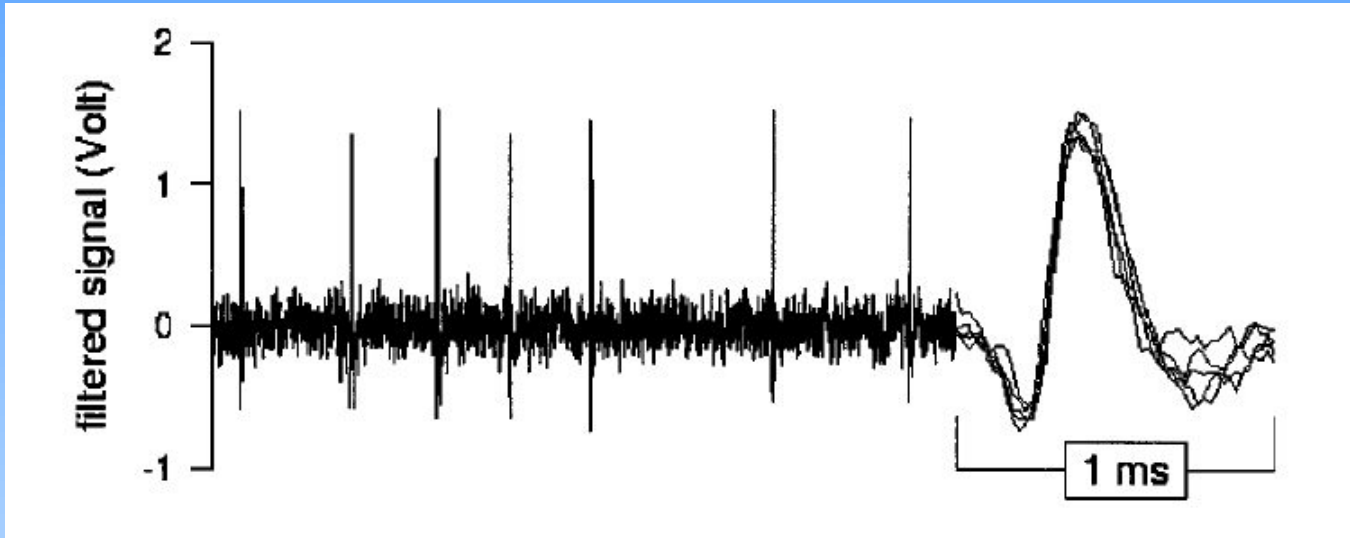

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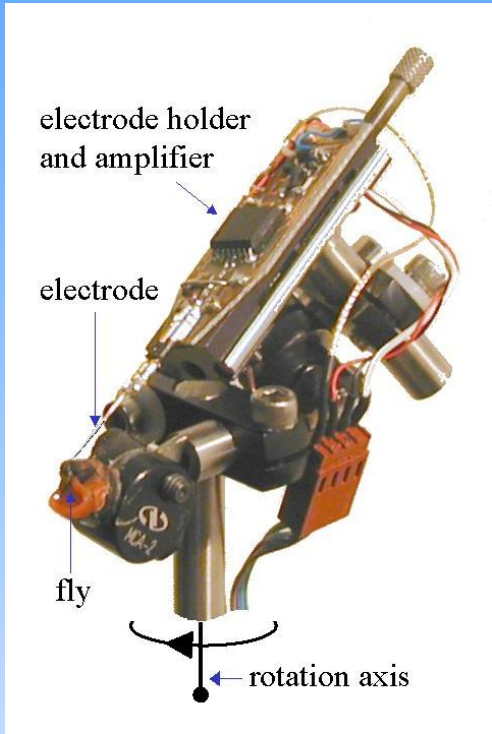
Neurons communicate by stereotypical pulses (spikes). Information is transmitted by spike rates and (possibly) precise positions of the spikes.

Experimental setup



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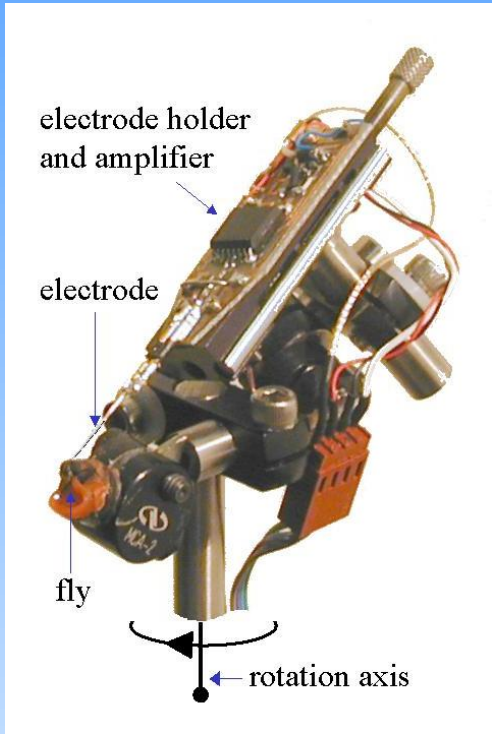

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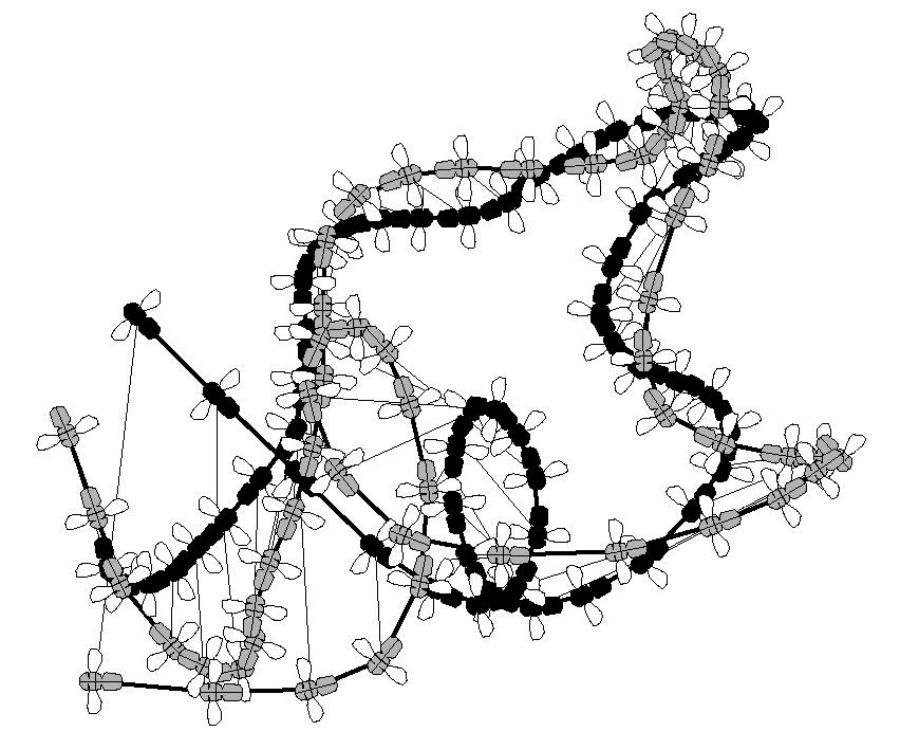
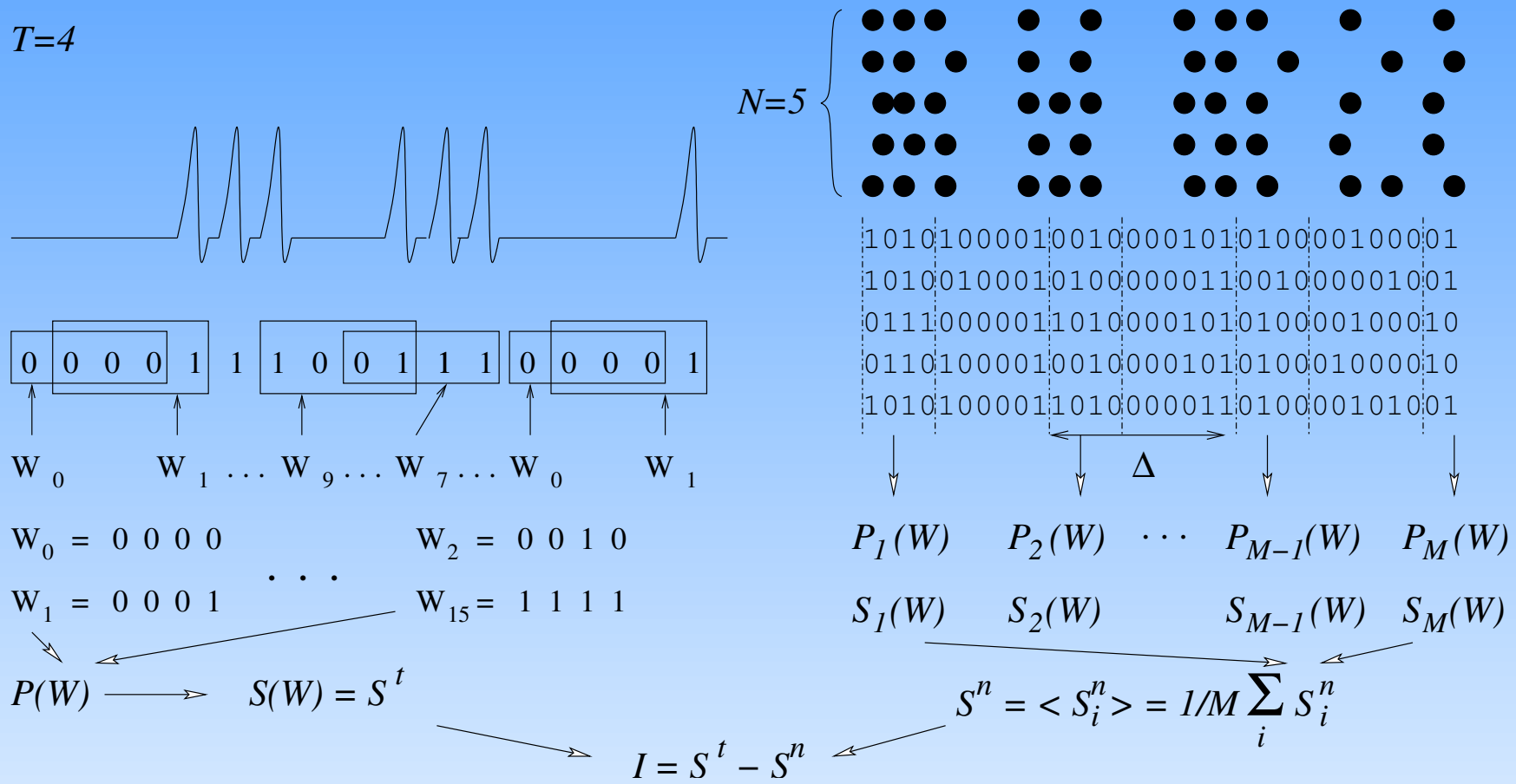


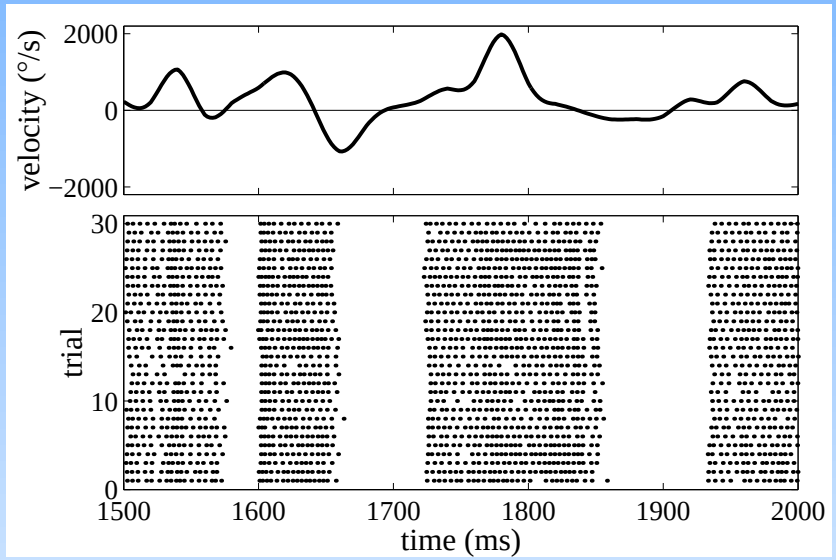
(Bialek and de Ruyter van Steveninck, 2002; Land and Collett, 1974)

Estimating information rate in spike trains



Recordings and problems

100–200 repeats of 5–10 s roller coasters rides



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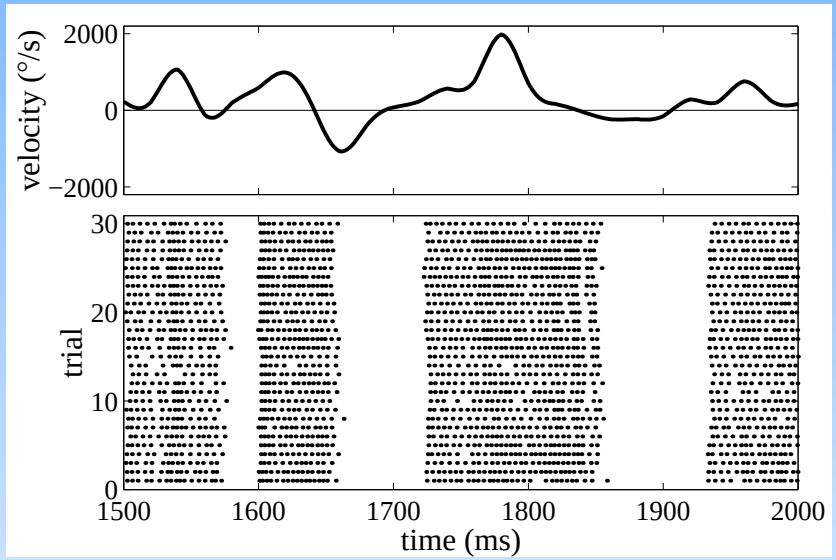

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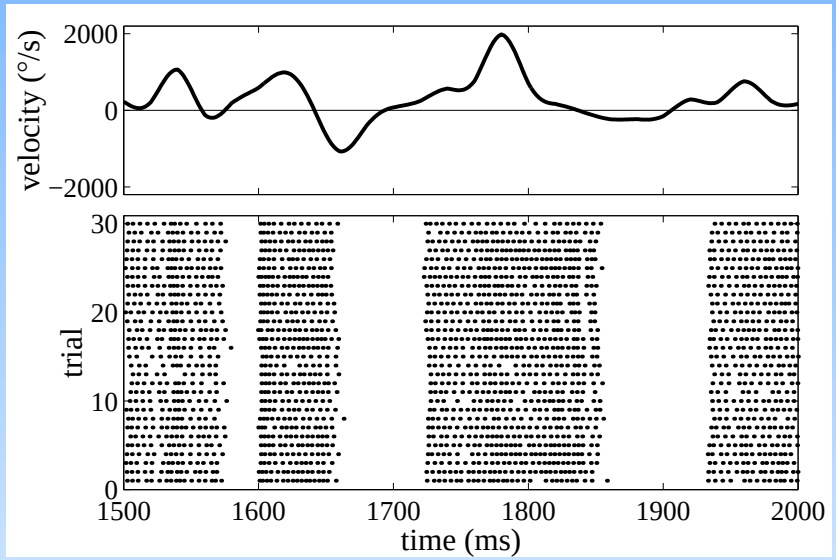

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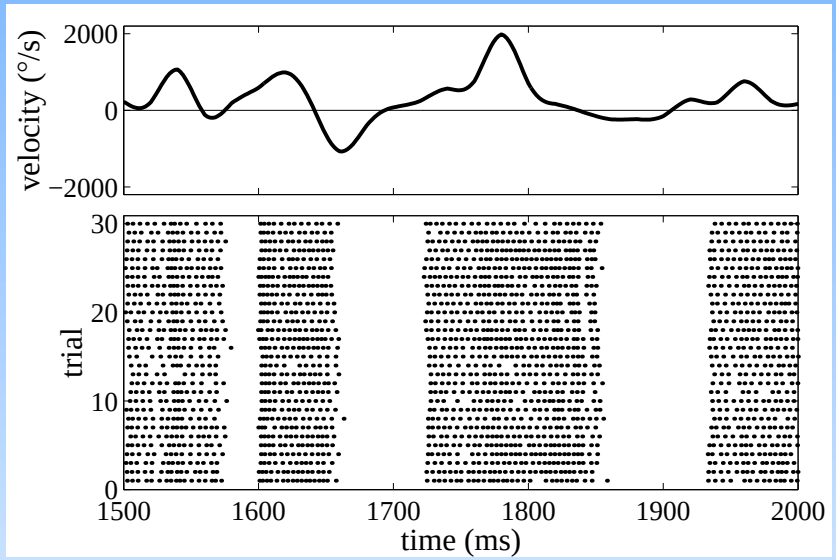

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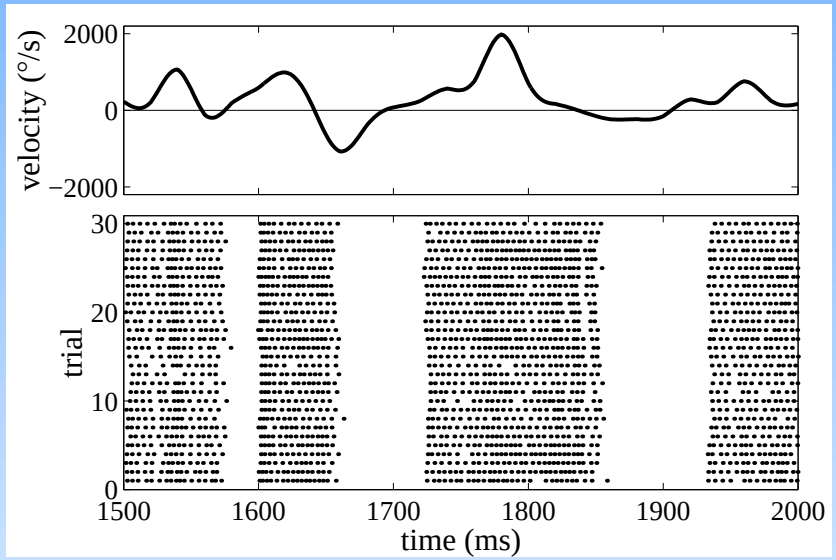

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Need to estimate entropies of words of length ~ 40 from < 200 samples. Undersampled!

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$$S_{\mathrm{ML}} \equiv -\hat{p}\log\hat{p} - (1-\hat{p})\log(1-\hat{p})$$ is convex

$$\Longrightarrow \quad E\,S_{\mathrm{ML}} < S(E\,\hat{p}) = S(p)$$

unknown negative bias, variance is much smaller

- no finite variance universally consistent unbiased entropy estimators for $N \ll K$, including string matching (Grassberger, 2003; Antos and Kontoyiannis, 2002; Wyner and Foster, 2003)
- no universally consistent multiplicative estimator (Batu et al., 2002)
- universal consistent entropy estimation is possible only for $K/N \to \mathrm{const}$, $K \to \infty$ (Paninski, 2003)
- bias–variance balanced estimators built for $K/N \to \mathrm{const}$, $K \to \infty$ (Paninski, 2003; Grassberger, 1989, 2003)

Correcting for bias

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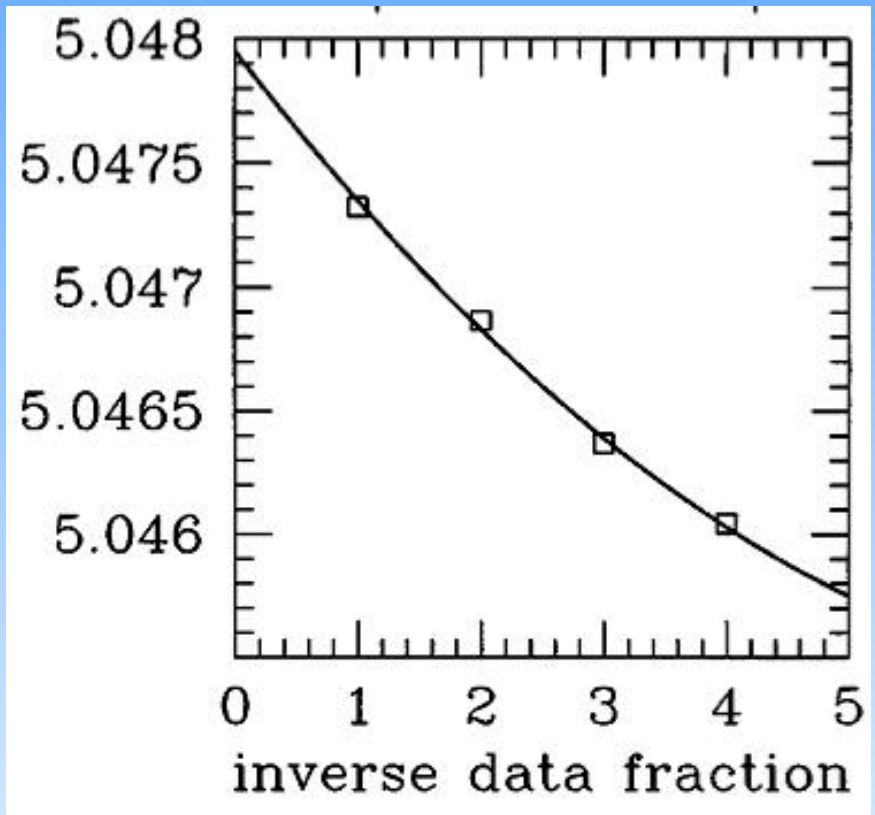

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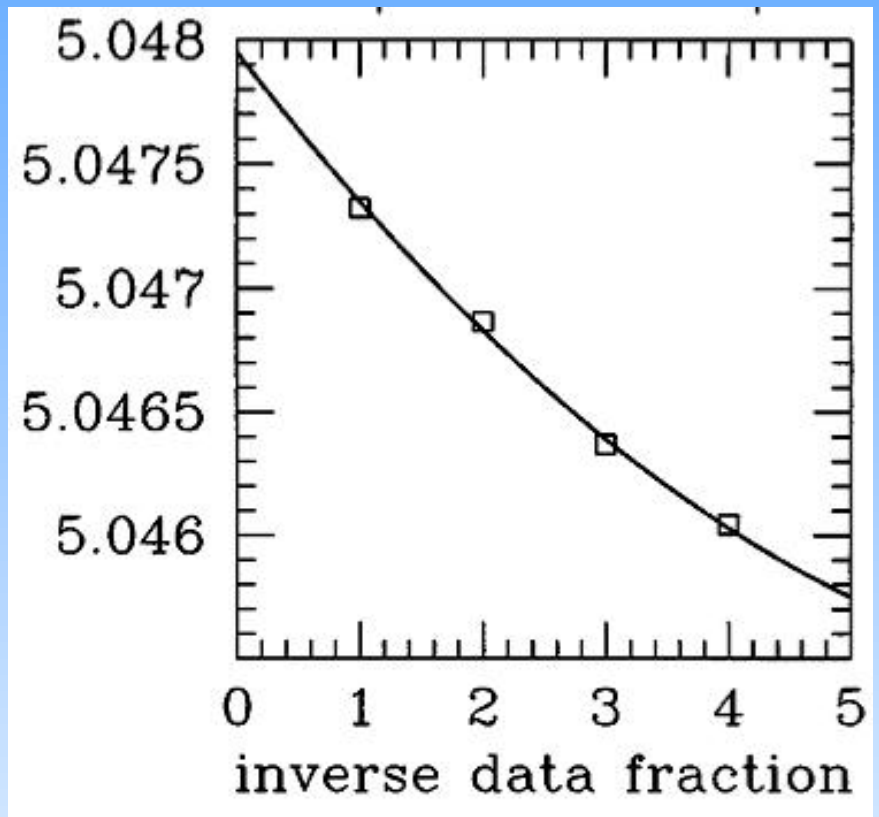
- ALL WORK FOR $2^S \ll N \ll K$



(Strong et al., 1998)

The hope

Ma's (1981) argument, the birthday problem.

For uniform K–bin distribution: for $N_c \sim \sqrt{K}$, probability of coincidences ~ 1.

$$S = \log K \approx \log N_c^2 = 2 \log N_c$$

Works in nonasymptotic regime $N \sim \sqrt{2^S}$. Better than it should!

$\delta S \sim 1$, but this is all we often need.

Extensions?

For Ma–type ideas to work for nonuniform cases

- forget universality, make assumptions about distributions
- do not learn distributions, learn entropies
- equate smoothness and long tails as high entropy (rapidly decaying Zipf plot)

Learning with nearly uniform priors

(ultra–local, Dirichlet priors)

$\{q_i\}$, $i = 1 \ldots K$:

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

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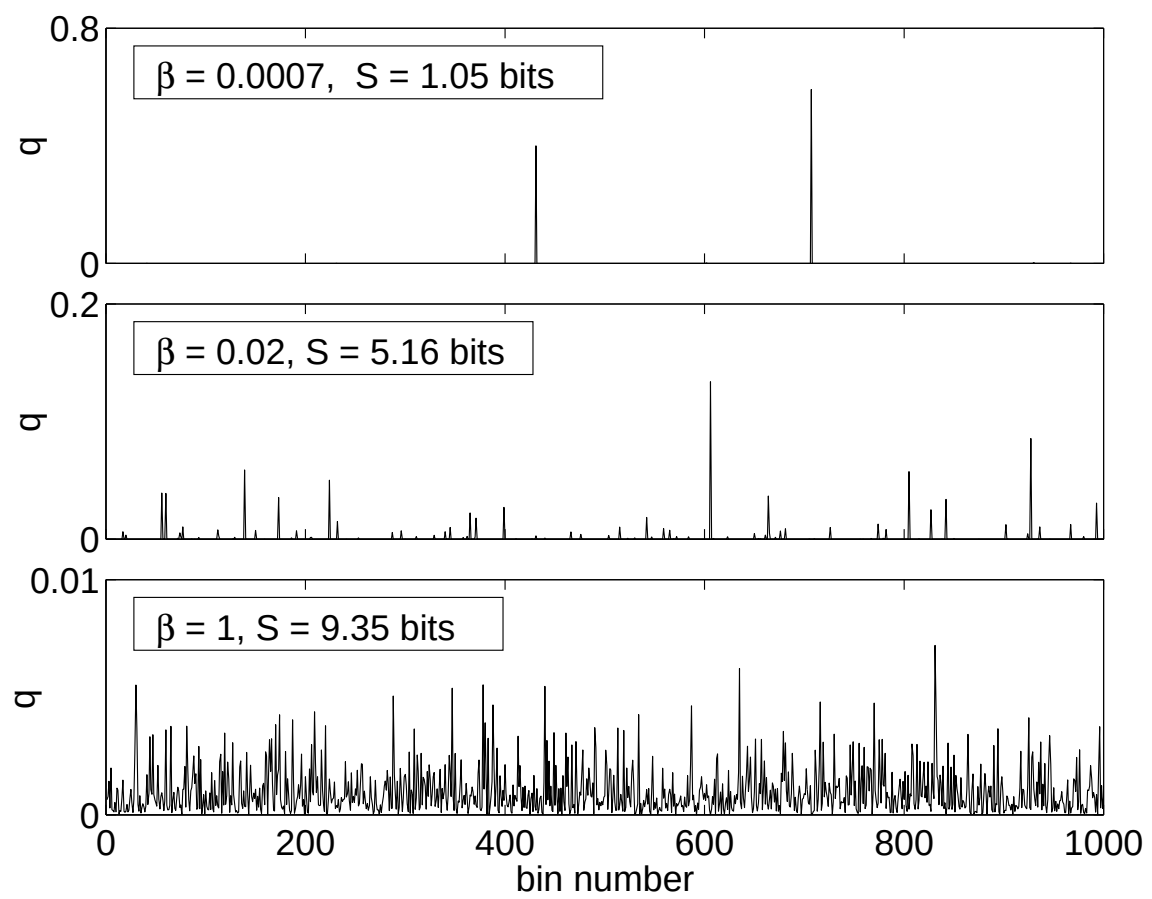
Some common choices:

Maximum likelihood	$\beta \to 0$
Laplace's successor rule	$\beta = 1$
Krichevsky–Trofimov (Jeffreys) estimator	$\beta = 1/2$
Schurmann–Grassberger estimator	$\beta = 1/K$

Typical distributions for $K = 1000, S \approx 9.97$



Typical rank–ordered plots

$$q_i \approx 1 - \left[\frac{\beta B(\beta, \kappa - \beta)(K-1)\, i}{K}\right]^{1/(\kappa-\beta)}, \quad i \ll K\,,$$

$$q_i \approx \left[\frac{\beta B(\beta, \kappa - \beta)(K-i+1)}{K}\right]^{1/\beta}, \quad K - i + 1 \ll K$$

Usually only the first regime is observed.

Gets to zero at finite i.

Faster decaying – too rough.

Slower decaying – too smooth.

Bayesian inference with Dirichlet priors

$$
\begin{aligned}
P_\beta(\{q_i\}|\{n_i\}) &= \frac{P(\{n_i\}|\{q_i\})\mathcal{P}_\beta(\{q_i\})}{P_\beta(\{n_i\})} \\
P(\{n_i\}|\{q_i\}) &= \prod_{i=1}^{K}(q_i)^{n_i} \\
\langle q_i \rangle_\beta &= \frac{n_i+\beta}{N+K\beta}
\end{aligned}
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\langle S \rangle_\beta &= \text{known (Wolpert and Wolf, 1995)} \\
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Equal pseudocounts added to each bin.

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Equal pseudocounts added to each bin.

Larger β means less sensitivity to data, thus more smoothing.

A problem: A priori entropy expectation

$$\mathcal{P}_\beta(S) = \int dq_1 dq_2 \cdots dq_K \, P_\beta(\{q_i\}) \, \delta \left[S + \sum_{i=1}^{K} q_i \log_2 q_i \right]$$

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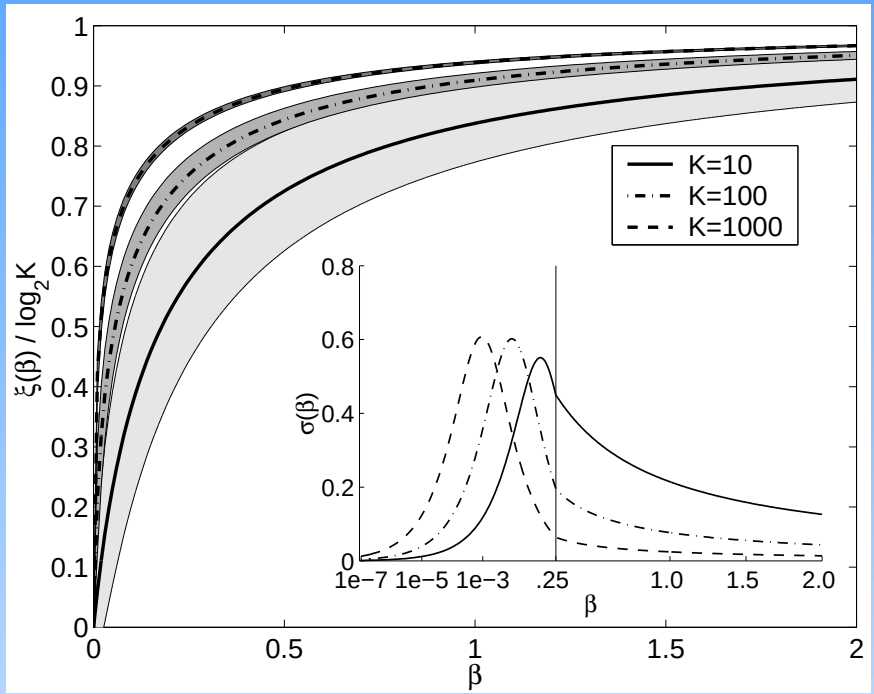
$$\xi(\beta) \equiv \langle \, S|_{N=0} \, \rangle_\beta = \psi_0(K\beta + 1) - \psi_0(\beta + 1)$$

$$\sigma^2(\beta) \equiv \langle \, (\delta S)^2 \big|_{N=0} \rangle_\beta = \frac{\beta + 1}{K\beta + 1} \psi_1(\beta + 1) - \psi_1(K\beta + 1)$$

$\psi_m(x) = (d/dx)^{m+1} \log_2 \Gamma(x)$ –the polygamma function

The problem: Analysis



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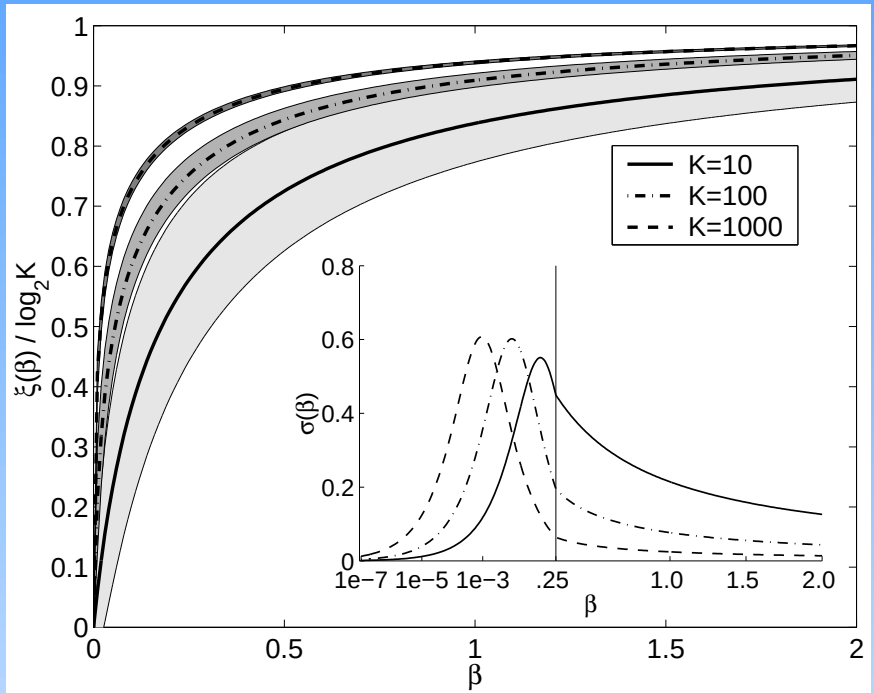

- Because of the Jacobian of $\{q_i\} \to S$, a priori distribution of entropy is strongly peaked.
- *Narrow* peak: $\sigma(\beta) \propto 1/\sqrt{K\beta}$, $\max \sigma(\beta) = 0.61\,\text{bits}$.
- As β varies from 0 to ∞, the peak smoothly moves from 0 to $\log_2 K$. For $\beta \sim 1$, $\xi(\beta) = \log_2 K - O(K^0)$.

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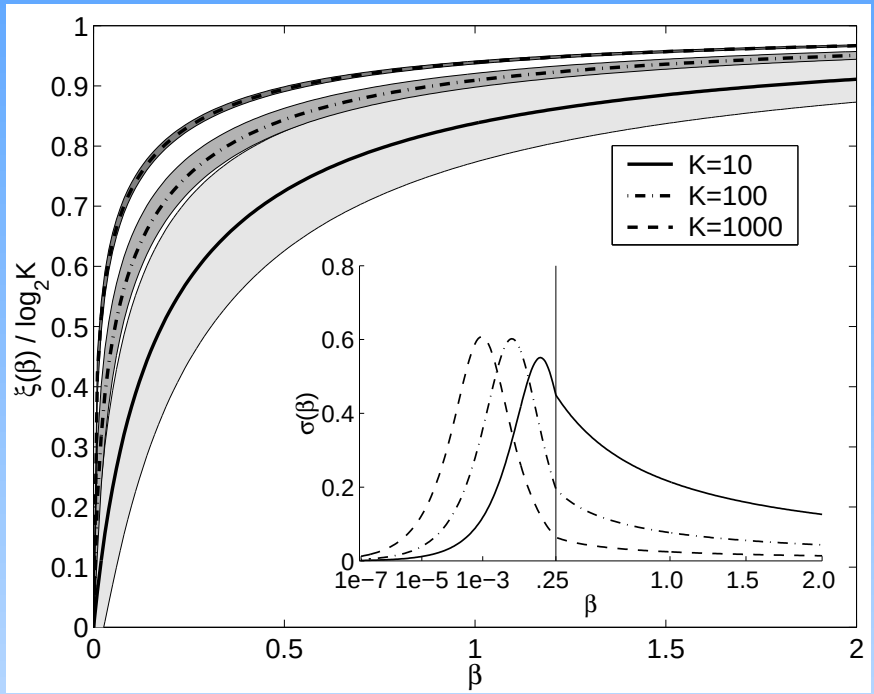

- Because of the Jacobian of $\{q_i\} \to S$, a priori distribution of entropy is strongly peaked.
- *Narrow* peak: $\sigma(\beta) \propto 1/\sqrt{K\beta}$, $\max \sigma(\beta) = 0.61\,\text{bits}$.
- As β varies from 0 to ∞, the peak smoothly moves from 0 to $\log_2 K$. For $\beta \sim 1$, $\xi(\beta) = \log_2 K - O(K^0)$.

- No a priori way to specify β.
- Choosing β fixes allowed "shapes" of $\{q_i\}$, and defines the a priori expectation of entropy.
- Such expectation dominates data until $N \gg K\beta$.
- All common estimators are bad for learning entropies.

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2. $\mathcal{P}(S) \sim 1 = \int \delta(S - \xi) d\xi$. Easy: $\mathcal{P}_\beta(S)$ is almost a δ-function!

Solution

Average over β — infinite Dirichlet mixtures.

$$\mathcal{P}(\{q_i\};\beta) = \frac{1}{Z}\delta\left(1-\sum_{i=1}^{K} q_i\right)\prod_{i=1}^{K} q_i^{\beta-1} \qquad \frac{d\xi(\beta)}{d\beta} \qquad \mathcal{P}(\xi(\beta))$$

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$$\widehat{S^m} = \frac{\int d\xi\,\rho(\xi,\{n_i\})\langle\, S^m[n_i]\,\rangle_{\beta(\xi)}}{\int d\xi\,\rho(\xi,[n_i])}$$

$$\rho(\xi,[n_i]) = \mathcal{P}\,(\xi)\,\frac{\Gamma(K\beta(\xi))}{\Gamma(N+K\beta(\xi))}\prod_{i=1}^{K}\frac{\Gamma(n_i+\beta(\xi))}{\Gamma(\beta(\xi))}\,.$$

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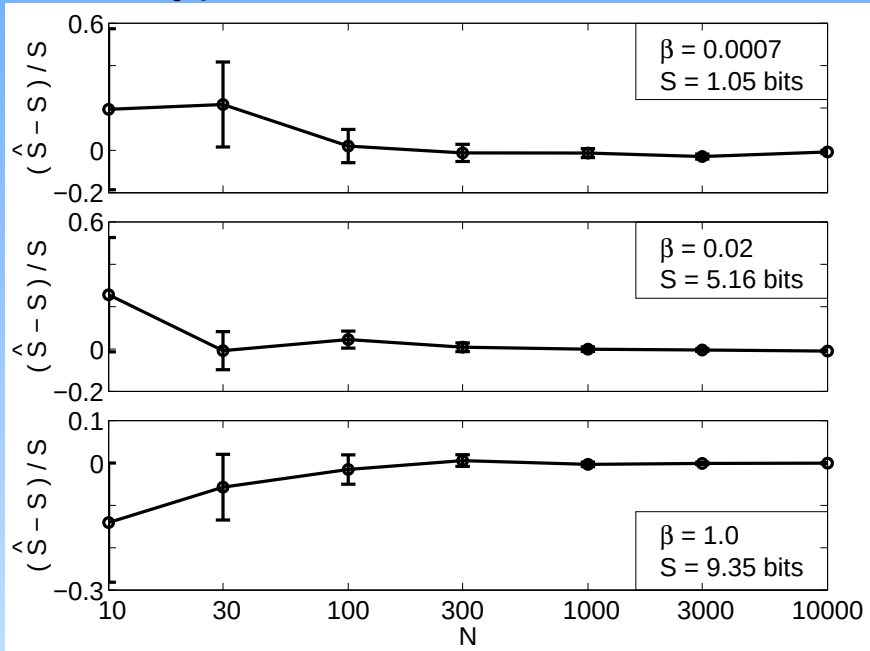
- Smaller β — larger allowed volume in the space of $\{q_i\}$. Thus averaging over β is *Bayesian model selection*.
- $\langle\delta^2 S\rangle$ is dominated by $\langle\delta^2\beta\rangle$ (not $\langle\delta^2 S\rangle_\beta$) which is small if a particular β (model) dominates (is "selected")

First attempts to estimate entropy

Typical distributions



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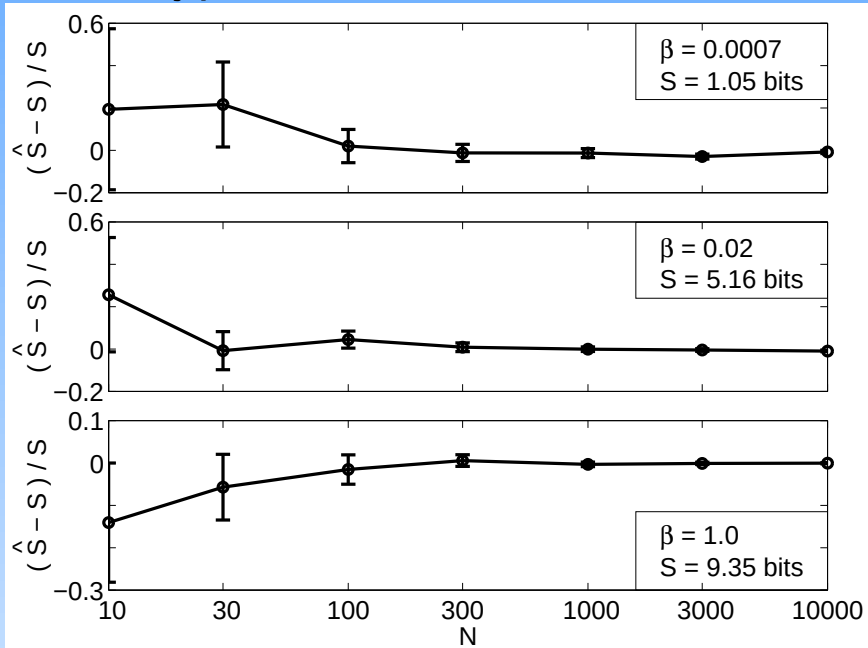
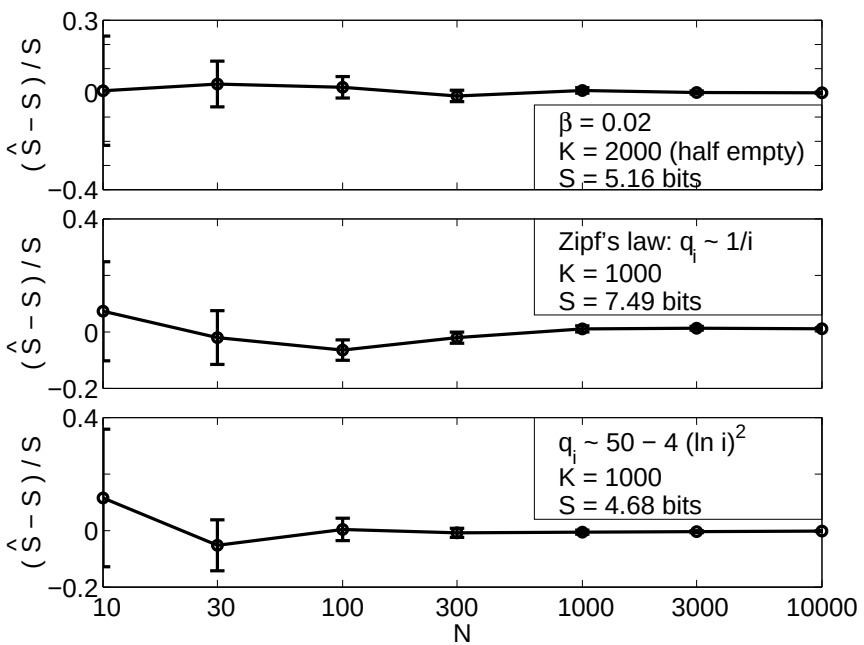


Atypical distributions



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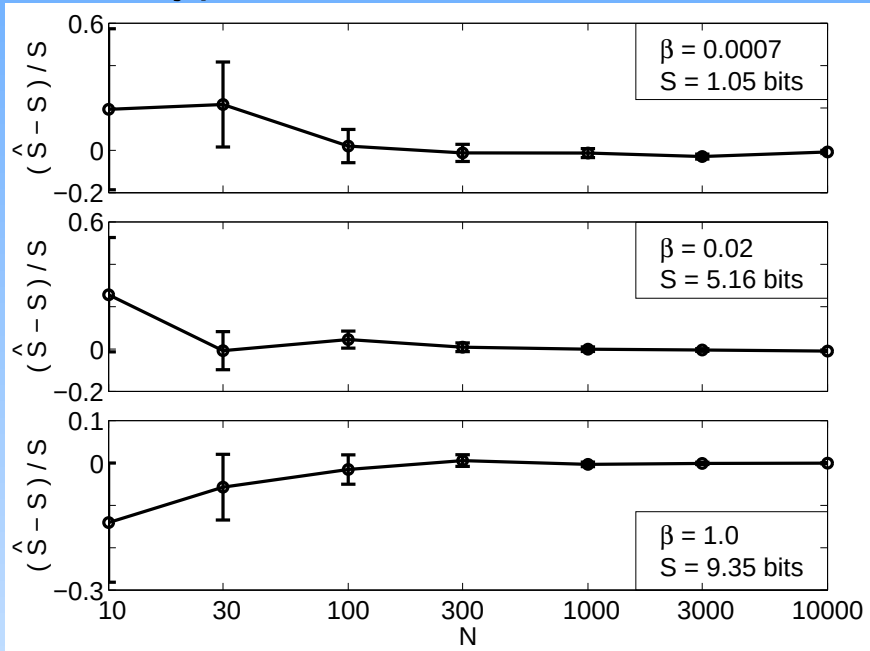

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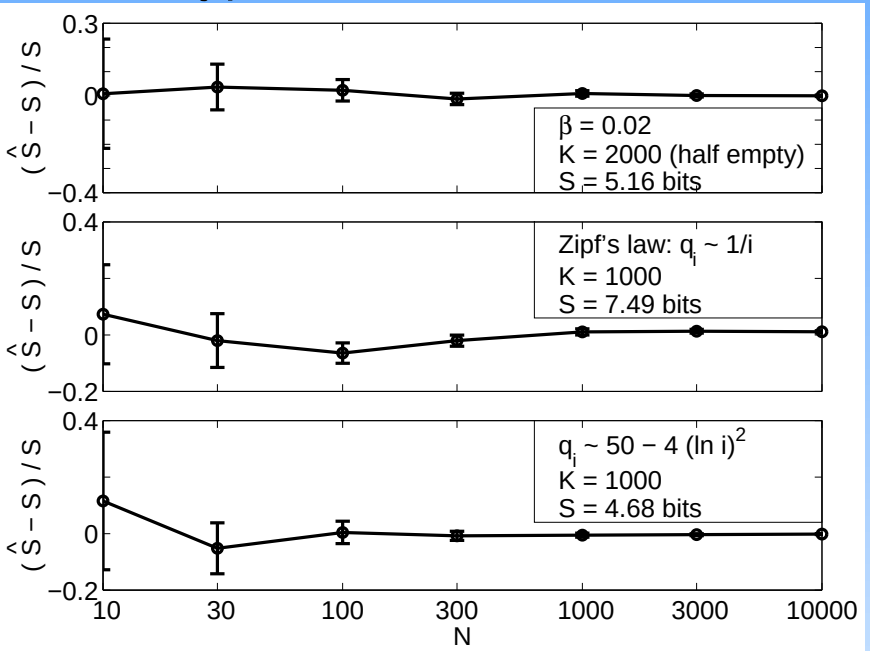

Supports understanding that smoothness = speed of decay of Zipf plot.

Estimating entropy: first observations

- Relative error $\sim 10\%$ at N as low as 30 for $K = 1000$.
- Reliable estimation of posterior error.
- *Little bias*. Exception: too smooth distributions.
- Key point: *learn entropies directly without finding* $\{q_i\}$*!*
- The dominant β stabilizes for typical distributions; drifts down (to complex models) for rough ones and up (to simpler models) for too smooth cases.

Asymptotics

$K \gg 1$, $\Delta \equiv N - K_{\text{counts}>0} \gg 1$

- saddle point works
- $\left.\frac{\partial^2(-\log\rho)}{\partial\xi^2}\right|_{\xi(\beta^*)} = \Delta + NO([\Delta/N]^2)$

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$K, N \gg 1,\ \Delta \sim 1$

- $\widehat{S} \approx (C_\gamma - \ln 2) + 2\ln N - \psi_0(\Delta) + O(\frac{1}{N}, \frac{1}{K})$
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Remember Ma's estimate!

Estimator: Properties

- Uniform prior on S *and* Bayesian model selection

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- Uniform prior on S *and* Bayesian model selection
- K can be infinite
- Works for $\Delta \ll N$ if distribution is not atypically smooth.
- Δ matters, not K or N.
- The estimator is consistent.
- Thus correct if self-consistent for subsamples.
- When works, works for $N \sim \sqrt{2^S}$.

Estimator: Synthetic test

Refractory Poisson process: $r = 0.26\text{ms}^{-1}$, $R = 1.8\text{ms}$, $T = 15\text{ms}$, $\tau = 0.5\text{ms}$.

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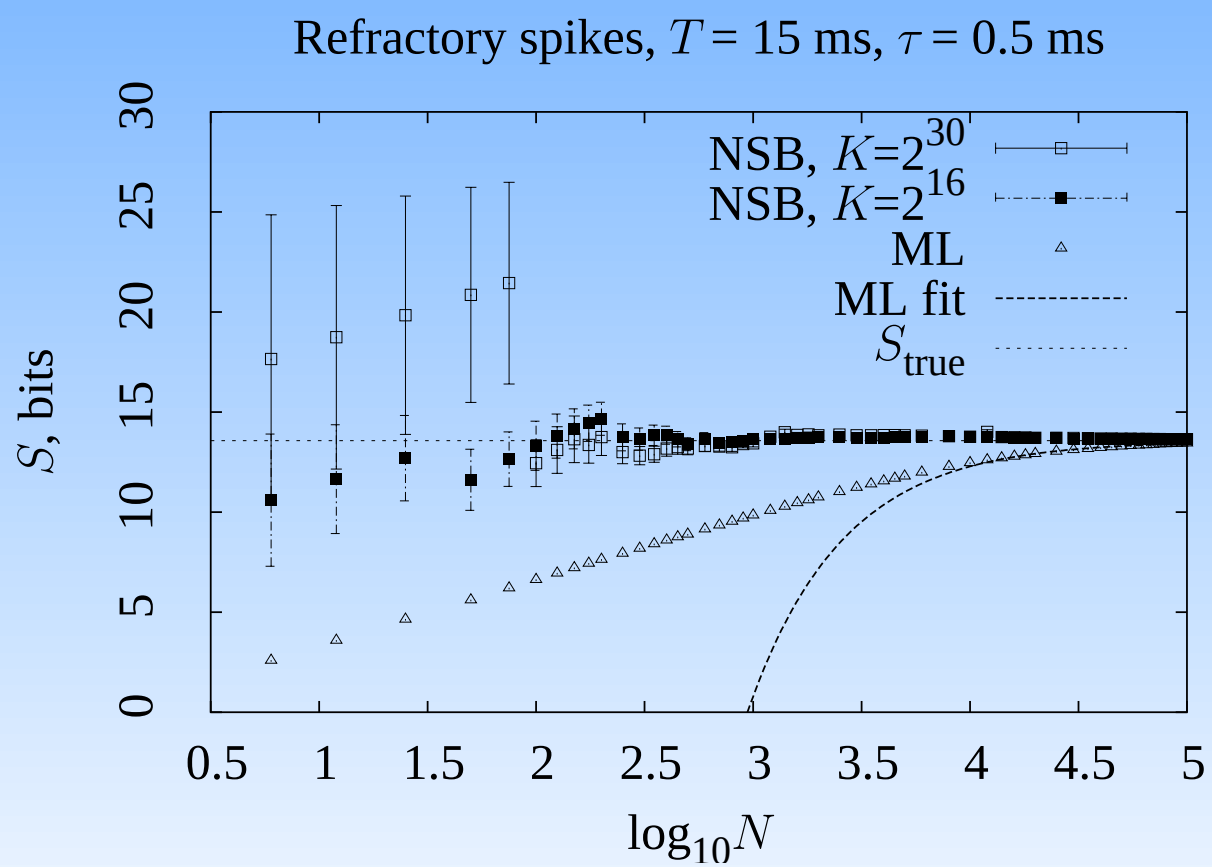

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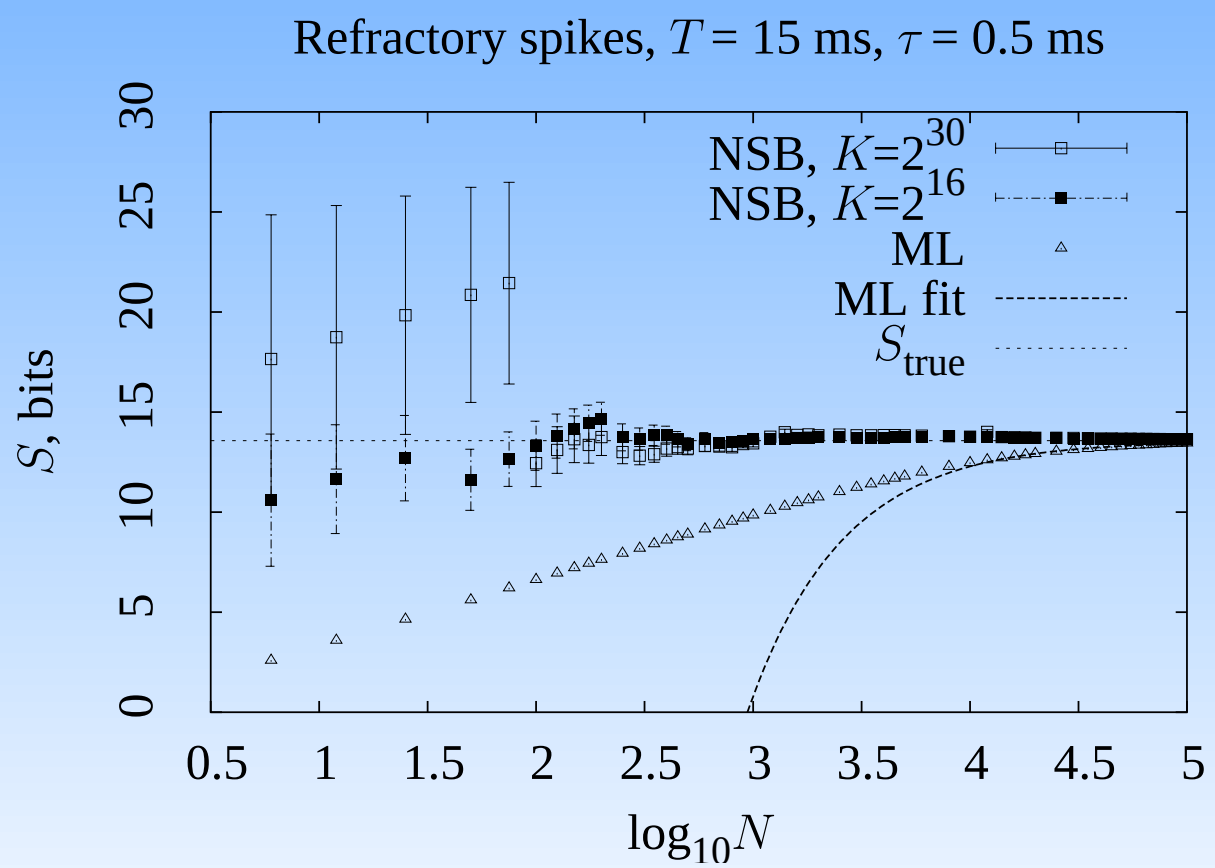
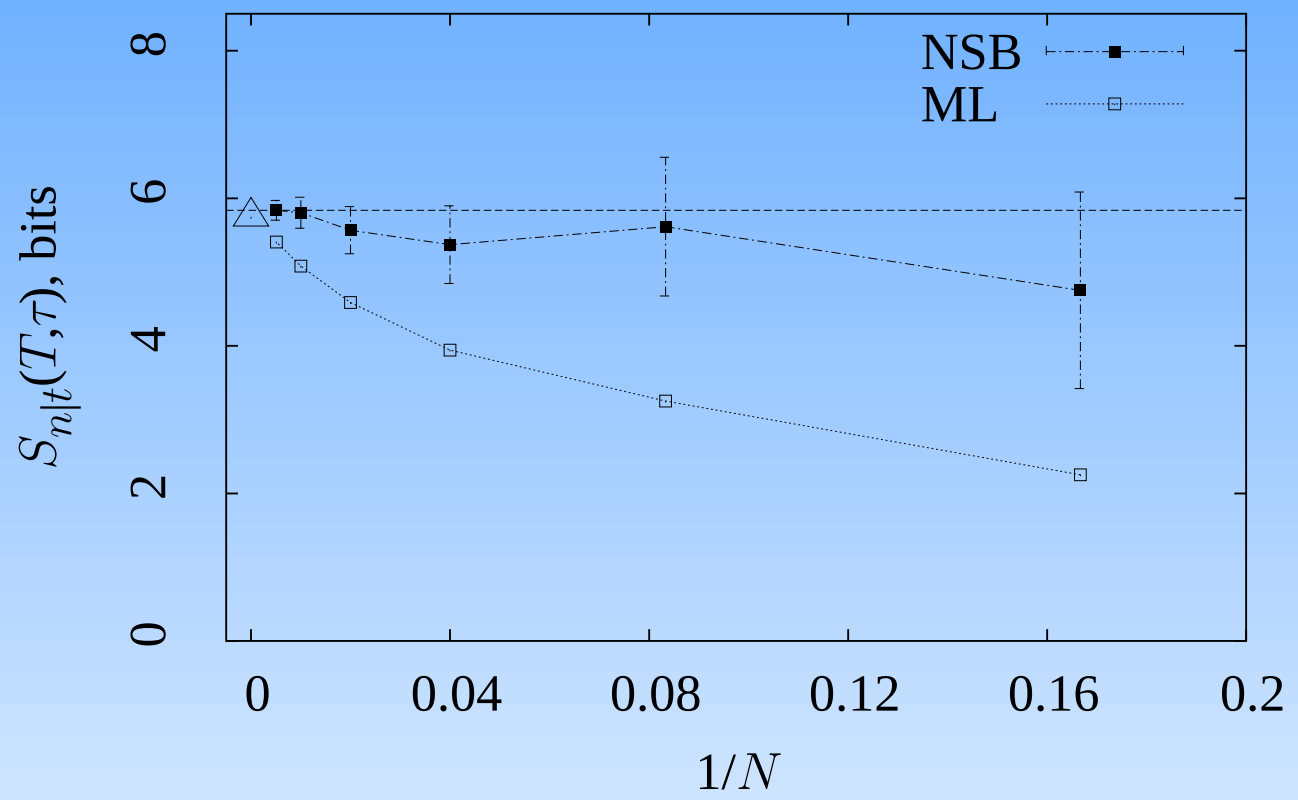


True value reached within the error bars for $N^2 \sim 2^S$, when coincidences start to occur.

Estimator is unbiased if it is consistent and agrees with itself for all N within error bars.

Natural data: Slice entropy vs. sample size

Slice at 1800 ms, τ = 2 ms, T = 16 ms

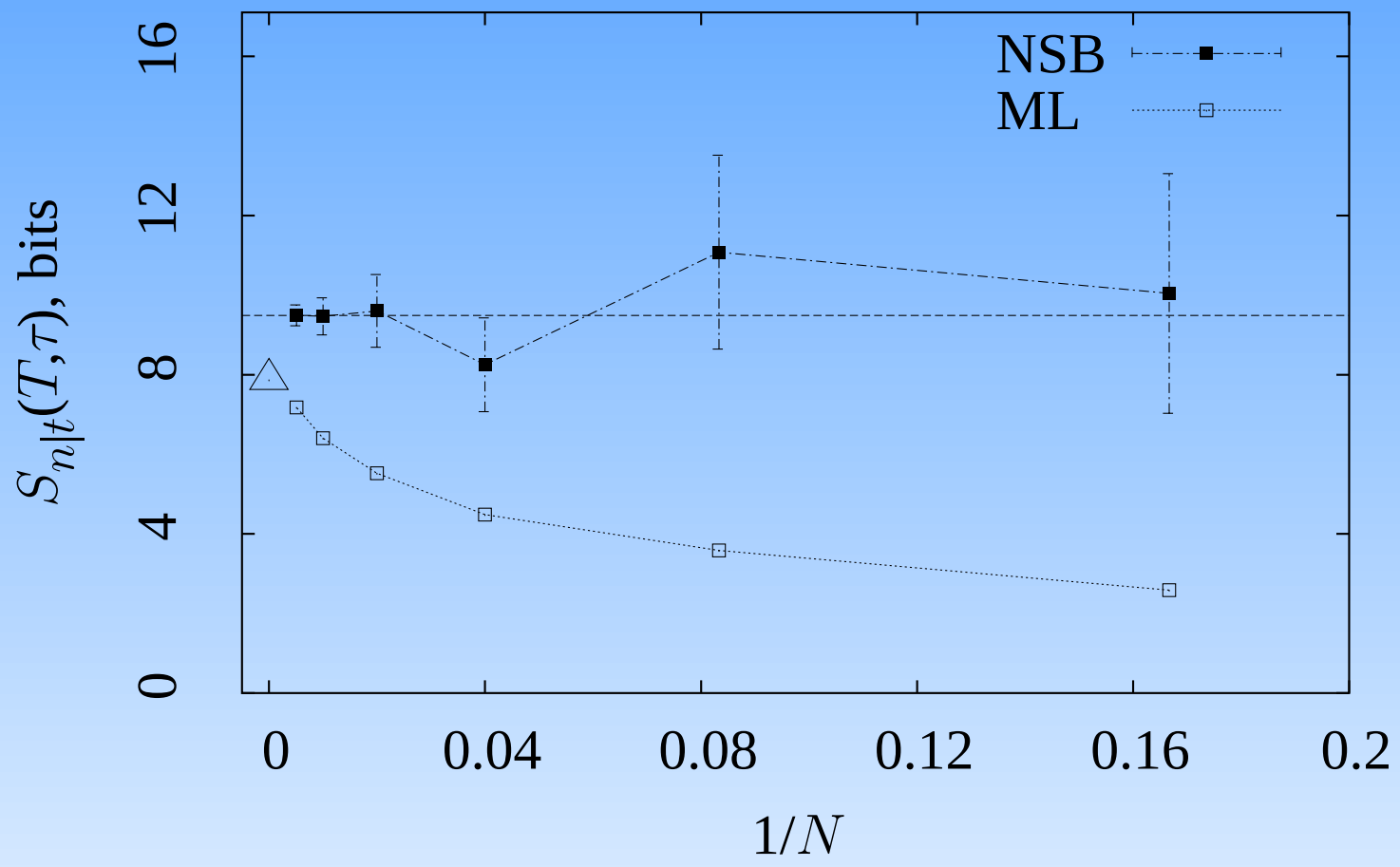


ML estimator converges with $\sim 1/N$ corrections.

NSB estimator is always within error bars.

$E(S^{\rm NSB} - S_{\rm ML})/\delta S^{\rm NSB} \approx 0$ if $S^{\rm ML}$ is reliably extrapolated ($N \gg 2^S$).

Slice at 1800 ms, τ = 2 ms, T = 30 ms



ML estimator cannot be extrapolated.

NSB estimator is always within error bars.

Natural data: Error vs. mean

$$\epsilon(N) \equiv \frac{S^{\mathrm{NSB}}(N) - S}{\delta S^{\mathrm{NSB}}(N)} \approx \frac{S^{\mathrm{NSB}}(N) - S^{\mathrm{NSB}}(196)}{\delta S^{\mathrm{NSB}}(N)}.$$ Remember: $\log_2 196 \approx 7.5\mathrm{bit}.$

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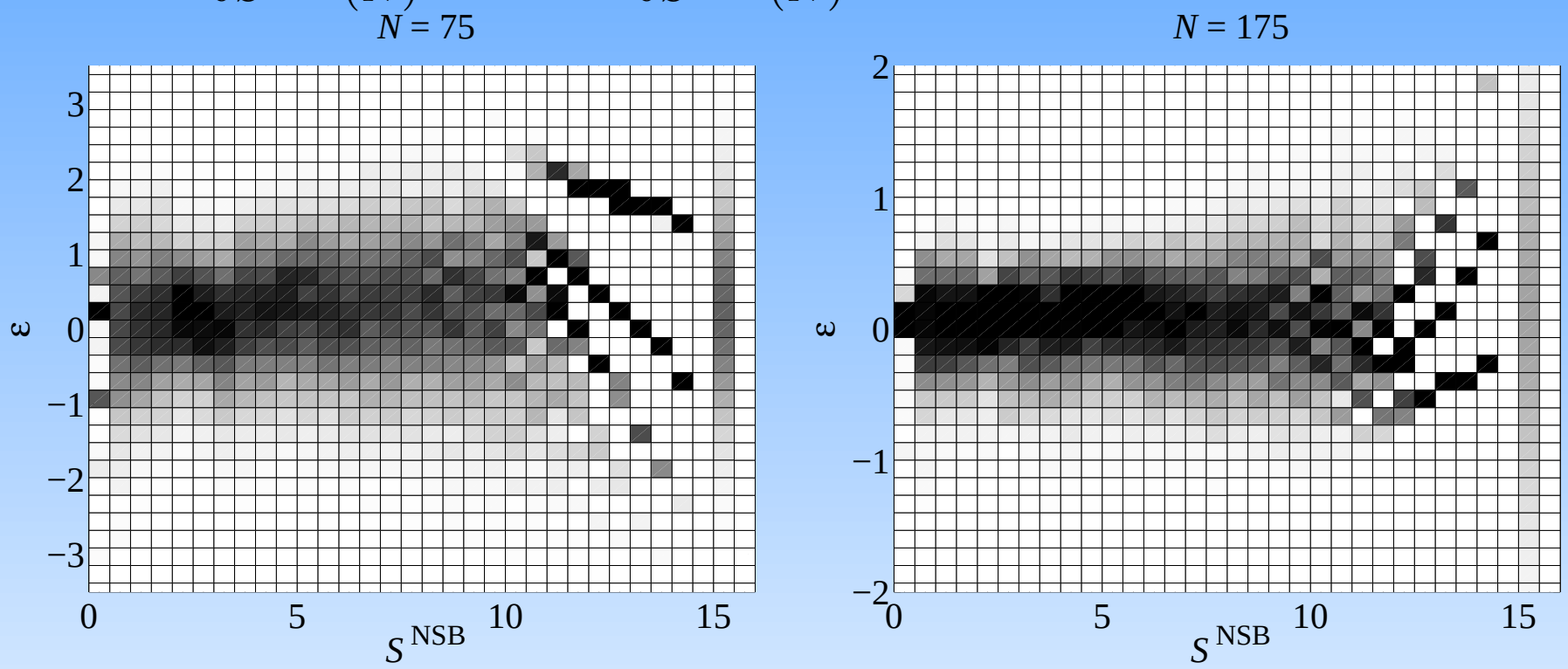


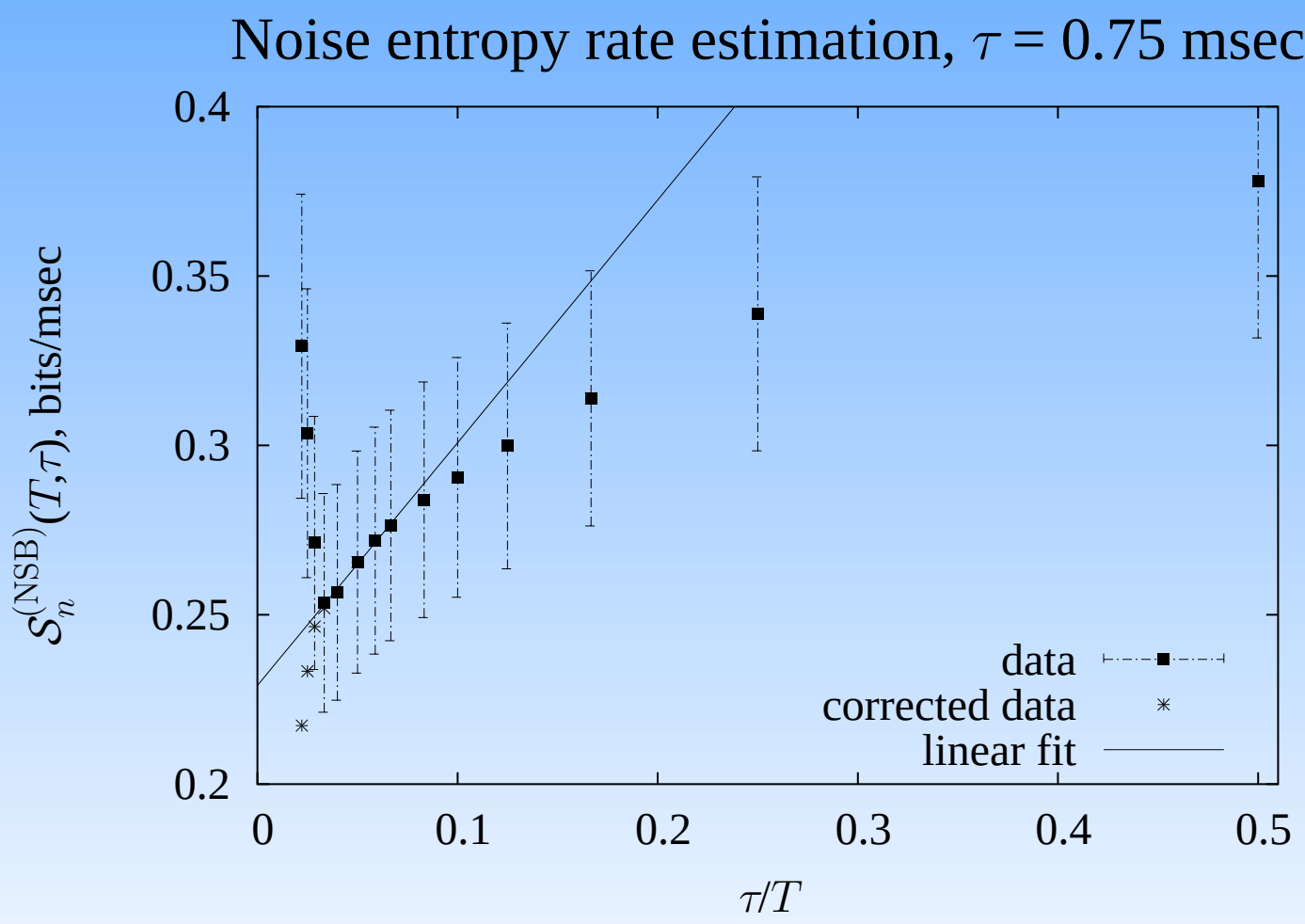
Almost no bias.

Empirical variance < 1 due to long tails in posterior, and $S \neq S^{\rm NSB}(196)$.

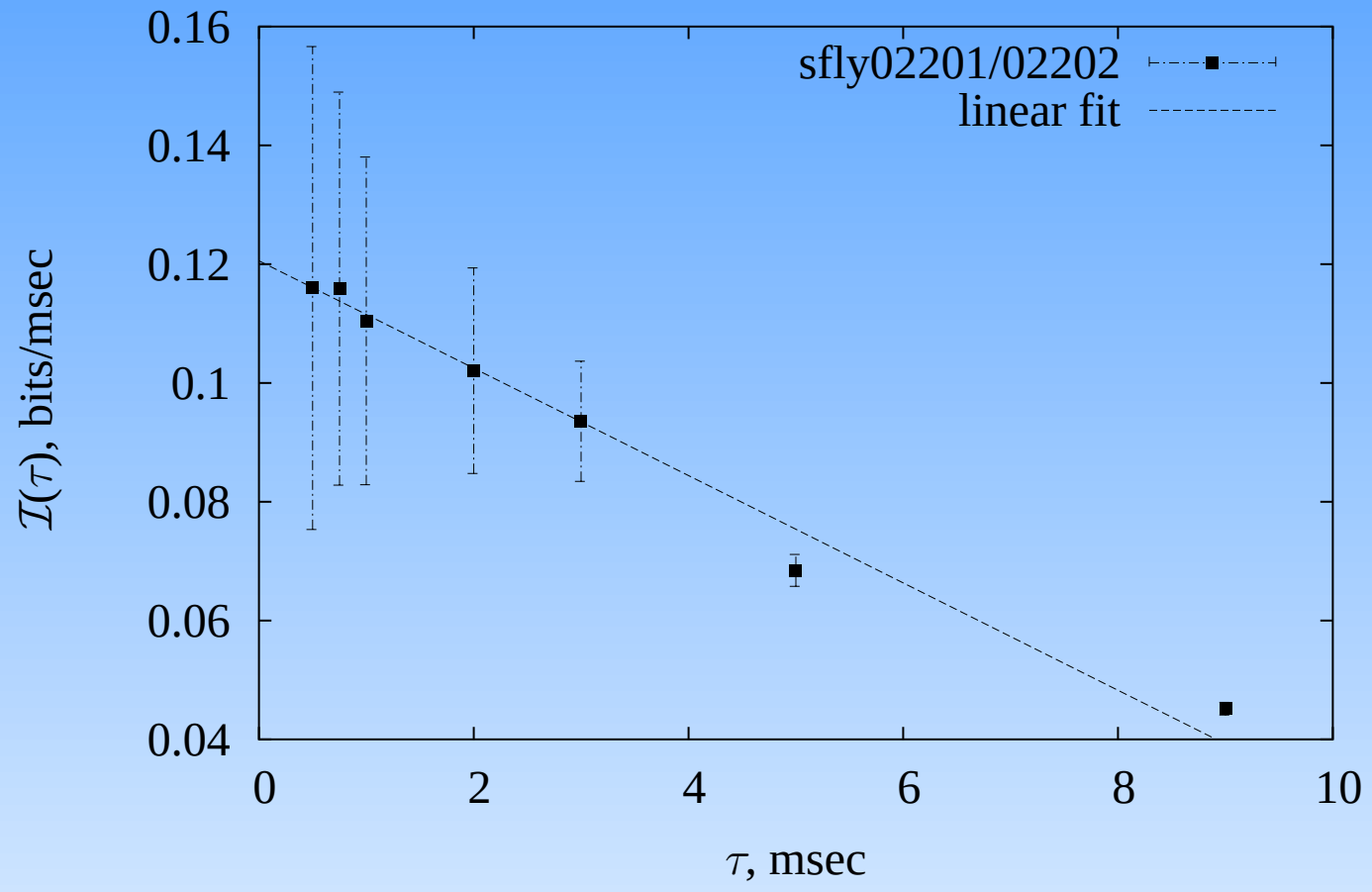
Bands are due to discrete nature of Δ.

Natural data: Rates

Further work is needed to properly estimate error bars due to signal correlations.



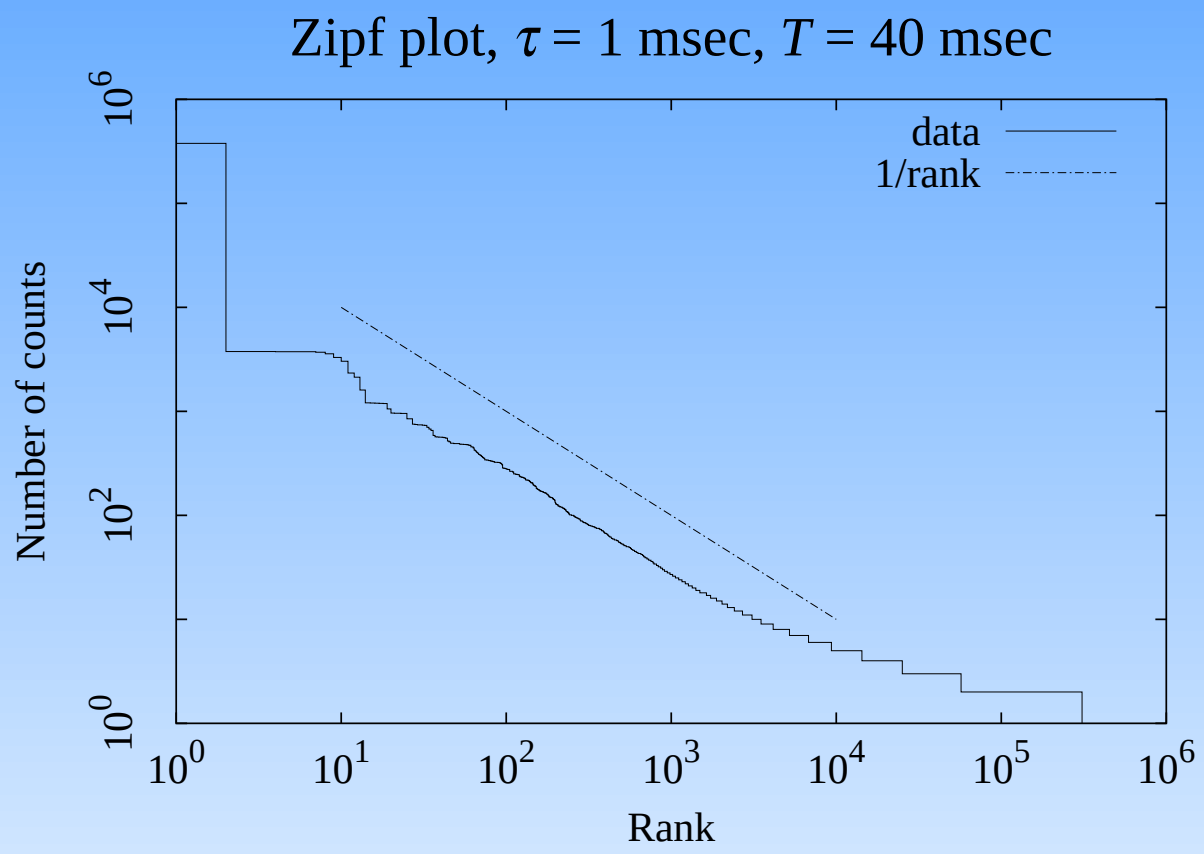
Information rate in the spike train



Conclusions

- Found new entropy estimator.
- Works in Ma regime.
- Produces error bars.
- Know if we should trust it.
- Neural data seems to be well matched to the estimator.
- Hope of similar progress on other biological data.

For amusement



Do not underestimate difficulty of working on real data!