Information Theory

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Quantifying a Code

- 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.

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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)

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How informative is R about S?

$$P(S|R) = \begin{bmatrix} 0, 0, 1, 0, \dots, 0 \end{bmatrix}$$
$$P(S|R) = \begin{bmatrix} \frac{1}{M}, \frac{1}{M}, \dots, \frac{1}{M} \end{bmatrix}$$

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We need to start by considering the uncertainty in a probability distribution \rightarrow called the $\ensuremath{\text{entropy}}$

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.

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,

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

$$\begin{array}{ccc} \log_2 M^N & B_N \leq & \log_2 M^N + 1 & 2 & M^N \\ & \rightarrow -N \log_2 \frac{1}{M} & \text{as } N \rightarrow \infty \\ & \Rightarrow B_s \rightarrow -\log_2 p \text{ bits} \end{array}$$

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.

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

$$P(S_1, S_2, \ldots, S_N) = \prod_m p_m^{n_m}$$

[where $n_m = (\# \text{ of } S_i = s_m)$].

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

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

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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

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

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

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

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so we can write

$$H[S|r] = -\sum_{s} P(s|r) \log_{2} P(s|r) = -\sum_{s,r} P(s) \int_{s,r} P(s) \int_{s,r}$$

It is easy to show that:

The average

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

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

Average Mutual Information

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Measures reduction in uncertainty due to R.

It follows from the definition that

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

Average Mutual Information



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.

Kullback-Leibler Divergence

Another useful information theoretic quantity measures the difference between two distributions. $\mu_{IO} = \frac{1}{2} R_O k_0 \frac{1}{2}$

$$\mathsf{KL}[P(S)||Q(S)] = \sum_{s} P(s) \log \frac{P(s)}{Q(s)}$$

$$= \sum_{s} P(s) \log \frac{1}{Q(s)} - \mathsf{H}[P]$$

$$E \quad \text{cross entropy} \quad \text{colcutor keyth under } Q$$

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

$$egin{aligned} -\mathsf{KL}[P\|Q] &= \sum_s P(s)\lograc{Q(s)}{P(s)} \ &\leq \log\sum_s P(s)rac{Q(s)}{P(s)} \ & ext{ by Jensen} \ &= \log\sum_s Q(s) = \log 1 = 0 \end{aligned}$$

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

Mutual Information and KL

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

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1. Mutual information is always non-negative

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Thus:

1. Mutual information is always non-negative

 $I[S; R] \ge 0$

2. Conditioning never increases entropy

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

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

$$R_1 \perp \perp R_2 \Rightarrow \mathbf{H}[R_1, R_2] = \mathbf{H}[R_1] + \mathbf{H}[R_2]$$
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$$\begin{array}{cccc} R_1 \perp \!\!\! \perp R_2 & R_1 \perp \!\!\! \perp R_2 | S \\ \text{no} & \text{yes} & \textit{I}_{12} < \textit{I}_1 + \textit{I}_2 & \text{redundant} \end{array}$$

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$R_1 \perp \perp R_2$	$R_1 \perp \perp R_2 S$		
no	yes	$I_{12} < I_1 + I_2$	redundant
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Two responses to the same stimulus, R_1 and R_2 , may provide either more or less information jointly than independently.

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

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

$$I_{12} = \mathbf{I}[S; H_1, H_2] = \mathbf{H}[H_1, H_2] - \mathbf{H}[H_1, H_2|S]$$

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$$S = \begin{pmatrix} \ell_1 & \ell_2 & \ell_1 \\ \ell_1 & \ell_1 \\ \ell_1 & \ell_2 & \ell_1 \\ \ell_1 & \ell_1 & \ell_2 \\ \ell_1 & \ell_1 & \ell_1 \\ \ell_1 & \ell_1 & \ell_2 \\ \ell_1 & \ell_1 & \ell_1 \\ \ell_1 & \ell_1 & \ell_2 \\ \ell_1 & \ell_1 & \ell_1 \\ \ell_1 & \ell$$

4.

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

Data Processing Inequality

Data Processing Inequality R_{AVINS} as $S = \frac{R_{A}}{2R_{A}}$

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

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

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

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Thus,

$$\begin{split} \mathbf{H}[S|R_2] &\geq \mathbf{H}[S|R_1, R_2] = \mathbf{H}[S|R_1] \\ &\Rightarrow \mathbf{I}[S; R_2] \leq \mathbf{I}[S; R_1] \end{split}$$

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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.

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

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

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

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

or alternatively as

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

If $S_i \stackrel{\text{iid}}{\sim} P(S)$ then H[S] = H[S]. If S is Markov (and stationary) then $H[S] = H[S_n|S_{n-1}]$.

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We define the differential entropy:

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

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

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The mutual information, however, is well-defined

$$I_{\Delta}[S; R] = H_{\Delta}[S] - H_{\Delta}[S|R]$$

$$= -\sum_{i} \Delta s \ p(s_{i}) \log p(s_{i}) - \log \Delta s$$

$$-\int dr \ p(r) \left(-\sum_{i} \Delta s \ p(s_{i}|r) \log p(s_{i}|r) - \log \Delta s \right)$$

$$\rightarrow h(S) - h(S|R)$$
as are other KL divergences.
$$= \int dr \ As \ p^{(r,s)} \int \frac{p(r,s)}{p(r,s)} dr$$

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$$\mathcal{L} = \int ds \, p(s) \log p(s) - \lambda_0 \left[\int ds \, p(s) - 1 \right] - \lambda_1 \left[\int ds \, p(s) f(s) - a \right]$$
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$$\begin{array}{ll} f(s) = s & \Rightarrow & p(s) = \frac{1}{Z} e^{\lambda_1 s}. & \text{Exponential (need } p(s) = 0 \text{ for } s < T). \\ f(s) = s^2 & \Rightarrow & p(s) = \frac{1}{Z} e^{\lambda_1 s^2}. & \text{Gaussian.} \end{array}$$

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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.

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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.

Joint source-channel coding theorem

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 $H[S] < C_{R|\tilde{S}}$ can be transmitted (in sufficiently long blocks) with $P_{error} \rightarrow 0$.

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

The channel coding problem

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

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

By data processing inequality, and defn of capacity:

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

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 $P(\tilde{S})$ that saturates $C_{R|\tilde{S}}$ for a general discrete channel.





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

$$\frac{\delta}{\delta p(r)} \left[h(r) - \mu \int_0^{r_{\max}} p(r) \right] = \begin{cases} -\log p(r) - 1 - \mu & r \in [0, r_{\max}] \\ 0 & \text{otherwise} \end{cases}$$



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i.e.
$$p(r) = \begin{cases} \frac{1}{r_{max}} & r \in [0, r_{max}] \\ 0 & \text{otherwise} \end{cases}$$

Histogram Equalisation

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 $p(r) = 1/r_{max}$?

$$\frac{1}{r_{\max}} = p(r) \approx p(\tilde{s}) = \frac{p(s)}{f'(s)} \qquad \Rightarrow f'(s) = r_{\max} p(s)$$
$$\Rightarrow f(s) = r_{\max} \int_{-\infty}^{s} ds' \ p(s')$$



Histogram Equalisation



Laughlin (1981)
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$$= \frac{1}{2} \log |2\pi\varepsilon|$$





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$$\Rightarrow \mathsf{I}[\tilde{S}; R] \le \frac{1}{2}\log 2\pi e(\mathsf{P} + \mathsf{k}_z) - \frac{1}{2}\log 2\pi e\mathsf{k}_z = \frac{1}{2}\log 2\pi e\left(1 + \frac{\mathsf{P}}{\mathsf{k}_z}\right)$$



$$\begin{split} \mathbf{I}[\widetilde{S};R] &= h(R) - h(R|\widetilde{S}) \\ &= h(R) - h(\widetilde{S} + Z|\widetilde{S}) \\ &= h(R) - h(Z) \\ \Rightarrow \mathbf{I}[\widetilde{S};R] &= h(R) - \frac{1}{2}\log 2\pi e \mathsf{k}_z. \end{split}$$

Without constraint, $h(R) \to \infty$ and $\mathbf{C}_{R|\widetilde{S}} = \infty$.

Therefore, constrain $\frac{1}{n} \sum_{i=1}^{n} \tilde{s}_i^2 \leq \mathsf{P}.$

Then,

$$\langle R^2 \rangle = \left\langle (\widetilde{S} + Z)^2 \right\rangle = \left\langle \widetilde{S}^2 + Z^2 + 2\widetilde{S}Z \right\rangle \le \mathsf{P} + \mathsf{k}_z + 0$$

$$\Rightarrow h(R) \le h(\mathcal{N}(0, \mathsf{P} + \mathsf{k}_z)) = \frac{1}{2}\log 2\pi e(\mathsf{P} + \mathsf{k}_z)$$

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The capacity is achieved iff $R \sim \mathcal{N}(0, \mathsf{P} + \mathsf{k}_z) \quad \Rightarrow \widetilde{S} \sim \mathcal{N}(0, \mathsf{P}).$

Now consider a vector Gaussian channel:

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

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Following the same approach as before:

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

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For **stationary** noise (wrt dimension indexed by *d*) this can be achieved by a Fourier transform \Rightarrow index diagonal elements by ω .

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

$$k_{\tilde{s}}^{*}(\omega) = \operatorname{argmax}\left[\sum_{\omega} \log\left(k_{\tilde{s}}(\omega) + k_{z}(\omega)\right) - \lambda\left(\frac{1}{d}\sum_{\omega}k_{\tilde{s}}(\omega) - P\right)\right]$$

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

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Assume that optimum is achieved for max. input power.

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

Waterfilling: choose ν so

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



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



Atick and Redlich (1992) argued that the retina decorrelates natural spatial statistics.

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RGCs exhibit roughly linear (centre-surround) processing:

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

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Therefore the correlation (covariance) between cells is

$$Q_{r}(\mathbf{a},\mathbf{b}) = \left\langle \int d\mathbf{x} \, d\mathbf{y} \, D_{s}(\mathbf{x}-\mathbf{a}) D_{s}(\mathbf{y}-\mathbf{b}) s(\mathbf{x}) s(\mathbf{y}) \right\rangle$$
$$= \int d\mathbf{x} \, d\mathbf{y} \, D_{s}(\mathbf{x}-\mathbf{a}) D_{s}(\mathbf{y}-\mathbf{b}) \underbrace{\langle s(\mathbf{x})s(\mathbf{y}) \rangle}_{Q_{s}(\mathbf{x},\mathbf{y})}$$

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

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

and thus output decorrelation requires

$$\left|\widetilde{D}_{s}(\mathbf{k})\right|^{2} \propto rac{1}{\widetilde{Q}_{s}(\mathbf{k})}$$

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

$$|\widetilde{D}_{s}(\mathbf{k})|^{2} \propto \frac{|\mathbf{k}|^{2} + k_{0}^{2}}{e^{-\alpha|\mathbf{k}|}} \sim e^{\frac{|\mathbf{k}|^{2}}{2}}$$

1 1

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Photodetection introduces noise. Therefore, cascade linear filters:

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

$$\widetilde{D}_{\eta}(\mathbf{k}) = \frac{\widetilde{Q}_{s}(\mathbf{k})}{\widetilde{Q}_{s}(\mathbf{k}) + \widetilde{Q}_{\eta}(\mathbf{k})} \qquad \underbrace{(\text{Wiener filter})}_{\text{(wiener filter)}} \qquad \underbrace{(\text{Wiener filter})}_{\text{(wiener filter)}}$$

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 (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



Related ideas

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