Information Theory

Maneesh Sahani maneesh@gatsby.ucl.ac.uk

Gatsby Computational Neuroscience Unit University College London

Term 1, Autumn 2010

- How much information does a neural response carry about a stimulus?
- How efficient is a hypothetical code, given the statistical behaviour of the components?
- How much better could another code do, given the same components?
- Is the information carried by different neurons complementary, synergistic (whole is greater than sum of parts), or redundant?
- Can further processing extract more information about a stimulus?

Information theory is the mathematical framework within which questions such as these can be framed and answered.

Information theory does not directly address:

- estimation (but there are some relevant bounds)
- computation (but "information bottleneck" might provide a motivating framework)
- representation (but redundancy reduction has obvious information theoretic connections)

Information is related to the removal of uncertainty.

$$S \to R \to P(S|R)$$

How informative is R about S?

$$\begin{split} P(S|R) = & \begin{bmatrix} 0, 0, 1, 0, \dots, 0 \end{bmatrix} & \Rightarrow \text{ high information?} \\ P(S|R) = & \begin{bmatrix} \frac{1}{M}, \frac{1}{M}, \dots, \frac{1}{M} \end{bmatrix} & \Rightarrow \text{ low information?} \end{split}$$

But also depends on P(S).

We need to start by considering the uncertainty in a probability distribution \rightarrow called the entropy

Let $S \sim P(S)$. The entropy is the minimum number of bits needed, on average, to specify the value S takes, assuming P(S) is known.

Equivalently, the minimum average number of yes/no questions needed to guess S.

Entropy

• Suppose there are M equiprobable stimuli: $P(s_m) = 1/M$. To specify which stimulus appears on a given trial, we would need assign each a (binary) number. This would take,

$$B_s \le \log_2 M + 1 \qquad [2^B \ge M]$$
$$= -\log_2 \frac{1}{M} + 1 \text{ bits}$$

 \bullet Now suppose we code N such stimuli, drawn iid, at once.

$$B_N \leq \log_2 M^N + 1$$

$$\rightarrow -N \log_2 \frac{1}{M} \quad \text{as } N \rightarrow \infty$$

$$\Rightarrow B_s \rightarrow -\log_2 p \text{ bits}$$

This is called block coding. It is useful for extracting theoretical limits. The nervous system is unlikely to use block codes in time, but may in space.

Entropy

• Now suppose stimuli are not equiprobable. Write $P(s_m) = p_m$. Then

$$P(S_1, S_2, \dots, S_N) = \prod_m p_m^{n_m}$$
 [where $n_m = (\# \text{ of } S_i = s_m)$].

Now, as $N \to \infty$ only "typical" sequences, with $n_m = p_m N$, have non-zero probability of occuring; and they are all equally likely. This is called the Asymptotic Equipartition Property (or AEP). Thus,

$$B_N \to -\log_2 \prod_m p_m^{n_m} = -\sum_m n_m \log_2 p_m$$
$$= -\sum_m p_m N \log_2 p_m = -N \underbrace{\sum_m p_m \log_2 p_m}_{-\mathbf{H}[s]}$$

 $H[S] = E[\log_2 P(S)]$, also written H[P(S)], is the **entropy** of the stimulus distribution.

Rather than appealing to typicality, we could instead have used the law of large numbers directly:

$$\frac{1}{N}\log_2 P(S_1, S_2, \dots, S_N) = \frac{1}{N}\log_2 \prod_i P(S_i) = \frac{1}{N}\sum_i \log_2 P(S_i) \xrightarrow{N \to \infty} \mathsf{E}[\log_2 P(S_i)]$$

Entropy is a measure of "available information" in the stimulus ensemble. Now suppose we measure a particular response r which depends on the stimulus according to P(R|S).

How uncertain is the stimulus once we know r? Bayes rule gives us

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

so we can write

$$\mathbf{H}[S|r] = -\sum_{s} P(s|r) \log_2 P(s|r)$$

The average uncertainty in S for $r \sim P(R) = \sum_s P(R|s) p(s)$ is then

$$\mathbf{H}[S|R] = \sum_{r} P(r) \left[-\sum_{s} P(s|r) \log_2 P(s|r) \right] = -\sum_{s,r} P(s,r) \log_2 P(s|r)$$

It is easy to show that:

1.
$$H[S|R] \le H[S]$$

2. $H[S|R] = H[S, R] - H[R]$
3. $H[S|R] = H[S]$ iff $S \perp R$

A natural definition of the average information gained about S from R is

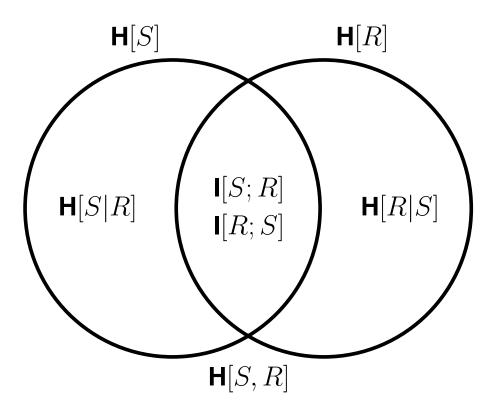
 $\mathbf{I}[S;R] = \mathbf{H}[S] - \mathbf{H}[S|R]$

Measures reduction in uncertainty due to R.

It follows from the definition that

$$\begin{split} \mathbf{I}[S;R] &= \sum_{s} P(s) \log \frac{1}{P(s)} - \sum_{s,r} P(s,r) \log \frac{1}{P(s|r)} \\ &= \sum_{s,r} P(s,r) \log \frac{1}{P(s)} + \sum_{s,r} P(s,r) \log P(s|r) \\ &= \sum_{s,r} P(s,r) \log \frac{P(s|r)}{P(s)} \\ &= \sum_{s,r} P(s,r) \log \frac{P(s,r)}{P(s)P(r)} \\ &= \mathbf{I}[R;S] \end{split}$$

The symmetry suggests a Venn-like diagram.



All of the additive and equality relationships implied by this picture hold for two variables. Unfortunately, we will see that this does not generalise to any more than two. Another useful information theoretic quantity measures the difference between two distributions.

$$\begin{split} \mathbf{KL}[P(S) \| Q(S)] &= \sum_{s} P(s) \log \frac{P(s)}{Q(s)} \\ &= \underbrace{\sum_{s} P(s) \log \frac{1}{Q(s)}}_{s} - \mathbf{H}[P] \end{split}$$

Excess cost in bits paid by encoding according to Q instead of P.

$$-\mathbf{KL}[P||Q] = \sum_{s} P(s) \log \frac{Q(s)}{P(s)}$$
$$\leq \log \sum_{s} P(s) \frac{Q(s)}{P(s)} \qquad \text{by Jensen}$$
$$= \log \sum_{s} Q(s) = \log 1 = 0$$

So $\mathbf{KL}[P \| Q] \ge 0$. Equality iff P = Q

$$\mathbf{I}[S;R] = \sum_{s,r} P(s,r) \log \frac{P(s,r)}{P(s)P(r)} = \mathbf{KL}[P(s,r) \| P(s)P(r)]$$

Thus:

1. Mutual information is always non-negative

 $\mathbf{I}[S;R] \geq 0$

2. Conditioning never increases entropy

 $\mathbf{H}[S|R] \le \mathbf{H}[S]$

Two responses to the same stimulus, R_1 and R_2 , may provide either more or less information jointly than independently.

$$I_{12} = \mathbf{I}[S; R_1, R_2] = \mathbf{H}[R_1, R_2] - \mathbf{H}[R_1, R_2|S]$$

$$R_1 \perp \!\!\!\perp R_2 \Rightarrow \mathbf{H}[R_1, R_2] = \mathbf{H}[R_1] + \mathbf{H}[R_2]$$
$$R_1 \perp \!\!\!\perp R_2 | S \Rightarrow \mathbf{H}[R_1, R_2 | S] = \mathbf{H}[R_1 | S] + \mathbf{H}[R_2 | S]$$

$R_1 \perp\!\!\!\perp R_2$	$R_1 \perp \!\!\!\perp R_2 S$		
no	yes	$I_{12} < I_1 + I_2$	redundant
yes	yes	$I_{12} = I_1 + I_2$	independent
yes	no	$I_{12} > I_1 + I_2$	synergistic
no	no	?	any of the above

 $I_{12} > \max(I_1, I_2)$: the second response cannot destroy information.

Thus, the Venn-like diagram with three variables is misleading.

Suppose $S \to R_1 \to R_2$ form a Markov chain; that is, $R_2 \perp \!\!\!\perp S | R_1$. Then,

$$P(R_2, S|R_1) = P(R_2|R_1)P(S|R_1)$$

 $\Rightarrow P(S|R_1, R_2) = P(S|R_1)$

Thus,

$$\mathbf{H}[S|R_2] \ge \mathbf{H}[S|R_1, R_2] = \mathbf{H}[S|R_1]$$
$$\Rightarrow \mathbf{I}[S; R_2] \le \mathbf{I}[S; R_1]$$

So any computation based on R_1 that does not have separate access to S cannot add information (in the Shannon sense) about the world.

Equality holds iff $S \to R_2 \to R_1$ as well. In this case R_2 is called a **sufficient statistic** for *S*.

So far we have discussed S and R as single (or iid) random variables. But real stimuli and responses form a time series.

Let $S = \{S_1, S_2, S_3 \dots\}$ form a stochastic process.

$$\mathbf{H}[S_1, S_2, \dots, S_n] = \mathbf{H}[S_n | S_1, S_2, \dots, S_{n-1}] + \mathbf{H}[S_1, S_2, \dots, S_{n-1}] \\ = \mathbf{H}[S_n | S_1, S_2, \dots, S_{n-1}] + \mathbf{H}[S_{n-1} | S_1, S_2, \dots, S_{n-2}] + \dots + \mathbf{H}[S_1]$$

The entropy rate of ${\mathcal S}$ is defined as

$$\mathbf{H}[\mathcal{S}] = \lim_{n \to \infty} \frac{\mathbf{H}[S_1, S_2, \dots, S_n]}{N}$$

or alternatively as

$$\mathbf{H}[\mathcal{S}] = \lim_{n \to \infty} \mathbf{H}[S_n | S_1, S_2, \dots, S_{n-1}]$$

If $S_i \stackrel{\text{iid}}{\sim} P(S)$ then $\mathbf{H}[S] = \mathbf{H}[S]$. If S is Markov (and stationary) then $\mathbf{H}[S] = \mathbf{H}[S_n|S_{n-1}]$. The discussion so far has involved discrete S and R. Now, let $S \in \mathbb{R}$ with density p(s). What is its entropy?

Suppose we discretise with length Δs :

$$\begin{aligned} \mathsf{H}_{\Delta}[S] &= -\sum_{i} p(s_{i})\Delta s \log p(s_{i})\Delta s \\ &= -\sum_{i} p(s_{i})\Delta s (\log p(s_{i}) + \log \Delta s) \\ &= -\sum_{i} p(s_{i})\Delta s \log p(s_{i}) - \log \Delta s \sum_{i} p(s_{i})\Delta s \\ &= -\sum_{i} \Delta s \ p(s_{i}) \log p(s_{i}) - \log \Delta s \\ &\to -\int ds \ p(s) \log p(s) + \infty \end{aligned}$$

We define the **differential entropy**:

$$h(S) = -\int ds \ p(s) \log p(s).$$

Note that h(S) can be < 0, and can be $\pm \infty$.

We can define other information theoretic quantities similarly. The conditional differential entropy is

$$h(S|R) = -\int ds \ dr \ p(s,r) \log p(s|r)$$

and, like the differential entropy itself, may be poorly behaved. The mutual information, however, is well-defined

$$\begin{split} \mathsf{I}_{\Delta}[S;R] &= \mathsf{H}_{\Delta}[S] - \mathsf{H}_{\Delta}[S|R] \\ &= -\sum_{i} \Delta s \; p(s_{i}) \log p(s_{i}) - \log \Delta s \\ &- \int dr \; p(r) \left(-\sum_{i} \Delta s \; p(s_{i}|r) \log p(s_{i}|r) - \log \Delta s \right) \\ &\to h(S) - h(S|R) \end{split}$$

as are other KL divergences.

- 1. $\mathbf{H}[R_1, R_2] = \mathbf{H}[R_1] + \mathbf{H}[R_2]$ with equality iff $R_1 \perp \!\!\!\perp R_2$.
- 2. Let $\int ds \ p(s)f(s) = a$ for some function f. What distribution has maximum entropy? Use Lagrange multipliers:

$$\mathcal{L} = \int ds \ p(s) \log p(s) - \lambda_0 \left[\int ds \ p(s) - 1 \right] - \lambda_1 \left[\int ds \ p(s) f(s) - a \right]$$
$$\frac{\delta \mathcal{L}}{\delta p(s)} = 1 + \log p(s) - \lambda_0 - \lambda_1 f(s) = 0$$
$$\Rightarrow \log p(s) = \lambda_0 + \lambda_1 f(s) - 1$$
$$\Rightarrow p(s) = \frac{1}{Z} e^{\lambda_1 f(s)}$$

The constants λ_0 and λ_1 can be found by solving the constraint equations. Thus,

$$f(s) = s \implies p(s) = \frac{1}{Z}e^{\lambda_1 s}$$
. Exponential (need $p(s) = 0$ for $s < T$).
 $f(s) = s^2 \implies p(s) = \frac{1}{Z}e^{\lambda_1 s^2}$. Gaussian.

Both results together \Rightarrow maximum entropy point process (for fixed mean arrival rate) is homogeneous Poisson – independent, exponentially distributed ISIs.

Channels

We now direct our focus to the conditional P(R|S) which defines the **channel** linking *S* to *R*.

$$S \xrightarrow{P(R|S)} R$$

The mutual information

$$\mathbf{I}[S;R] = \sum_{s,r} P(s,r) \log \frac{P(s,r)}{P(s)P(r)} = \sum_{s,r} \frac{P(s)P(r|s) \log \frac{P(r|s)}{P(r)}}{P(r)}$$

depends on marginals P(s) and $P(r) = \sum_{s} P(r|s)P(s)$ as well and thus is unsuitable to characterise the conditional alone.

Instead, we characterise the channel by its capacity

 $\mathbf{C}_{R|S} = \sup_{P(s)} \mathbf{I}[S;R]$

Thus the capacity gives the theoretical limit on the amount of information that can be transmitted over a channel. Clearly, this is limited by the properties of the noise.

The remarkable central result of information theory.

$$S \xrightarrow{encoder} \widetilde{S} \xrightarrow{channel} R \xrightarrow{decoder} \widehat{T}$$

Any source ensemble S with entropy $\mathbf{H}[S] < \mathbf{C}_{R|\tilde{S}}$ can be transmitted (in sufficiently long blocks) with $P_{error} \to 0$.

The proof is beyond our scope.

Some of the key ideas that appear in the proof are:

- block coding
- error correction
- joint typicality
- random codes

$$S \xrightarrow{encoder} \widetilde{S} \xrightarrow{channel} R \xrightarrow{decoder} \widehat{T}$$

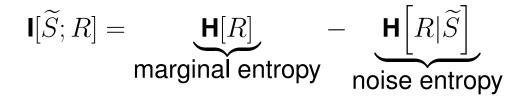
Given channel $P(R|\widetilde{S})$ and source P(S), find **encoding** $P(\widetilde{S}|S)$ (may be deterministic) to maximise I[S;R].

By data processing inequality, and defn of capacity:

$$\mathbf{I}[S;R] \leq \mathbf{I}[\widetilde{S};R] \leq \mathbf{C}_{R|\widetilde{S}}$$

By JSCT, equality can be achieved (in the limit of increasing block size). Thus $I[\widetilde{S}; R]$ should saturate $C_{R|\widetilde{S}}$.

See homework for an algorithm (Blahut-Arimoto) to find $P(\widetilde{S})$ that saturates $\mathbf{C}_{R|\widetilde{S}}$ for a general discrete channel.



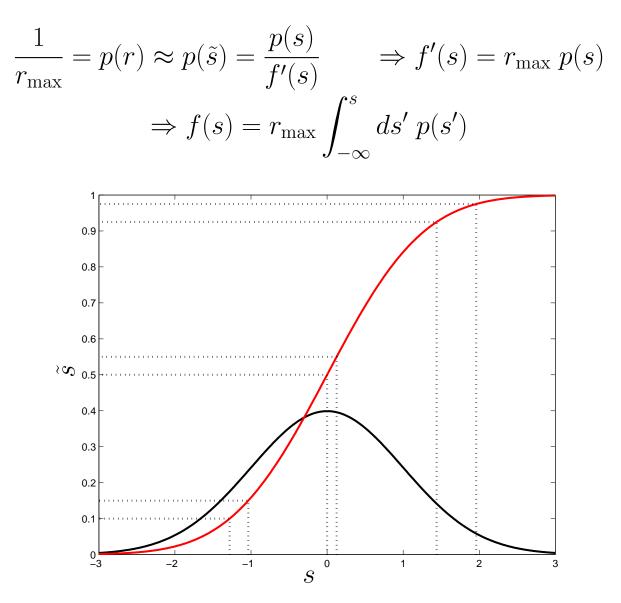
If noise is small and "constant" \Rightarrow maximise marginal entropy \Rightarrow maximise $\mathbf{H}\left[\widetilde{S}\right]$ Consider a (rate coding) neuron with $r \in [0, r_{\max}]$.

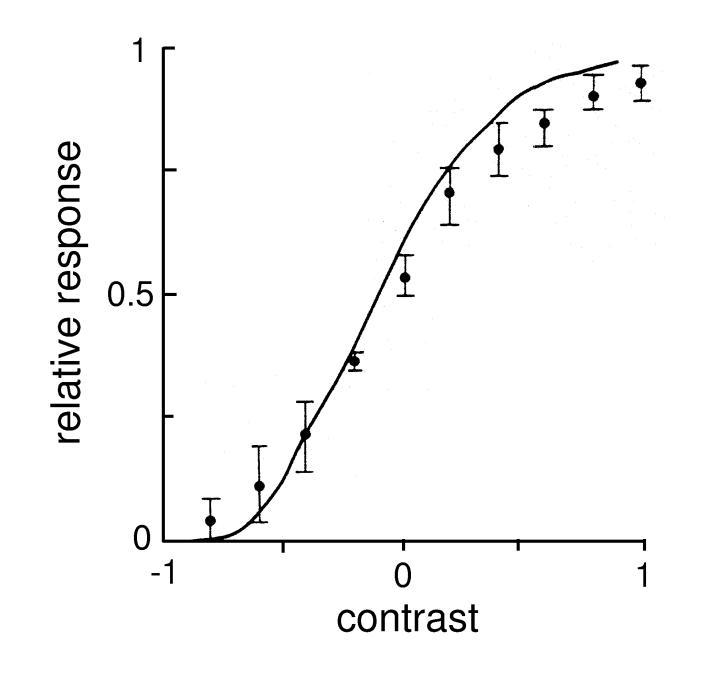
$$h(r) = -\int_0^{r_{\max}} dr \, p(r) \log p(r)$$

To maximise the marginal entropy, we add a Lagrange multiplier (μ) to enforce normalisation and then differentiate

$$\begin{split} \frac{\delta}{\delta p(r)} \begin{bmatrix} h(r) - \mu \int_0^{r_{\max}} p(r) \end{bmatrix} &= \begin{cases} -\log p(r) - 1 - \mu & r \in [0, r_{\max}] \\ 0 & \text{otherwise} \end{cases} \\ \Rightarrow p(r) &= const \text{ for } r \in [0, r_{\max}] \\ \text{i.e.} \\ p(r) &= \begin{cases} \frac{1}{r_{\max}} & r \in [0, r_{\max}] \\ 0 & \text{otherwise} \end{cases} \end{split}$$

Suppose $r = \tilde{s} + \eta$ where η represents a (relatively small) source of noise. Consider deterministic encoding $\tilde{s} = f(s)$. How do we ensure that $p(r) = 1/r_{\text{max}}$?





Laughlin (1981)

A similar idea of output-entropy maximisation appears in the theory of Gaussian channel coding, where it is called the **water filling** algorithm.

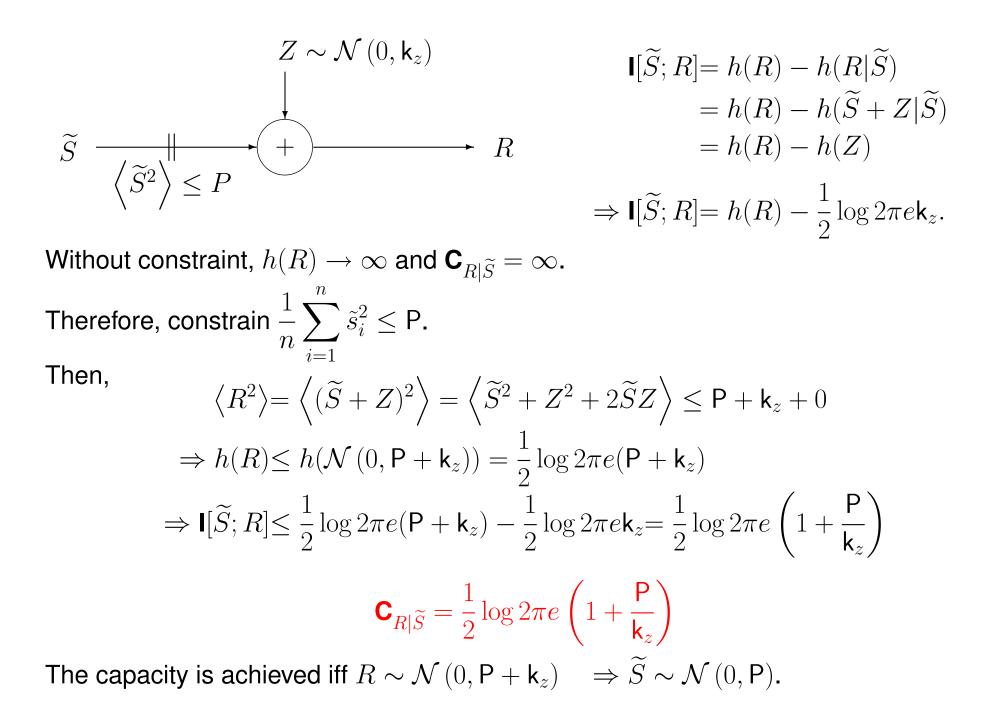
We will need the differential entropy of a (multivariate) Gaussian distribution:

$$p(\mathbf{Z}) = |2\pi\Sigma|^{-1/2} \exp\left[-\frac{1}{2}(\mathbf{Z}-\boldsymbol{\mu})^{\mathsf{T}}\Sigma^{-1}(\mathbf{Z}-\boldsymbol{\mu})\right],$$

then,

Let

$$\begin{split} h(\mathbf{Z}) &= -\int d\mathbf{Z} \ p(\mathbf{Z}) \left[-\frac{1}{2} \log |2\pi\Sigma| - \frac{1}{2} (\mathbf{Z} - \boldsymbol{\mu})^{\mathsf{T}} \Sigma^{-1} (\mathbf{Z} - \boldsymbol{\mu}) \right] \\ &= \frac{1}{2} \log |2\pi\Sigma| + \frac{1}{2} \int d\mathbf{Z} \ p(\mathbf{Z}) \mathsf{Tr} \left[\Sigma^{-1} (\mathbf{Z} - \boldsymbol{\mu}) (\mathbf{Z} - \boldsymbol{\mu})^{\mathsf{T}} \right] \\ &= \frac{1}{2} \log |2\pi\Sigma| + \frac{1}{2} \mathsf{Tr} \left[\Sigma^{-1} \Sigma \right] \\ &= \frac{1}{2} \log |2\pi\Sigma| + \frac{1}{2} d \quad (\log e) \\ &= \frac{1}{2} \log |2\pie\Sigma| \end{split}$$



Now consider a vector Gaussian channel:

$$\widetilde{\mathbf{S}} = (S_1, \dots, S_d) \xrightarrow[\frac{1}{d}]{\mathsf{Tr}} [\widetilde{\mathbf{S}}\widetilde{\mathbf{S}}^{\mathsf{T}}] \leq P \qquad \mathbf{R} = (R_1, \dots, R_d)$$

Following the same approach as before:

$$\mathbf{I}[\widetilde{\mathbf{S}};\mathbf{R}] = h(\mathbf{R}) - h(\mathbf{Z}) \leq \frac{1}{2} \log\left[(2\pi e)^n |\mathbf{K}_{\widetilde{s}} + \mathbf{K}_z|\right] - \frac{1}{2} \log\left[(2\pi e)^n |\mathbf{K}_z|\right],$$

 $\Rightarrow \mathbf{C}_{R|S}$ achieved when $\widetilde{\mathbf{S}}$ (and thus \mathbf{R}) $\sim \mathcal{N}$, with $|\mathbf{K}_{\tilde{s}} + \mathbf{K}_{z}|$ max given $\frac{1}{d} \operatorname{Tr} [\mathbf{K}_{\tilde{s}}] \leq P$. Diagonalise $\mathbf{K}_{z} \Rightarrow \mathbf{K}_{\tilde{s}}$ is diagonal in same basis. For **stationary** noise (wrt dimension indexed by *d*) this can be achieved by a Fourier transform \Rightarrow index diagonal elements by ω .

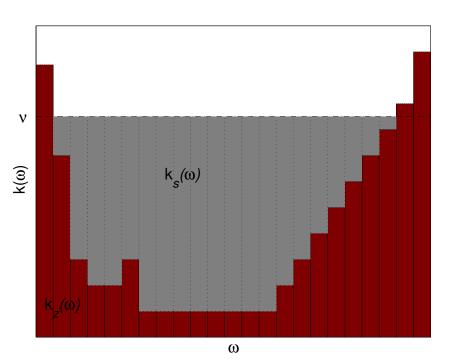
$$\mathbf{k}_{\tilde{s}}^{*}(\omega) = \operatorname{argmax} \prod_{\omega} \left(\mathbf{k}_{\tilde{s}}(\omega) + \mathbf{k}_{z}(\omega) \right) \qquad \text{such that } \frac{1}{d} \sum \mathbf{k}_{\tilde{s}}(\omega) \leq P$$

Assume that optimum is achieved for max. input power.

$$\begin{aligned} \mathbf{k}_{\tilde{s}}^{*}(\omega) =& \arg\max\left[\sum_{\omega} \log\left(\mathbf{k}_{\tilde{s}}(\omega) + \mathbf{k}_{z}(\omega)\right) - \lambda\left(\frac{1}{d}\sum_{\omega}\mathbf{k}_{\tilde{s}}(\omega) - P\right)\right] \\ \Rightarrow \frac{1}{\mathbf{k}_{\tilde{s}}^{*}(\omega) + \mathbf{k}_{z}(\omega)} - \frac{\lambda}{d} = 0 \\ \Rightarrow \mathbf{k}_{\tilde{s}}^{*}(\omega) + \mathbf{k}_{z}(\omega) = \nu \quad (const.) \\ (\mathbf{k}_{\tilde{s}} \geq 0) \Rightarrow \mathbf{k}_{\tilde{s}}^{*}(\omega) = [\nu - \mathbf{k}_{z}(\omega)]^{+} \end{aligned}$$

Waterfilling: choose ν so

$$\sum_{\omega} \mathsf{k}_{\tilde{s}}(\omega) = d \cdot P$$



R is white or decorrelated (within power budget) \Rightarrow variance equalisation.

Atick and Redlich (1992) argued that the retina decorrelates natural spatial statistics. RGCs exhibit roughly linear (centre-surround) processing:

$$r_{\mathbf{a}} - \langle r_{\mathbf{a}} \rangle = \int d\mathbf{x} \underbrace{D_s(\mathbf{x} - \mathbf{a})}_{\text{filter}} \underbrace{s(\mathbf{x})}_{\text{stimulus}}$$

Therefore the correlation (covariance) between cells is

$$Q_r(\mathbf{a}, \mathbf{b}) = \left\langle \int d\mathbf{x} \, d\mathbf{y} \, D_s(\mathbf{x} - \mathbf{a}) D_s(\mathbf{y} - \mathbf{b}) s(\mathbf{x}) s(\mathbf{y}) \right\rangle$$
$$= \int d\mathbf{x} \, d\mathbf{y} \, D_s(\mathbf{x} - \mathbf{a}) D_s(\mathbf{y} - \mathbf{b}) \underbrace{\langle s(\mathbf{x}) s(\mathbf{y}) \rangle}_{Q_s(\mathbf{x}, \mathbf{y})}$$

Using (spatial) stationarity, we can transform to the Fourier domain:

$$\widetilde{Q}_r(\mathbf{k}) = |\widetilde{D}_s(\mathbf{k})|^2 \widetilde{Q}_s(\mathbf{k})$$

and thus output decorrelation requires

$$|\widetilde{D}_s({f k})|^2 \propto rac{1}{\widetilde{Q}_s({f k})}$$

Spatial correlations of natural images fall off with f^{-2} :

$$\widetilde{Q}_s(\mathbf{k}) \propto rac{1}{|\mathbf{k}|^2 + k_0^2}$$

and the optical filter of the eye introduces (crudely) a low-pass term $\propto e^{-\alpha |\mathbf{k}|}$. So decorrelation requires

$$\widetilde{D}_s(\mathbf{k})|^2 \propto rac{|\mathbf{k}|^2 + k_0^2}{e^{-lpha|\mathbf{k}|}}$$

But: not all input is signal.

Photodetection introduces noise. Therefore, cascade linear filters:

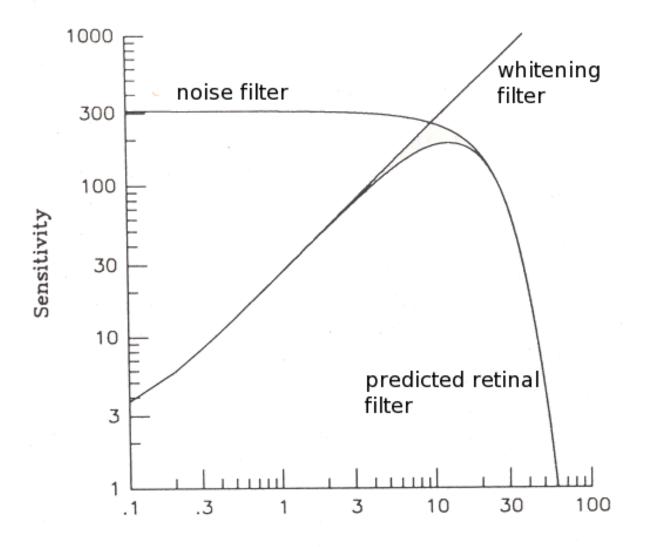
$$\mathbf{s} + \boldsymbol{\eta} \xrightarrow[D_{\eta}]{} \hat{\mathbf{s}} \xrightarrow[D_{s}]{} \mathbf{r}$$

with

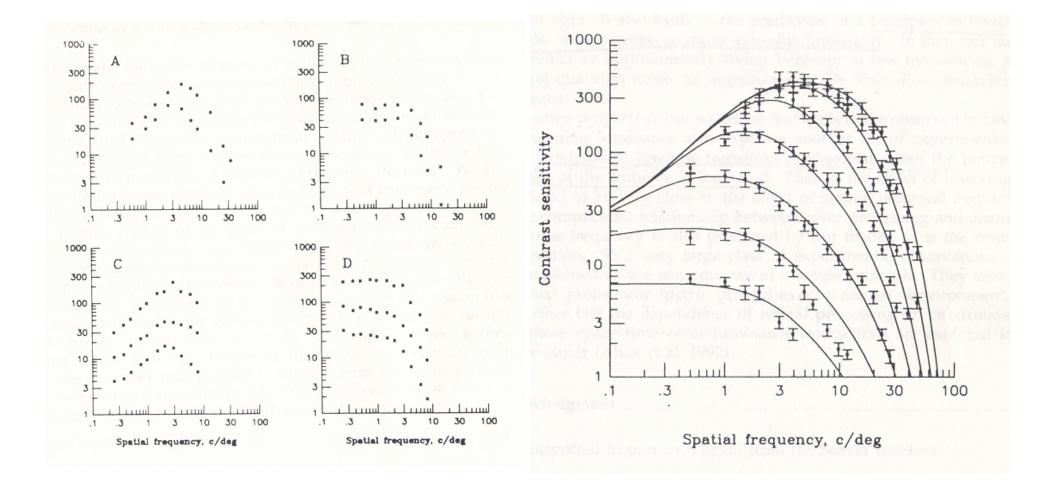
$$\widetilde{D}_{\eta}(\mathbf{k}) = rac{\widetilde{Q}_{s}(\mathbf{k})}{\widetilde{Q}_{s}(\mathbf{k}) + \widetilde{Q}_{\eta}(\mathbf{k})}$$
 (Wiener filter)

Thus the combined RGC filter is predicted to be:

$$|\widetilde{D}_{s}(\mathbf{k})|\widetilde{D}_{\eta}(\mathbf{k}) \propto rac{\sqrt{\widetilde{Q}_{s}(\mathbf{k})}}{\widetilde{Q}_{s}(\mathbf{k}) + \widetilde{Q}_{\eta}(\mathbf{k})}$$



Spatial frequency, c/deg



- efficient channel utilisation
- output entropy maximisation
- variance equalisation
- redundancy reduction
- decorrelation
- discovery of independent projections or components