Information Theory

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Why information theory?

Understanding the neural code.

- Encoding and decoding. We imposed coding schemes, such as a linear kernel, or a GLM. We possibly lost information in doing so.
- Instead, use information:
  - Don't need to impose encoding or decoding scheme (non-parametric).
    In particular important for 1) spike timing codes, 2) higher areas.
  - Estimate how much information is present in a recorded signal.

  Caveats:
  - The decoding process is ignored (upper bound only)
  - Requires more data, and biases are tricky

Overview

- Entropy, Mutual Information
- Entropy Maximization for a Single Neuron
- Maximizing Mutual Information
- Estimating information
- Reading: Dayan and Abbott ch 4, Rieke

Definitions

For the probability of an event $P(x)$, the quantity

$$h(p) = -\log p(x)$$

is called ‘surprise‘ or ‘information‘.

- Measures the information gained when observing x.
- Additive for independent events.
- Often $\log_2$ is used, then unit is bits ($\log_e$ has unit nats).

Surprise

i	a_i	p_i	$h(p_i)$
1	a	.0575	4.1
2	b	.0128	6.3
3	c	.0263	5.2
4	d	.0285	5.1
5	e	.0913	3.5
6	f	.0173	5.9
7	g	.0133	6.2
8	h	.0313	5.0
9	i	.0599	4.1
10	j	.0006	10.7
11	k	.0084	6.9
12	l	.0335	4.9
13	m	.0235	5.4
14	n	.0596	4.1
15	o	.0689	3.9
16	p	.0192	5.7
17	q	.0008	10.3
18	r	.0508	4.3
19	s	.0567	4.1
20	t	.0706	3.8
21	u	.0334	4.9
22	v	.0069	7.2
23	w	.0119	6.4
24	x	.0073	7.1
25	y	.0164	5.9
26	z	.0007	10.4
27	-	.1928	2.4

Definitions

The *entropy* of a quantity is the average

$$H(X) = -\sum_{x} P(x) \log_2 P(x)$$

Properties:

- Continuous, non-negative, $H(1) = 0$
- If $p_i = \frac{1}{n}$, it increases monotonically with n. $H = \log_2 n$.
- Parallel independent events add.

[Shannon and Weaver, 1949, Cover and Thomas, 1991, Rieke et al., 1996]

Entropy

Discrete variable

$$H(R) = -\sum_r p(r) \log_2 p(r)$$

Continuous variable at resolution Δr

$$H(R) = -\sum_r p(r)\Delta r \log_2(p(r)\Delta r) = -\sum_r p(r)\Delta r \log_2 p(r) - \log_2 \Delta r$$

letting $\Delta r \to 0$ we have

$$\lim_{\Delta r \to 0}[H + \log_2 \Delta r] = -\int p(r) \log_2 p(r) dr$$

(also called differential entropy)

Joint, Conditional entropy

Joint entropy:

$$H(S,R) = -\sum_{r,s} P(S,R) \log_2 P(S,R)$$

Conditional entropy:

$$\begin{aligned} H(S|R) &= \sum_r P(R=r) H(S|R=r) \\ &= -\sum_r P(r) \sum_s P(s|r) \log_2 P(s|r) \\ &= H(S,R) - H(R) \end{aligned}$$

If S, R are independent

$$H(S,R) = H(S) + H(R)$$

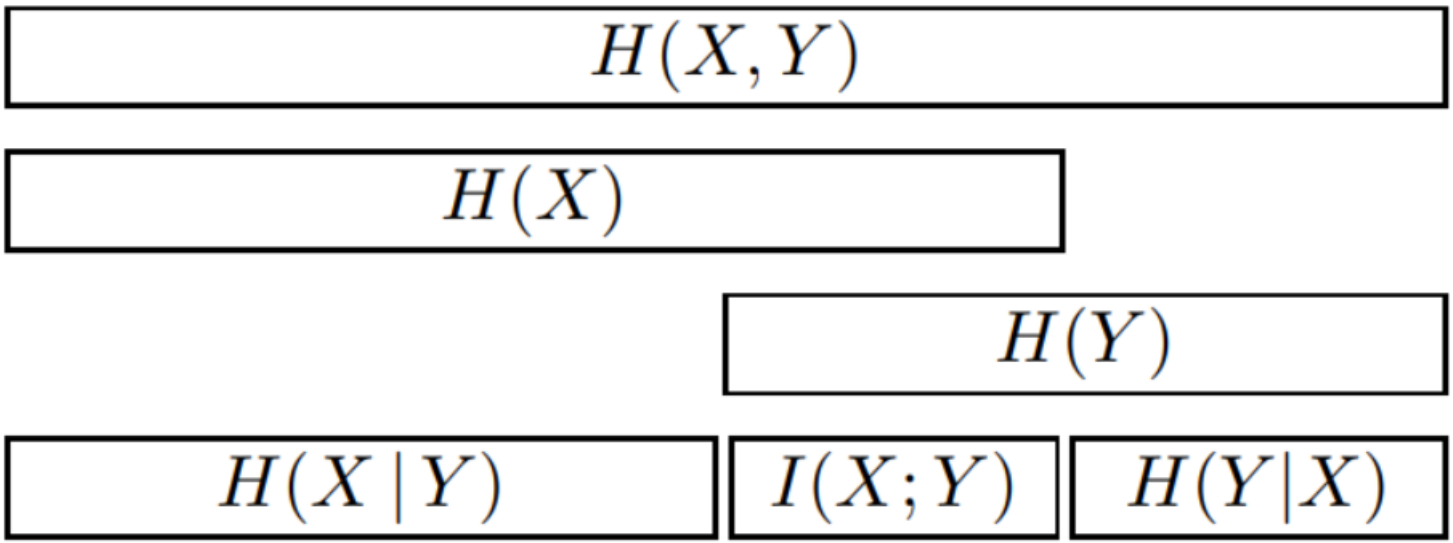
Mutual information

Mutual information:

$$I_m(R;S) = \sum_{r,s} p(r,s) \log_2 \frac{p(r,s)}{p(r)p(s)}$$
$$= H(R) - H(R|S) = H(S) - H(S|R)$$

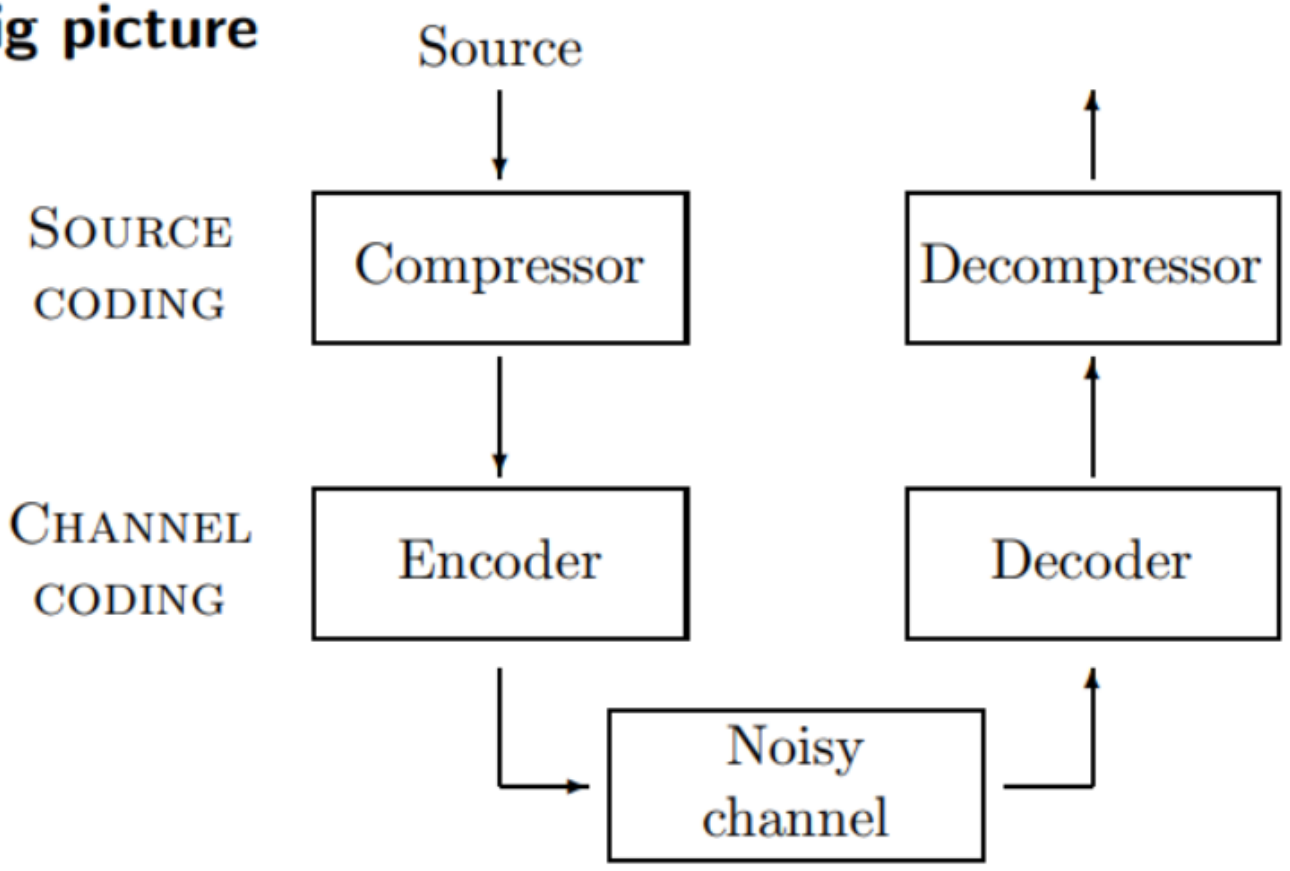
- Measures reduction in uncertainty of R by knowing S (or vice versa)
- $H(R|S)$ is called *noise entropy*, the part of the response not explained by the stimulus.
- $I_m(R;S) \geq 0$
- The continuous version is the *difference* of two entropies, the Δr divergence cancels

Relationships between information measures



Coding channels

The big picture



Coding channels

Can we reconstruct the stimulus? We need a en/decoding model:

$$P(s|r) = \frac{P(r|s)P(s)}{P(r)}$$

How much information is conveyed? This can be addressed non-parametrically:

$$I_m(S;R) = H(S) - H(S|R) = H(R) - H(R|S)$$

Kullback-Leibler divergence

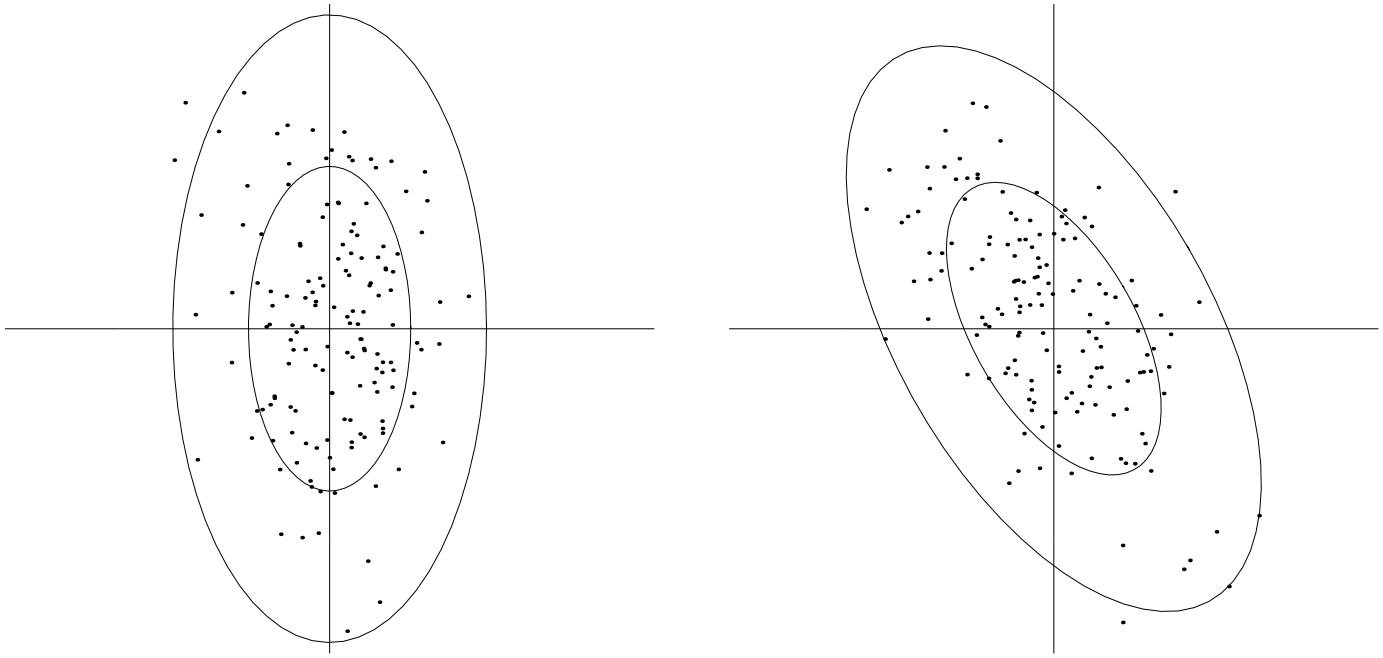
- KL-divergence measures distance between two probability distributions

$$D_{KL}(P||Q) = \int P(x) \log_2 \frac{P(x)}{Q(x)} dx$$

$$D_{KL}(P||Q) \equiv \sum_i P_i \log_2 \frac{P_i}{Q_i}$$

- Not symmetric (Jensen Shannon divergence is the symmetrised form)
- $I_m(R;S) = D_{KL}(p(r,s)||p(r)p(s))$, hence measures KLD to independent model.
- Often used as probabilistic cost function: $D_{KL}(data||model)$.

Mutual info between jointly Gaussian variables



$$I(Y_1; Y_2) = \int \int P(y_1, y_2) \log_2 \frac{P(y_1, y_2)}{P(y_1)P(y_2)} \, dy_1 \, dy_2 = -\frac{1}{2} \log_2(1 - \rho^2)$$

ρ is (Pearson-r) correlation coefficient.

Populations of Neurons

Given

$$H(\mathbf{R}) = -\int p(\mathbf{r}) \log_2 p(\mathbf{r}) d\mathbf{r} - N \log_2 \Delta r$$

and

$$H(R_i) = -\int p(r_i) \log_2 p(r_i) d\mathbf{r} - \log_2 \Delta r$$

We have

$$H(\mathbf{R}) \leq \sum_i H(R_i)$$

(proof, consider KL divergence)

Mutual information in populations of Neurons

Reduncancy can be defined as (compare to above)

$$R = \sum_{i=1}^{n_r} I(r_i; \mathbf{s}) - I(\mathbf{r}; \mathbf{s}).$$

Some codes have $R > 0$ (redundant code), others $R < 0$ (synergistic)
Example of synergistic code:
$P(r_1, r_2, s)$ with $P(0,0,1) = P(0,1,0) = P(1,0,0) = P(1,1,1) = \frac{1}{4}$,
other probabilities zero

Entropy Maximization for a Single Neuron

$$I_m(R;S) = H(R) - H(R|S)$$

- If noise entropy $H(R|S)$ is independent of the transformation $S \to R$, we can maximize mutual information by maximizing $H(R)$ under given constraints
- Possible constraint: response r is $0 < r < r_{\max}$. Maximal $H(R)$ if $\Rightarrow p(r) \sim U(0, r_{\max})$ (U is uniform dist)
- If average firing rate is limited, and $0 < r < \infty$: exponential distribution is optimal $p(x) = 1/\bar{x} exp(-x/\bar{x})$. $H = \log_2 e\bar{x}$
- If variance is fixed and $-\infty < r < \infty$: Gaussian distribution. $H = \frac{1}{2}\log_2(2\pi e\sigma^2)$

- Let $r = f(s)$ and $s \sim p(s)$. Which f (assumed monotonic) maximizes $H(R)$ using max firing rate constraint? Require: $P(r) = \frac{1}{r_{\max}}$

$$p(s) = p(r)\frac{dr}{ds} = \frac{1}{r_{\max}}\frac{df}{ds}$$

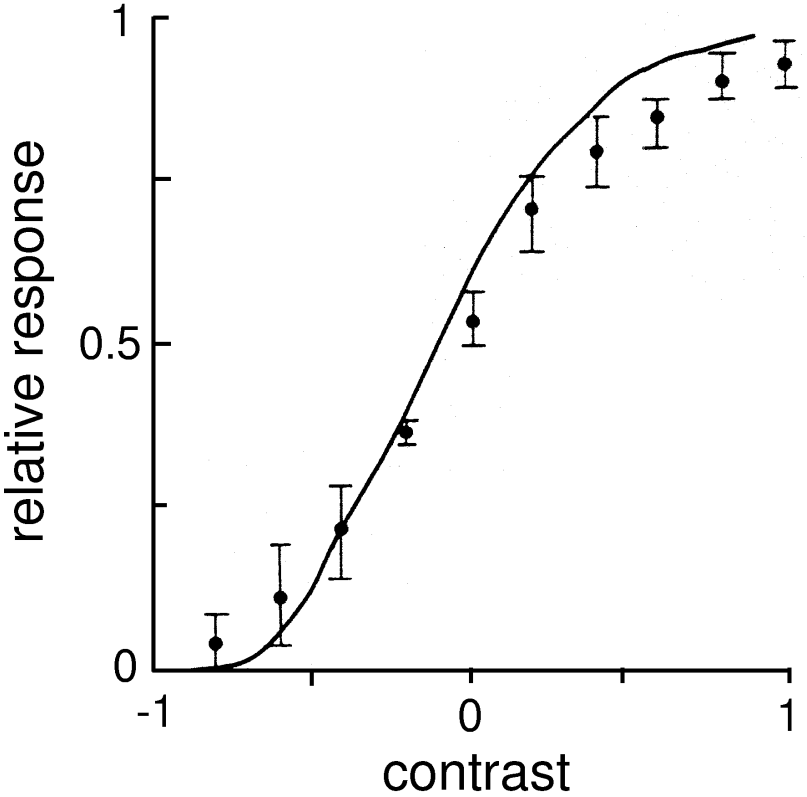
Thus $df/ds = r_{\max} p(s)$ and

$$f(s) = r_{\max} \int_{s_{\min}}^{s} p(s')ds'$$

- This strategy is known as *histogram equalization* in signal processing

Fly retina

Evidence that the large monopolar cell in the fly visual system carries out histogram equalization



Contrast response for fly large monopolar cell (points) matches environment statistics (line) [Laughlin, 1981] (but changes in high noise conditions)

V1 contrast responses

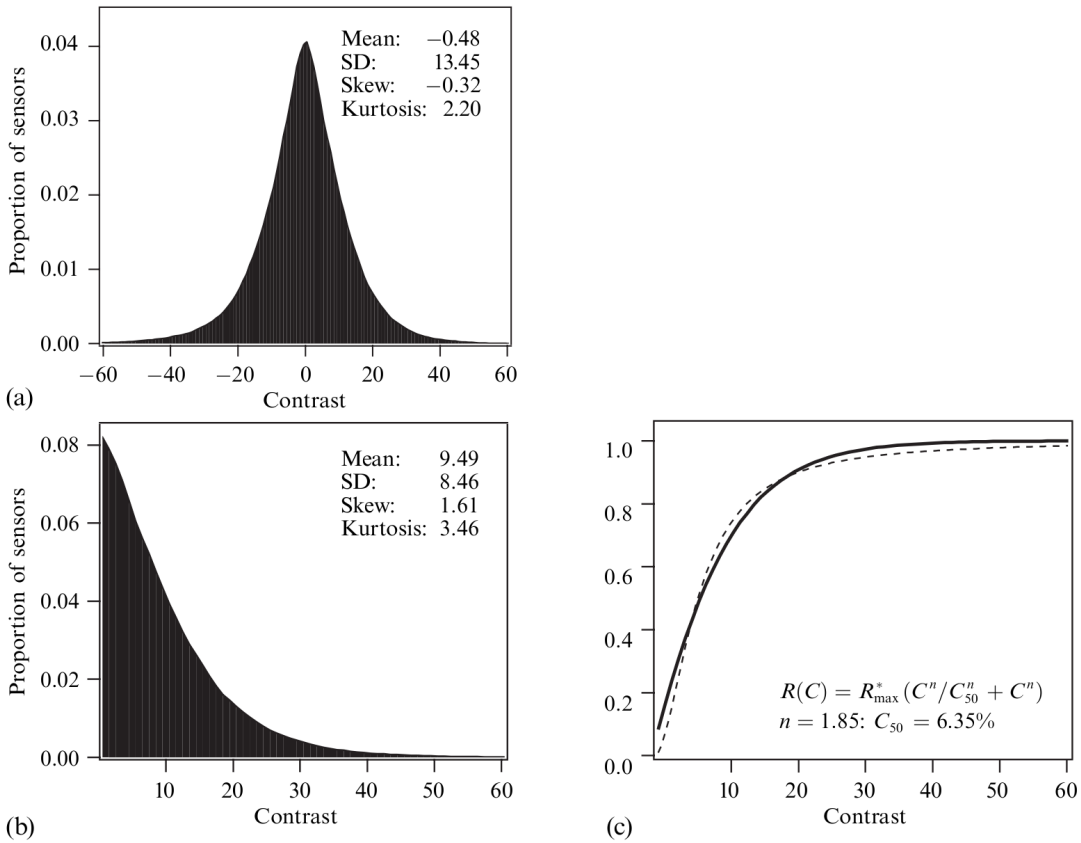


Figure 3. The distribution of image contrast in natural scenes: (a) both positive and negative, and (b) positive alone. In this study, sensor responses were pooled across 46 images, 5 spatial frequencies, and 4 orientations. The contrast bin width was 1%. (c) The integral of the positive-contrast histogram shown by the solid line defines the optimal contrast-response function. A hyperbolic function shown by the dotted line with $R_{max} = 1.0$, $C_{50} = 6.35\%$, and $n = 1.85$ provides a good fit to the data. SD = standard deviation.

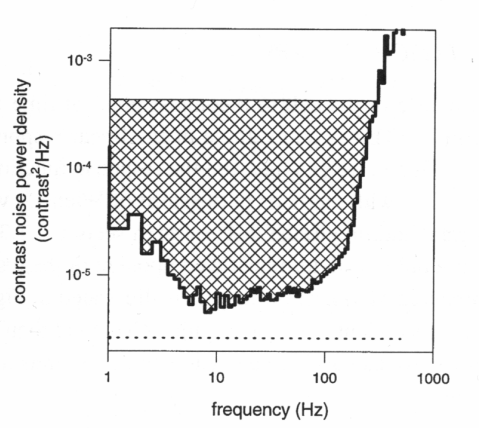
Similar in V1, but On and Off channels [Brady and Field, 2000]

Information of time varying signals

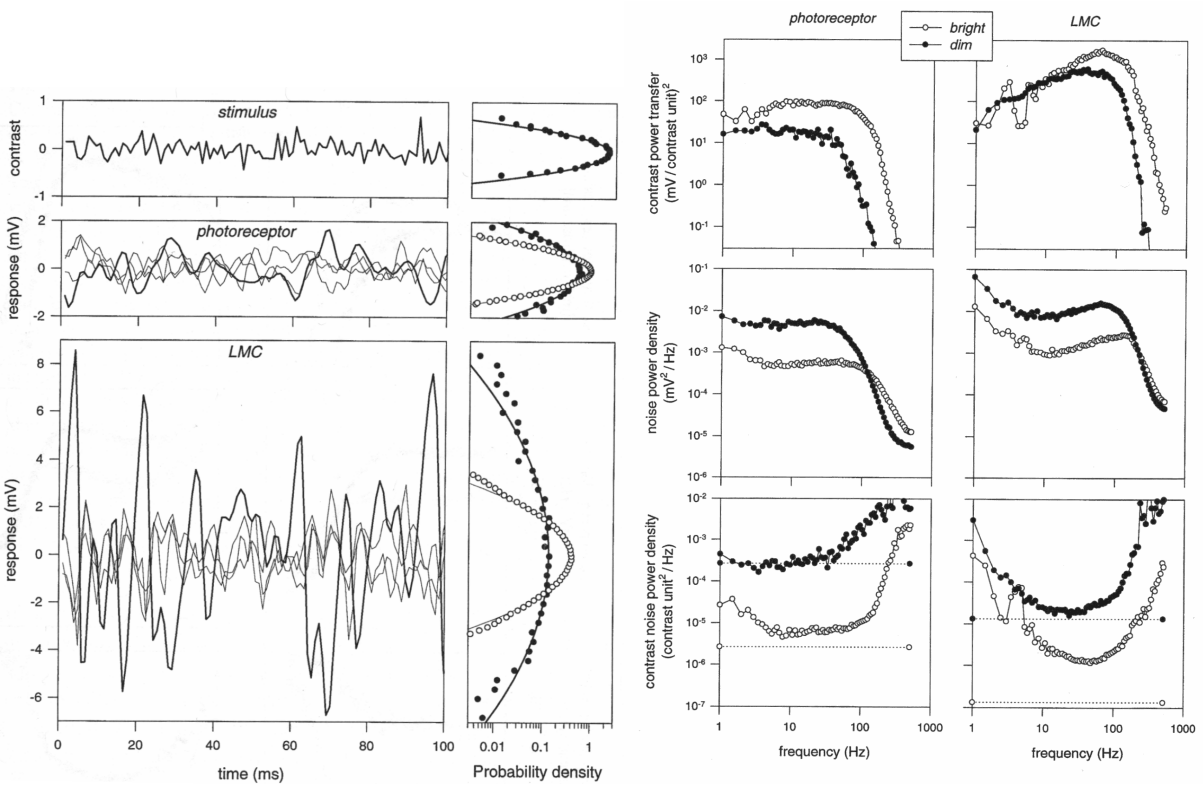
Single analog channel with Gaussian signal s and Gaussian noise η:
$r = s + \eta$

$$I = \frac{1}{2}\log_2(1 + \frac{\sigma_s^2}{\sigma_\eta^2}) = \frac{1}{2}\log_2(1 + SNR)$$

For time dependent signals $I = \frac{1}{2}T\int \frac{d\omega}{2\pi}\log_2(1 + \frac{s(\omega)}{n(\omega)})$
To maximize information, *when* variance of the signal is constrained, use all frequency bands such that signal+noise = constant.
Whitening. Water filling analog:



Information of graded synapses



Light - (photon noise) - photoreceptor - (synaptic noise) - LMC

At low light levels photon noise dominates, synaptic noise is negligible.

Information rate: 1500 bits/s

[de Ruyter van Steveninck and Laughlin, 1996].

Spiking neurons: maximal information

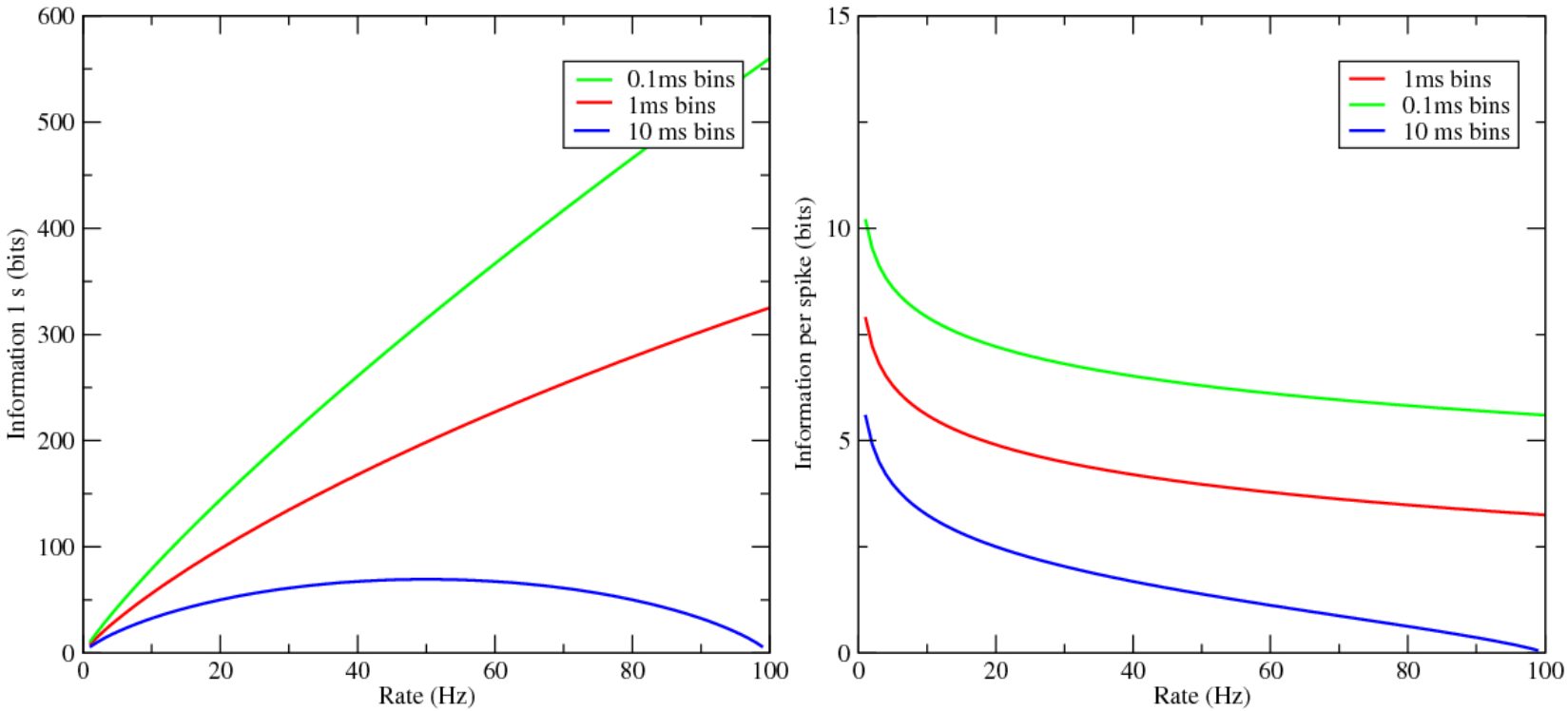
Spike train with $N = T/\delta t$ bins [Mackay and McCullogh, 1952] δt *"time-resolution".*
$pN = N_1$ events, #words $= \frac{N!}{N_1!(N-N_1)!}$
Maximal entropy if all words are equally likely.
$H = \sum p_i \log_2 p_i = \log_2 N! - \log_2 N_1! - \log_2(N - N_1)!$
Use for large x that $\log x! \approx x(\log x - 1)$

$$H = \frac{-T}{\delta t}[p \log_2 p + (1-p)\log_2(1-p)]\log_2(e)$$

For low rates $p \ll 1$, setting $\lambda = (\delta t)p$:

$$H = T\lambda \log_2(\frac{e}{\lambda \delta t})$$

Spiking neurons



Calculation incorrect when multiple spikes per bin.

Spiking neurons: rate code

[Stein, 1967]

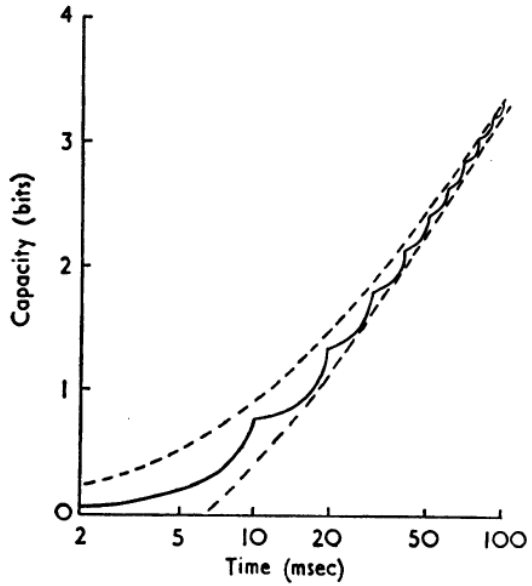


FIGURE 2 Information capacity of a completely regular neuron (solid line) as a function of the duration of a maintained stimulus. The dashed lines are upper and lower limits which converge rapidly as time (on a logarithmic scale) increases. The values were calculated for the example described in the text. The range of neuronal impulse frequencies was from 10 to 100 impulses/sec.

- Measure rate in window T, during which stimulus is constant.
- Periodic neuron can maximally encode $[1 + (f_{max} - f_{min})T]$ stimuli
- $H \approx log_2[1 + (f_{max} - f_{min})T]$. Note, only $\propto \log(T)$

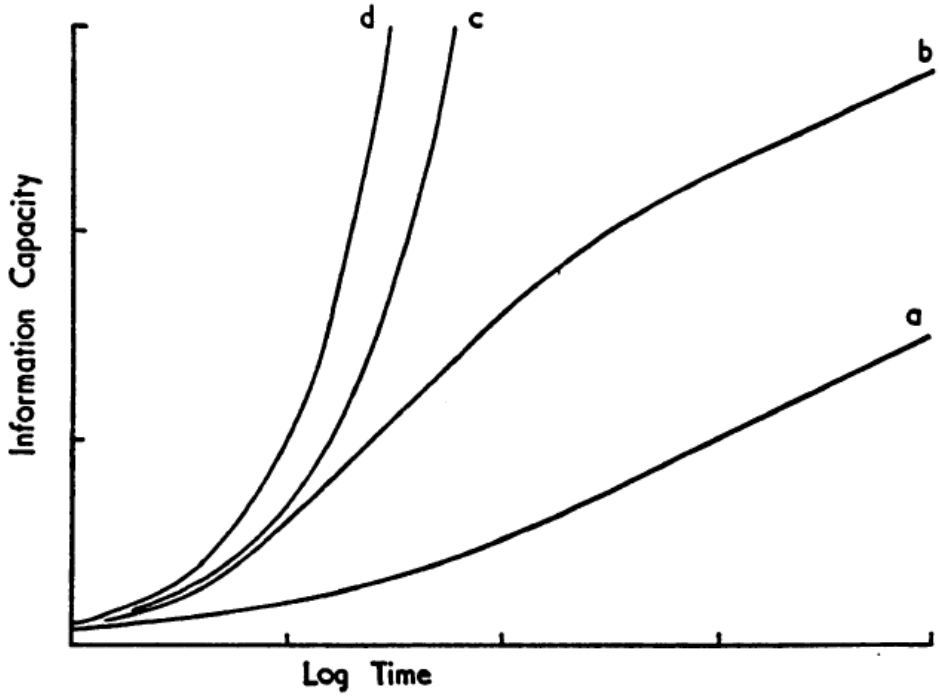
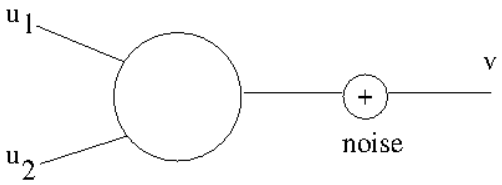


FIGURE 7 Schematic representation of the information capacity as a function of stimulus duration for a neuron, (*a*) discharging randomly and using a frequency code, (*b*) discharging fairly regularly and using a frequency code, (*c*) using a binary pulse code, and (*d*) using an interval code. Explanation in text.

[Stein, 1967]

Similar behaviour for Poisson : $H \propto \log(T)$

Maximizing Information Transmission: single output



Single linear neuron with post-synaptic noise

$$v = \mathbf{w} \cdot \mathbf{u} + \eta$$

where η is an independent noise variable

$$I_m(\mathbf{u}; v) = H(v) - H(v|\mathbf{u})$$

- Second term depends only on $p(\eta)$
- To maximize I_m need to maximize $H(v)$; sensible constraint is that $\|\mathbf{w}\|^2 = 1$
- If $\mathbf{u} \sim N(\mathbf{0}, Q)$ and $\eta \sim N(0, \sigma_\eta^2)$ then $v \sim N(0, \mathbf{w}^T Q \mathbf{w} + \sigma_\eta^2)$

- For a Gaussian RV with variance σ^2 we have $H = \frac{1}{2} \log 2\pi e \sigma^2$. To maximize $H(v)$ we need to maximize $\mathbf{w}^T Q \mathbf{w}$ subject to the constraint $\|\mathbf{w}\|^2 = 1$
- Thus $\mathbf{w} \propto \mathbf{e}_1$ so we obtain PCA
- If v is non-Gaussian then this calculation gives an *upper bound* on $H(v)$ (as the Gaussian distribution is the maximum entropy distribution for a given mean and covariance)

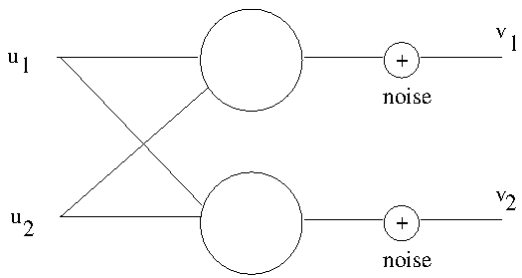
Infomax

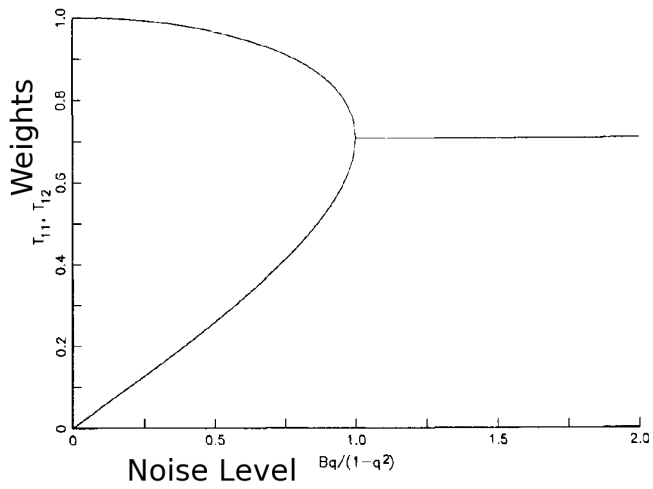
Infomax: maximize information in *multiple* outputs wrt weights [Linsker, 1988]

$$\mathbf{v} = W\mathbf{u} + \eta$$

$$H(v) = \frac{1}{2} \log \det(\langle \mathbf{v}\mathbf{v}^T \rangle)$$

Example: 2 inputs and 2 outputs. Input is correlated. $w_{k1}^2 + w_{k2}^2 = 1$.

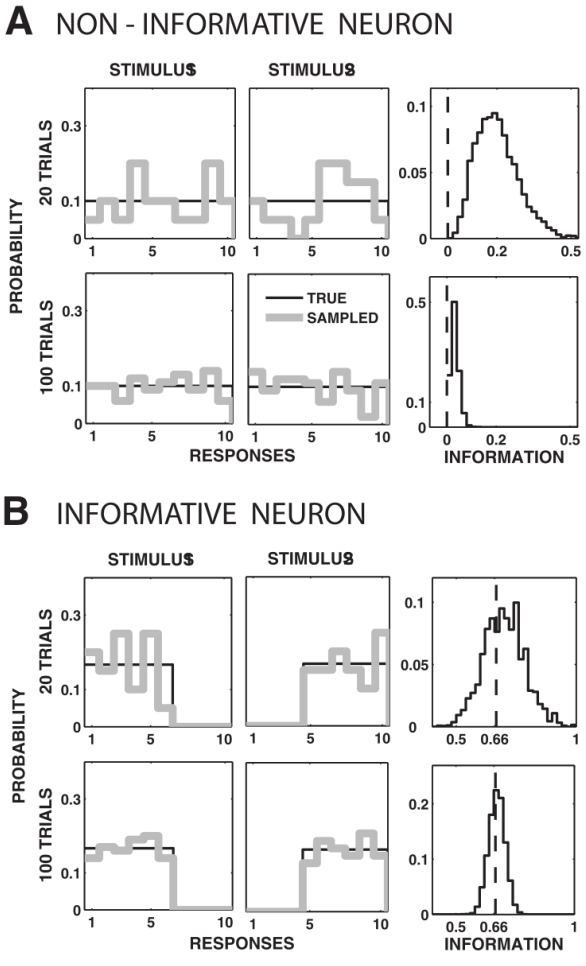




At low noise independent coding, at high noise joint coding.

Estimating information

Information estimation requires a lot of data.
Most statistical quantities are unbiased (mean, var,...).
But both entropy and noise entropy have bias.



[Panzeri et al., 2007]

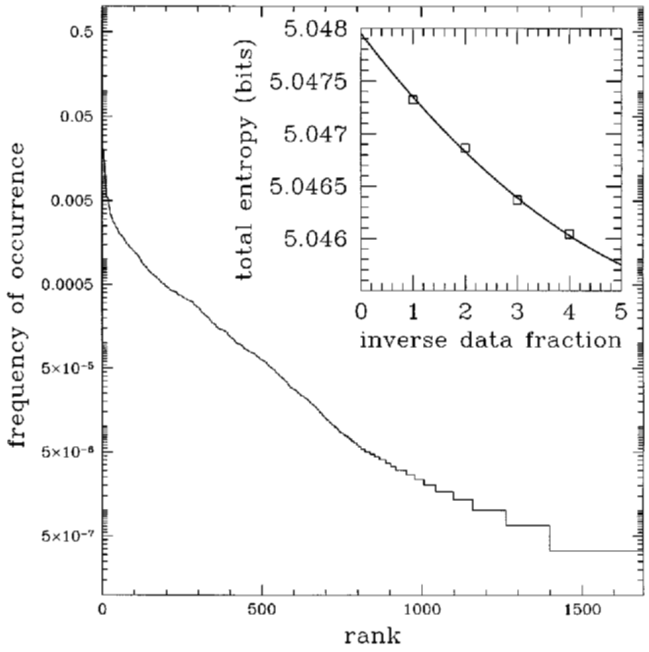


FIG. 2. The frequency of occurrence for different words in the spike train, with $\Delta\tau = 3$ ms and $T = 30$ ms. Words are placed in order so that the histogram is monotonically decreasing; at this value of T the most likely word corresponds to no spikes. Inset shows the dependence of the entropy, computed from this histogram according to Eq. (1), on the fraction of data included in the analysis. Also plotted is a least squares fit to the form $S = S_0 + S_1/\text{size} + S_2/\text{size}^2$. The intercept S_0 is our extrapolation to the true value of the entropy with infinite data [11].

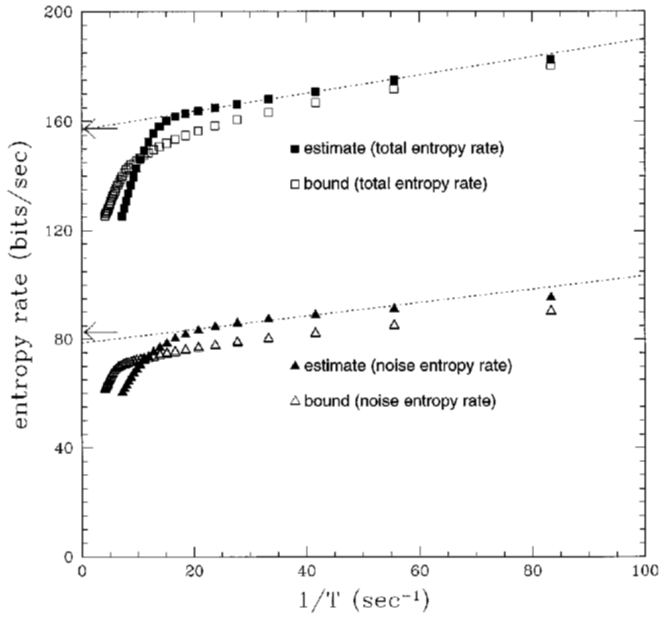


FIG. 3. The total and noise entropies per unit time are plotted versus the reciprocal of the window size, with the time resolution held fixed at $\Delta\tau = 3$ ms. Results are given both for the direct estimate and for the bounding procedure described in the text, and for each data point we apply the extrapolation procedures of Fig. 2 (inset). Dashed lines indicate extrapolations to infinite word length, as discussed in the text, and arrows indicate upper bounds obtained by differentiating $S(T)$ [7].

Try to fit $1/N$ correction [Strong et al., 1998]

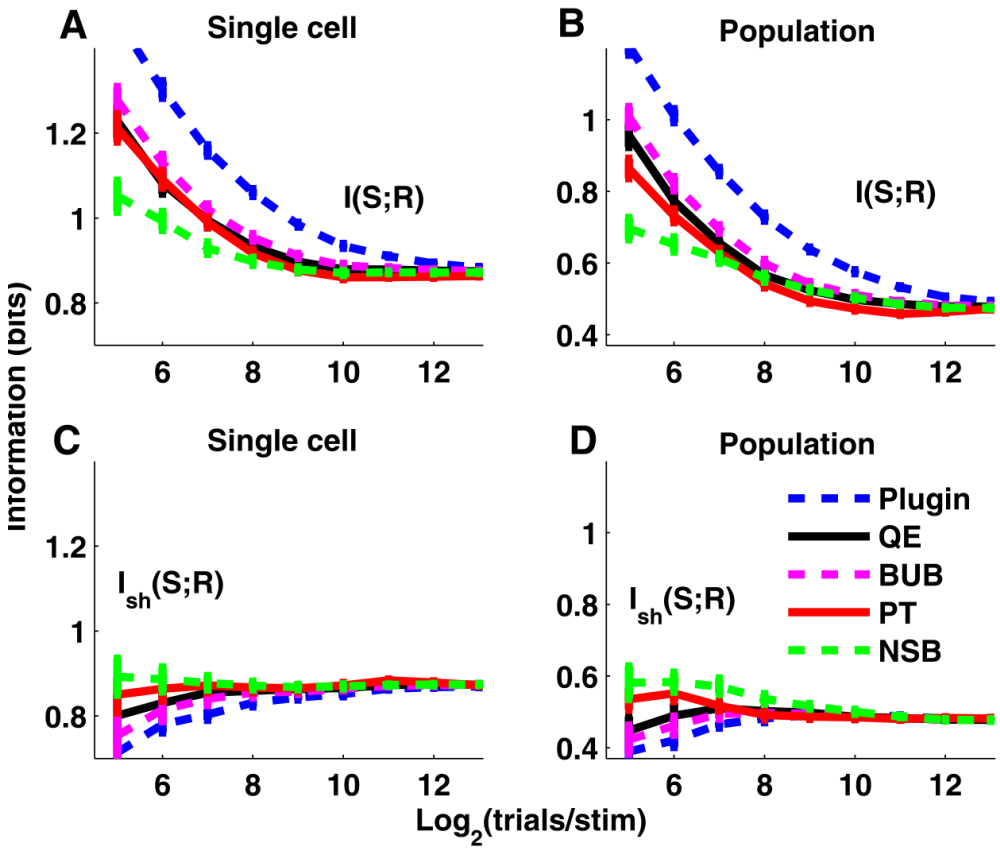


FIG. 3. Comparison of the performance of different bias correction methods. The information estimates $\mathbf{I(S;R)}$ and $\mathbf{I}_{sh}\mathbf{(S;R)}$ are plotted as a function of the available number of trials per stimulus. *A* and *B*: mean ± SD (over 50 simulations) of $\mathbf{I(S;R)}$. *C* and *D*: mean ± SD (over 50 simulations) of $\mathbf{I}_{sh}\mathbf{(S;R)}$. Various methods were used to correct for the bias: plug-in estimation (i.e., no bias correction), PT, QE, BUB, and NSB (see text). *A* and *C* and *B* and *D* report results using realistically simulated single-cell and population cortical spike trains, respectively (see main text).

Common technique for I_m: shuffle correction [Panzeri et al., 2007]
See also: [Paninski, 2003, Nemenman et al., 2002]

Summary

- Information theory provides non parametric framework for coding
- Optimal coding schemes depend strongly on noise assumptions and optimization constraints
- In data analysis biases can be substantial

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