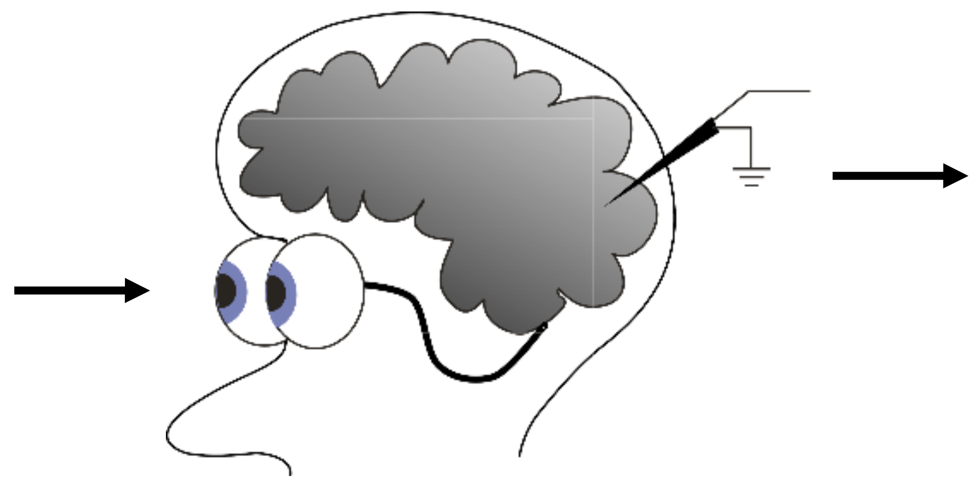
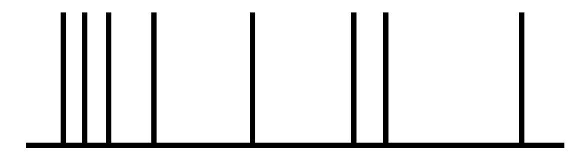
THE NEURAL CODING PROBLEM

stimulus s

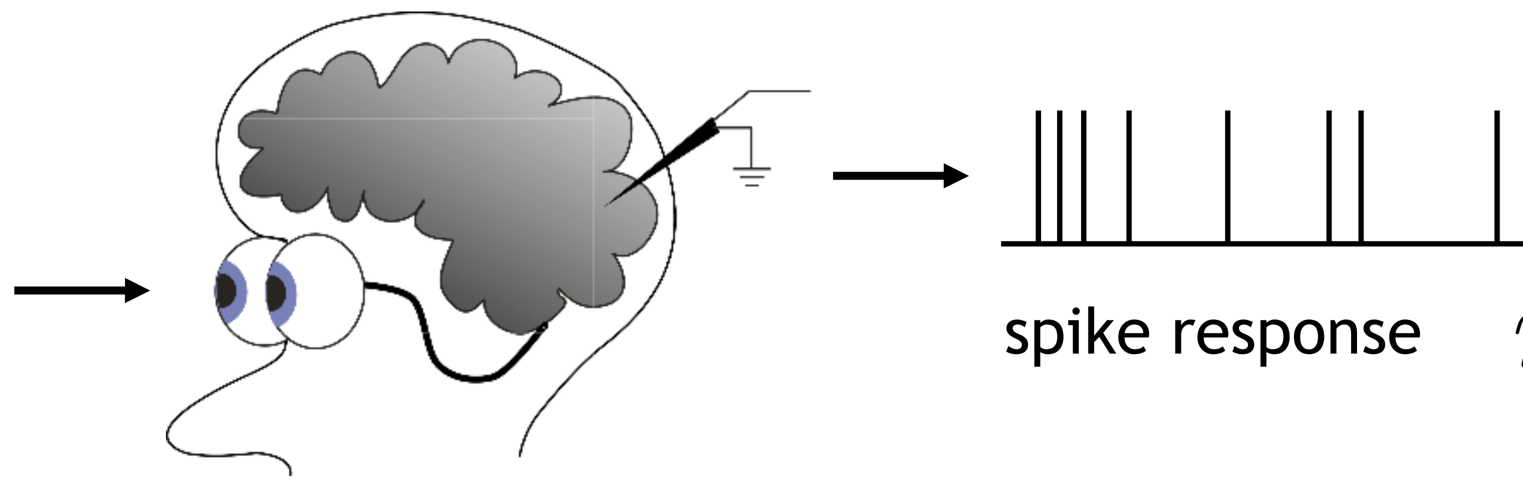




spike response r

THE NEURAL CODING PROBLEM

What is the relationship between environmental stimuli and neural activity?



spike response r

stimulus s

THE NEURAL CODING PROBLEM

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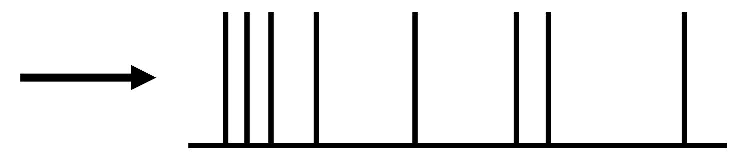
stimulus s

$\mathrm{P}(r|s)$



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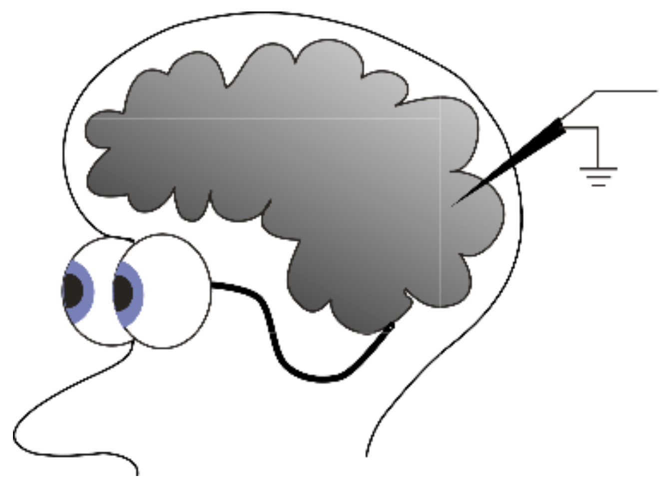
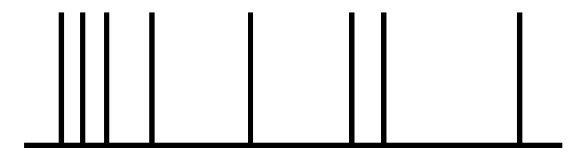


$\mathrm{P}(r|s)$



spike response r

What is the codebook for neural responses?

THE NEURAL CODING PROBLEM

What is the relationship between environmental stimuli and neural activity?

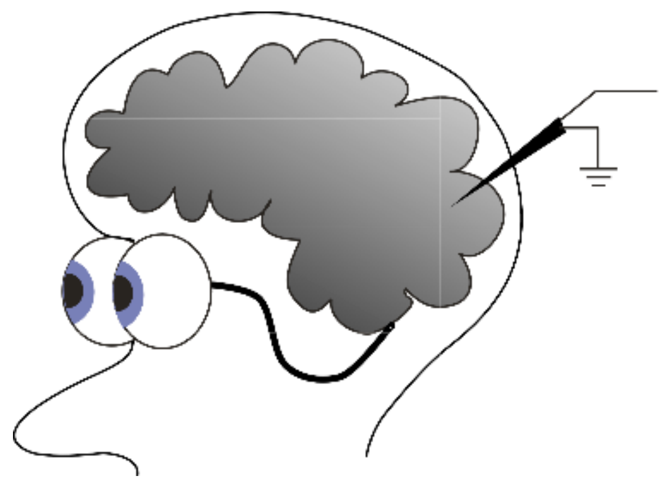
Codebook: $\mathrm{P}(r|s)$

(encoding distribution)

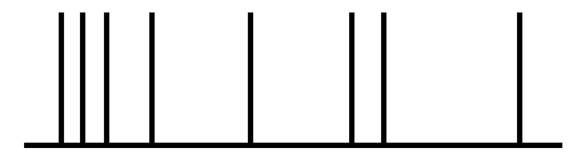
THE NEURAL CODING PROBLEM

What is the relationship between environmental stimuli and neural activity?

stimulus s



$$\mathrm{P}(r|s)$$



spike response r

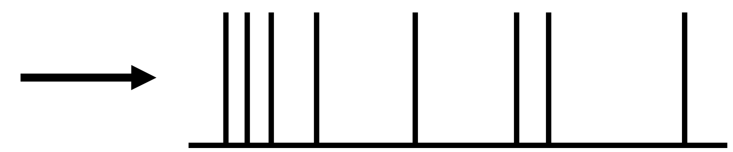
What is the codebook for neural responses?

THE EFFICIENT CODING PROBLEM

What is the relationship between environmental stimuli and neural activity?

stimulus s

$\mathrm{P}(r|s)$



spike response r

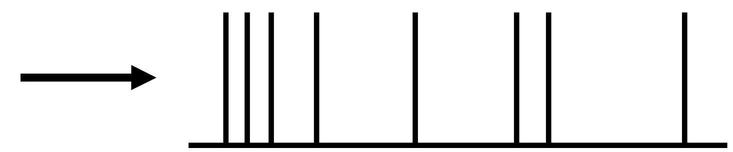
What is the codebook for neural responses?

THE EFFICIENT CODING PROBLEM

What is the optimal relationship between environmental stimuli and neural activity?

stimulus s

$\mathrm{P}(r|s)$



spike response r

What is the codebook for neural responses?

THE EFFICIENT CODING PROBLEM

optimal
What is the relationship between environmental stimuli and neural activity?

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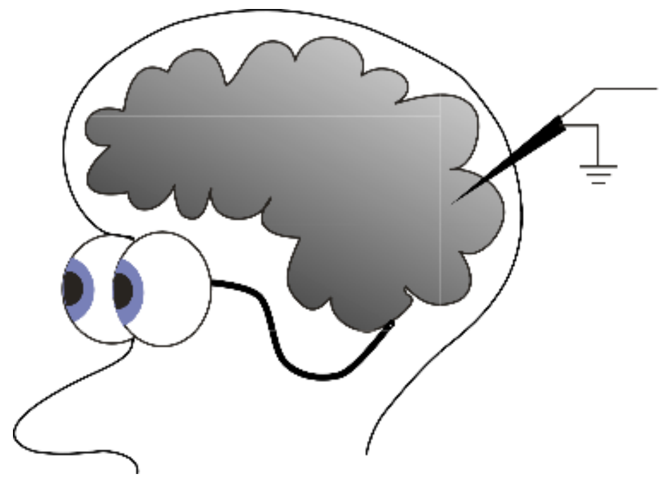
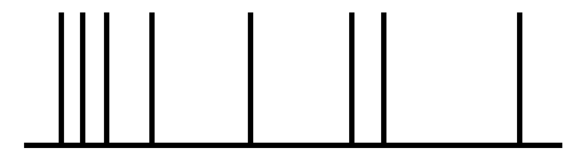


$\mathrm{P}(r|s)$



spike response r

What is the codebook for neural responses?
that allows preserving the most information in r about s

INFORMATION THEORY PRIMER

discrete random variables — probability distributions

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discrete random variables — probability distributions

'surprise' when observing a particular r

$$h(r) = -\log_2(\mathrm{P}(r)) \qquad 0 \leq h(r)$$

INFORMATION THEORY PRIMER

discrete random variables — probability distributions

'surprise' when observing a particular r

$$h(r) = -\log_2(\mathrm{P}(r))$$

$$0 \leq h(r)$$

entropy = uncertainty about r = average surprise when observing some r

$$0 \leq H_\mathrm{r}$$

$$H_\mathrm{r} = -\sum_r \mathrm{P}(r) \log_2(\mathrm{P}(r))$$

INFORMATION THEORY PRIMER

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$$H_\mathrm{r} = H_{f(\mathrm{r})}$$

f is invertible

$$H_{\mathrm{r}_1,\mathrm{r}_2} = H_{\mathrm{r}_1} + H_{\mathrm{r}_2} \text{ iff } r_1 \perp r_2$$

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uncertainty about r when a particular s is known

$$H_{\mathrm{r}}|\mathrm{s} \quad = \quad -\sum_r \mathrm{P}(r|s)\,\log_2(\mathrm{P}(r|s))$$

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$$H_{\mathrm{r}} = H_{f(\mathrm{r})}$$ f is invertible

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uncertainty about r when a particular s is known

$$H_{\mathrm{r}}|\mathrm{s} \quad = \quad -\sum_{r} \mathrm{P}(r|s) \, \log_2(\mathrm{P}(r|s))$$

conditional entropy = average uncertainty about r when some s is known

$$\begin{aligned} H_{\mathrm{r}|\mathrm{s}} \quad &= \quad -\sum_{s} \mathrm{P}(s) \sum_{r} \mathrm{P}(r|s) \, \log_2(\mathrm{P}(r|s)) \\ &= \quad -\sum_{r,s} \mathrm{P}(r,s) \, \log_2(\mathrm{P}(r|s)) \end{aligned}$$

$$0 \leq H_{\mathrm{r}|\mathrm{s}} \leq H_{\mathrm{r}}$$

$$H_{\mathrm{r}|\mathrm{s}} = 0 \text{ iff } r = f(s)$$

$$H_{\mathrm{r}|\mathrm{s}} = H_{\mathrm{r}} \text{ iff } r \perp s$$

MUTUAL INFORMATION

MUTUAL INFORMATION

mutual information = average reduction in uncertainty about r by knowing s

$$
\begin{aligned}
I_{\mathrm{r,s}} &= H_{\mathrm{r}} - H_{\mathrm{r|s}} = H_{\mathrm{s}} - H_{\mathrm{s|r}} \\
&= \sum_{r,s} \mathrm{P}(r,s) \log_2 \frac{\mathrm{P}(r,s)}{\mathrm{P}(r)\,\mathrm{P}(s)} \\
\text{or} &\quad \int_{-\infty}^{\infty} \mathrm{P}(r,s) \log_2 \frac{\mathrm{P}(r,s)}{\mathrm{P}(r)\,\mathrm{P}(s)}\, dr\, ds
\end{aligned}
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$$
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symmetric $\quad I_{\mathrm{r,s}} = I_{\mathrm{s,r}}$

non-negative $\quad 0 \leq I_{\mathrm{r,s}}$

$I_{\mathrm{r,s}} = 0 \text{ iff } r \perp s$

invariant $\quad I_{\mathrm{r,s}} = I_{f(\mathrm{r}),g(\mathrm{s})}$ $\quad f$ and g are bijective

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Kullback-Leibler divergence (aka relative entropy)

$$
D_{\mathrm{KL}}(\mathrm{P}(\cdot)\,\|\mathrm{Q}(\cdot)) = \sum_x \mathrm{P}(x) \log_2 \frac{\mathrm{P}(x)}{\mathrm{Q}(x)} \quad \text{or} \quad \int_{-\infty}^{\infty} \mathrm{P}(x) \log_2 \frac{\mathrm{P}(x)}{\mathrm{Q}(x)}\, dx
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$$D_{\mathrm{KL}}(\mathrm{P}(\cdot)\,\|\mathrm{Q}(\cdot)) \geq 0$$
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relationship between mutual information and KL-divergence

$$x = (r,s)\,, \quad \mathrm{P}(x) = \mathrm{P}(r,s)\,, \quad \mathrm{Q}(x) = \mathrm{P}(r)\,\mathrm{P}(s)$$

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STATISTICALLY EFFICIENT CODING

$$\mathrm{P}(s) \longrightarrow \underbrace{s \longrightarrow \mathrm{P}(r|s) \longrightarrow r}_{I_{\mathrm{r,s}}}$$

natural stimulus statistics

neural response characteristics

STATISTICALLY EFFICIENT CODING

$$\mathrm{P}(s) \longrightarrow s \longrightarrow \mathrm{P}(r|s) \longrightarrow r$$

natural stimulus statistics

neural response characteristics

$I_{\mathrm{r,s}}$

what is the $\mathrm{P}(r|s)$ that maximises $I_{\mathrm{r,s}}$ for a given $\mathrm{P}(s)$ under appropriate constraints?

STATISTICALLY EFFICIENT CODING

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simple example:

$$\begin{aligned} s &\sim \mathcal{N}(0, \sigma_s^2) \\ r &= as + \epsilon, \quad \epsilon \sim \mathcal{N}(0, \sigma_r^2) \end{aligned}$$

STATISTICALLY EFFICIENT CODING

$$\begin{tikzcd}
\mathrm{P}(s) \arrow[r] & s \arrow[r] \arrow[rr, dash, bend right, "I_{\mathrm{r,s}}"'] & \mathrm{P}(r|s) \arrow[r] & r
\end{tikzcd}$$

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$$\downarrow$$

$$r|s \sim \mathcal{N}(as, \sigma_r^2)$$

$$r \sim \mathcal{N}(0, a^2\sigma_s^2 + \sigma_r^2)$$

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trade-off between increasing H_{r} and decreasing $H_{\mathrm{r|s}}$

STATISTICALLY EFFICIENT CODING

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degenerate solutions

$$a \rightarrow \infty$$

$$\sigma_r^2 \rightarrow 0$$

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degenerate solutions

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$$\sigma_r^2 \to 0$$

need constraints

MAXIMUM ENTROPY FOR AN INDIVIDUAL NEURON

$$I_{\mathrm{r,s}} = H_{\mathrm{r}} - H_{\mathrm{r|s}}$$

MAXIMUM ENTROPY FOR AN INDIVIDUAL NEURON

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assume: $\mathrm{P}(r|s) \to \delta(r - f(s))$

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2. find $f(s)$ that yields desired $\mathrm{P}_{\mathrm{r}}(r)$

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HISTOGRAM EQUALISATION

maximum entropy with $0 \leq r \leq r_{\max}$ constraint

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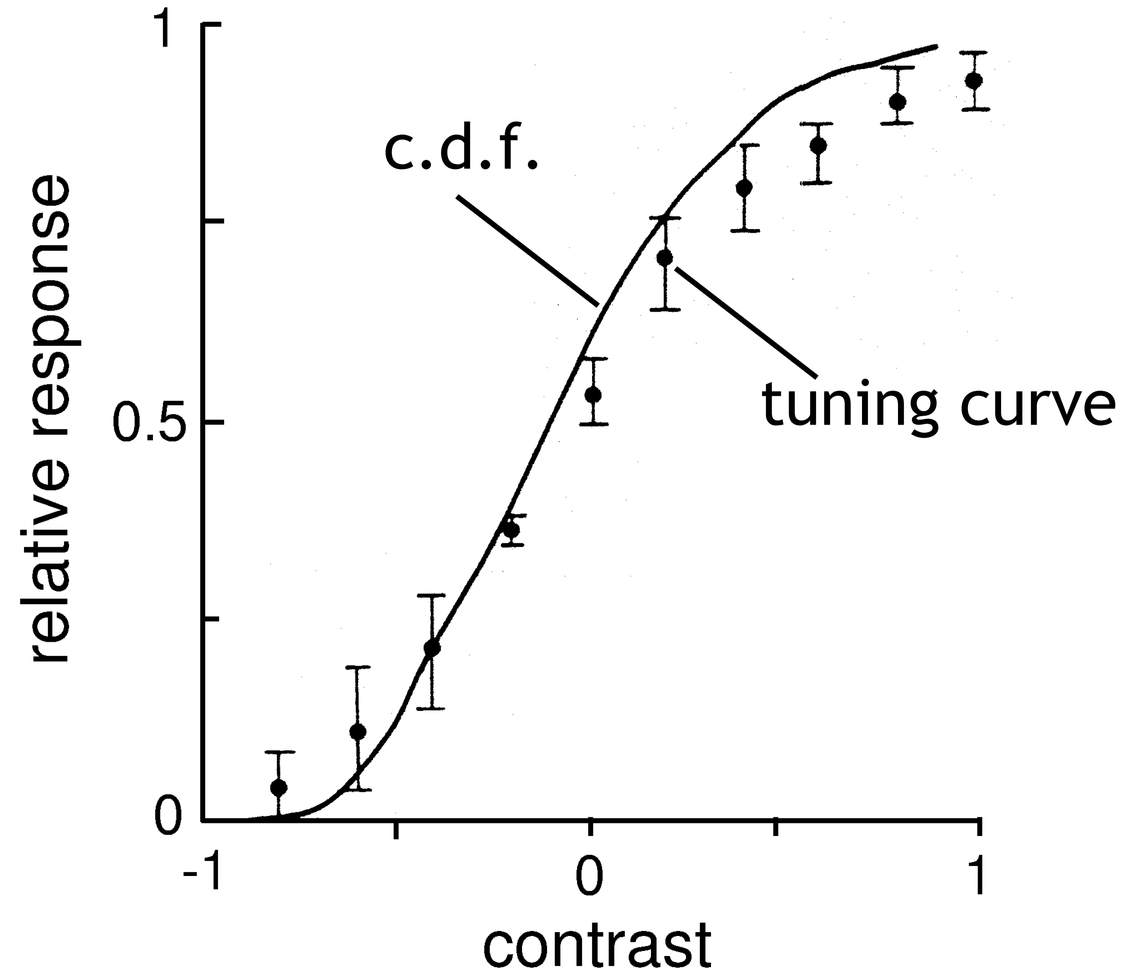
large monopolar cell in fly retina
(Laughlin, 1981)



WHITENING IN THE RETINA

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continuous neural field
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stimulus correlation function

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$e^{-\alpha\,|\boldsymbol{\kappa}|} \leftarrow$ optics of the eye

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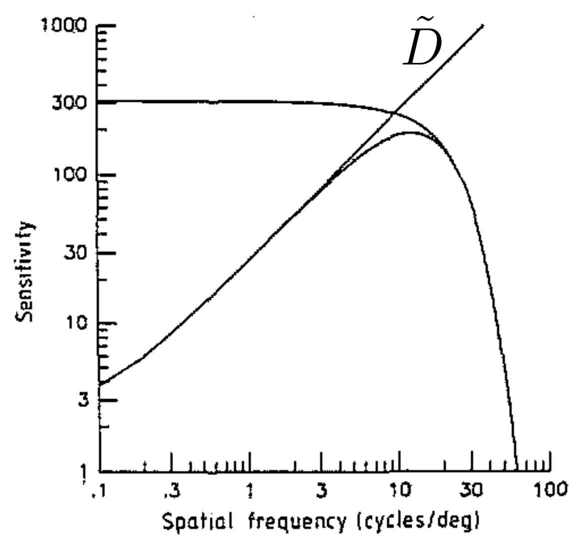

κ

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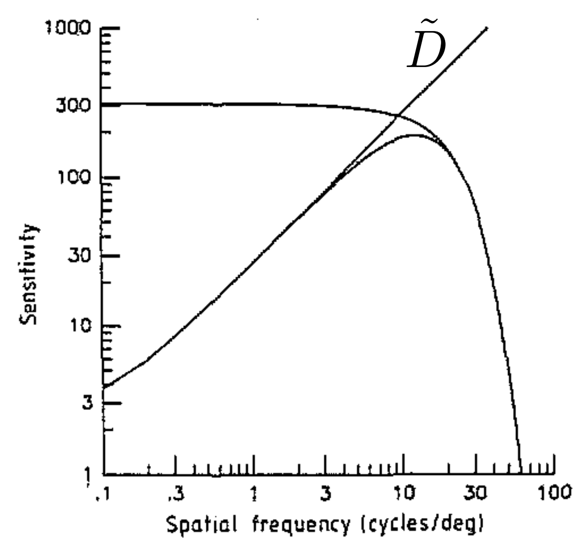
input noise

$$\eta \rightarrow s_\eta,\quad s^* \rightarrow s_\eta,\quad s_\eta \xrightarrow{D_\eta} s \xrightarrow{D} r$$



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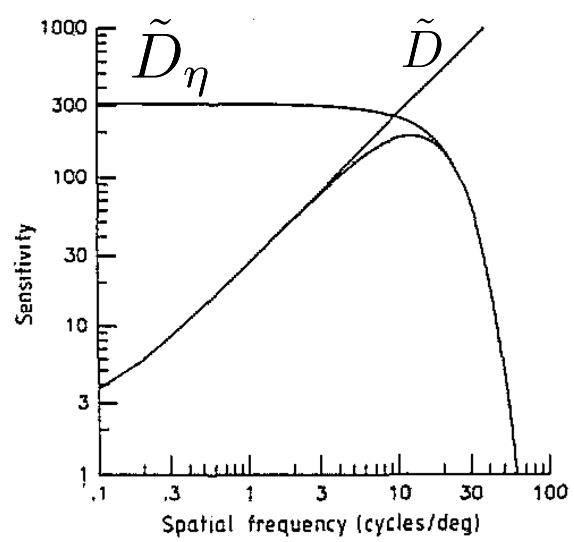

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$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

factorial code

$$H_{\mathbf{r}} = \sum_a H_{\mathrm{r}_a} \text{ iff } \mathrm{P}(\mathbf{r}) = \prod_{a=1}^{N} \mathrm{P}(r_a)$$

probability equalisation $\mathrm{P}(r_a) = \mathrm{P}(r_b)\ \forall a, b$ if constraints are same

$\approx$ decorrelation and variance equalisation

stimulus correlation function

$$Q(\mathbf{a},\mathbf{b}) = \sigma_{\mathrm{r}}^2\, \delta(\mathbf{a}-\mathbf{b}) = \int\!\!\int \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}\, D(\mathbf{x}-\mathbf{a})\, D(\mathbf{y}-\mathbf{b})\, C(\mathbf{x}-\mathbf{y})$$

continuous neural field performing filtering

$$r_{\mathbf{a}} = f_{\mathbf{a}}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$$

constraint directly on $f(s)$ rather than on $\mathrm{P}_{\mathrm{r}}(r)$

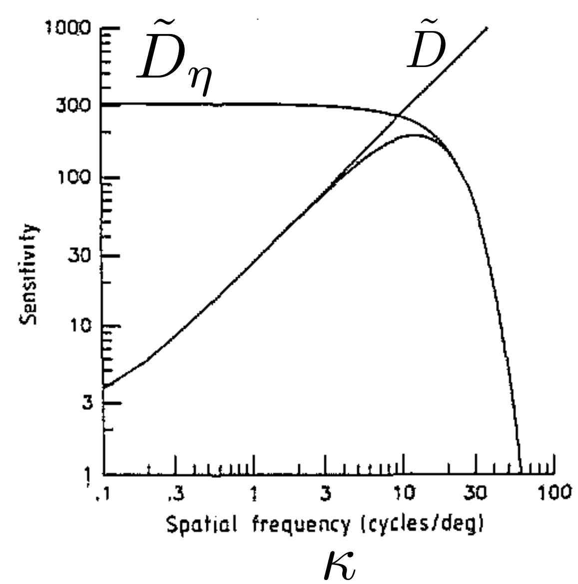
what is the optimal filter $D(\mathbf{x})$?

input noise

$$\begin{array}{l} \eta \searrow \\ \quad\quad s_\eta \xrightarrow{D_\eta} s \xrightarrow{D} r \\ s^* \nearrow \end{array}$$

$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

$$\left|\tilde{D}(\boldsymbol{\kappa})\right| = \frac{\sigma_{\mathrm{r}}}{\sqrt{\tilde{C}(\boldsymbol{\kappa})}}$$



$$\tilde{C}(\boldsymbol{\kappa}) \propto \frac{e^{-\alpha\,|\boldsymbol{\kappa}|}}{|\boldsymbol{\kappa}|^2 + \kappa_0^2}$$

$e^{-\alpha\,|\boldsymbol{\kappa}|}$ ← optics of the eye

$|\boldsymbol{\kappa}|^2 + \kappa_0^2$ ← natural images

WHITENING IN THE RETINA

and denoising

$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

factorial code

$$H_{\mathbf{r}} = \sum_a H_{\mathrm{r}_a} \text{ iff } \mathrm{P}(\mathbf{r}) = \prod_{a=1}^{N} \mathrm{P}(r_a)$$

probability equalisation

$$\mathrm{P}(r_a) = \mathrm{P}(r_b)\ \forall a, b$$ if constraints are same

stimulus correlation function

$\approx$ decorrelation and variance equalisation

$$Q(\mathbf{a},\mathbf{b}) = \sigma_{\mathrm{r}}^2\, \delta(\mathbf{a}-\mathbf{b}) = \int\!\!\int \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}\, D(\mathbf{x}-\mathbf{a})\, D(\mathbf{y}-\mathbf{b})\, C(\mathbf{x}-\mathbf{y})$$

continuous neural field performing filtering

$$r_{\mathbf{a}} = f_{\mathbf{a}}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$$

constraint directly on $f(s)$ rather than on $\mathrm{P}_{\mathrm{r}}(r)$

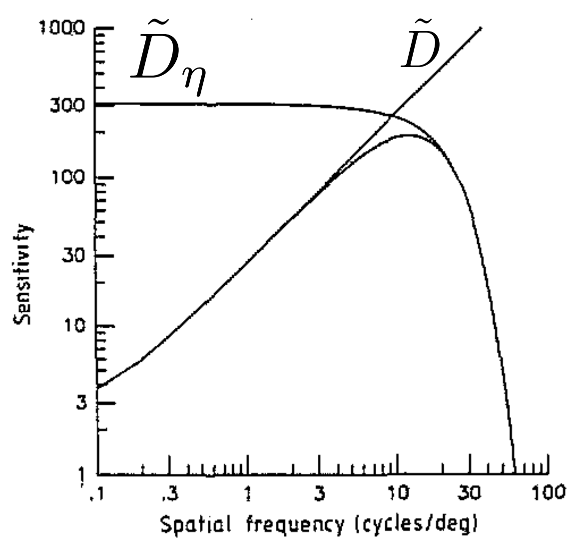
what is the optimal filter $D(\mathbf{x})$?

white input noise

$$\begin{matrix} \eta \searrow & & & & \\ & s_\eta \xrightarrow{D_\eta} & s & \xrightarrow{D} & r \\ s^* \nearrow & & & & \end{matrix}$$

$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

$$\left|\tilde{D}(\boldsymbol{\kappa})\right| = \frac{\sigma_{\mathrm{r}}}{\sqrt{\tilde{C}(\boldsymbol{\kappa})}}$$



κ

$$\tilde{C}(\boldsymbol{\kappa}) \propto \frac{e^{-\alpha\,|\boldsymbol{\kappa}|}}{|\boldsymbol{\kappa}|^2 + \kappa_0^2}$$

$e^{-\alpha\,|\boldsymbol{\kappa}|}$ ← optics of the eye

$|\boldsymbol{\kappa}|^2 + \kappa_0^2$ ← natural images

WHITENING IN THE RETINA
and denoising

$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

factorial code
$$H_{\mathbf{r}} = \sum_a H_{\mathrm{r}_a} \text{ iff } \mathrm{P}(\mathbf{r}) = \prod_{a=1}^{N} \mathrm{P}(r_a)$$

probability equalisation
$$\mathrm{P}(r_a) = \mathrm{P}(r_b)\ \forall a, b$$ if constraints are same

stimulus correlation function

decorrelation
≈ and variance equalisation
$$Q(\mathbf{a},\mathbf{b}) = \sigma_\mathrm{r}^2\,\delta(\mathbf{a}-\mathbf{b}) = \int\!\!\int \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}\, D(\mathbf{x}-\mathbf{a})\, D(\mathbf{y}-\mathbf{b})\, C(\mathbf{x}-\mathbf{y})$$

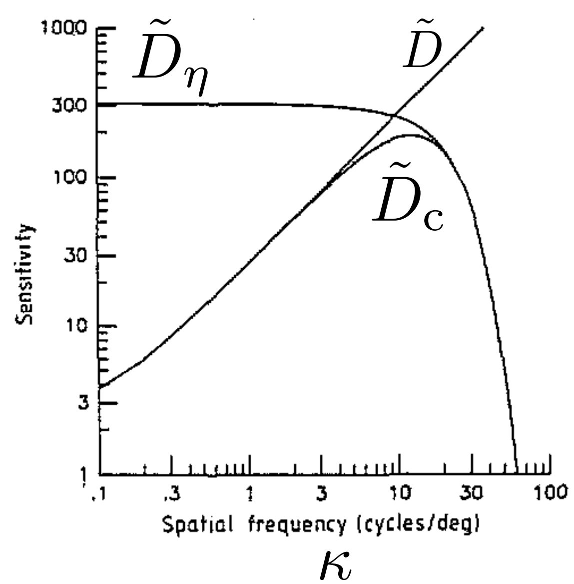
continuous neural field performing filtering
$$r_\mathbf{a} = f_\mathbf{a}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$$

constraint directly on $f(s)$ rather than on $\mathrm{P}_\mathrm{r}(r)$

what is the optimal filter $D(\mathbf{x})$?

white input noise η

$$\eta,\ s^* \rightarrow s_\eta \overbrace{\xrightarrow{D_\eta} s \xrightarrow{D}}^{D_\mathrm{c}} r$$



$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

$$\left|\tilde{D}(\boldsymbol{\kappa})\right| = \frac{\sigma_\mathrm{r}}{\sqrt{\tilde{C}(\boldsymbol{\kappa})}}$$

$$\tilde{C}(\boldsymbol{\kappa}) \propto \frac{e^{-\alpha\,|\boldsymbol{\kappa}|}}{|\boldsymbol{\kappa}|^2 + \kappa_0^2}$$

← optics of the eye

← natural images

WHITENING IN THE RETINA

and denoising

$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

factorial code

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probability equalisation

$$\mathrm{P}(r_a) = \mathrm{P}(r_b)\ \forall a, b$$

if constraints are same

stimulus correlation function

$\approx$ decorrelation and variance equalisation

$$Q(\mathbf{a},\mathbf{b}) = \sigma_{\mathrm{r}}^2\,\delta(\mathbf{a}-\mathbf{b}) = \int\!\!\int \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}\, D(\mathbf{x}-\mathbf{a})\, D(\mathbf{y}-\mathbf{b})\, C(\mathbf{x}-\mathbf{y})$$

continuous neural field performing filtering

$$r_{\mathbf{a}} = f_{\mathbf{a}}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$$

constraint directly on $f(s)$ rather than on $\mathrm{P}_{\mathrm{r}}(r)$

what is the optimal filter $D(\mathbf{x})$?

white input noise η

$$\eta,\ s^* \rightarrow s_\eta \overbrace{\xrightarrow{D_\eta} s \xrightarrow{D}}^{D_{\mathrm{c}}} r$$

$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

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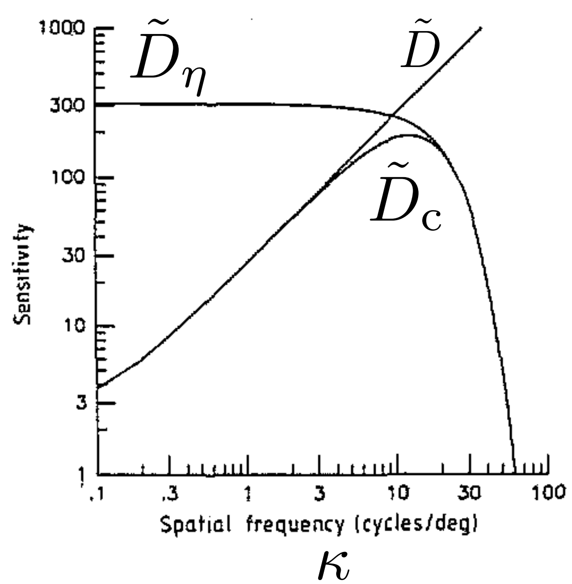

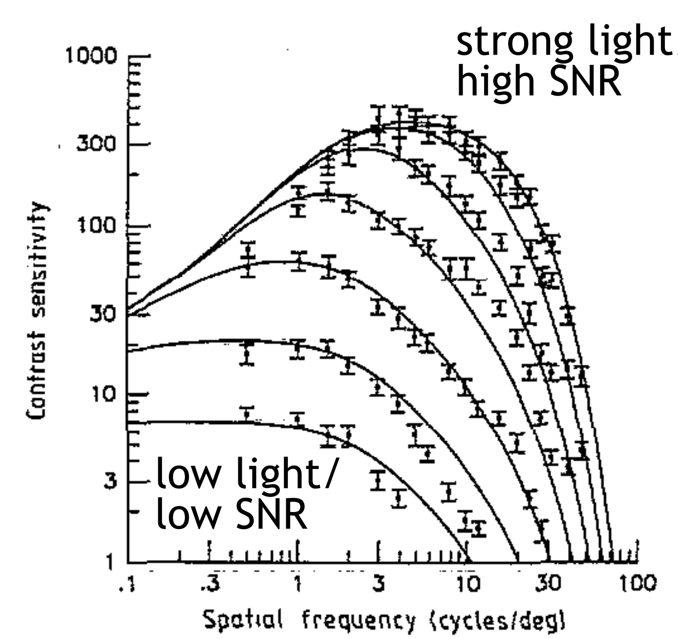

$$\tilde{C}(\boldsymbol{\kappa}) \propto \frac{e^{-\alpha\,|\boldsymbol{\kappa}|}}{|\boldsymbol{\kappa}|^2 + \kappa_0^2}$$

$\leftarrow$ optics of the eye

$\leftarrow$ natural images

WHITENING IN THE RETINA

and denoising

$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

- factorial code $\quad H_{\mathbf{r}} = \sum_a H_{\mathrm{r}_a}$ iff $\mathrm{P}(\mathbf{r}) = \prod_{a=1}^{N} \mathrm{P}(r_a)$
- probability equalisation $\quad \mathrm{P}(r_a) = \mathrm{P}(r_b)\ \forall a, b \quad$ if constraints are same
- $\approx$ decorrelation and variance equalisation $\quad Q(\mathbf{a},\mathbf{b}) = \sigma_{\mathrm{r}}^2\,\delta(\mathbf{a}-\mathbf{b}) = \int\!\!\int \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}\, D(\mathbf{x}-\mathbf{a})\, D(\mathbf{y}-\mathbf{b})\, C(\mathbf{x}-\mathbf{y})$

stimulus correlation function

continuous neural field performing filtering $\quad r_{\mathbf{a}} = f_{\mathbf{a}}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$

constraint directly on $f(s)$ rather than on $\mathrm{P}_{\mathrm{r}}(r)$

what is the optimal filter $D(\mathbf{x})$?

white input noise

$$\begin{array}{l} \eta \searrow \\ s^* \nearrow \end{array} s_\eta \xrightarrow{D_\eta} s \xrightarrow{D} r, \qquad \underbrace{D_\eta \;\; D}_{D_{\mathrm{c}}}$$

$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

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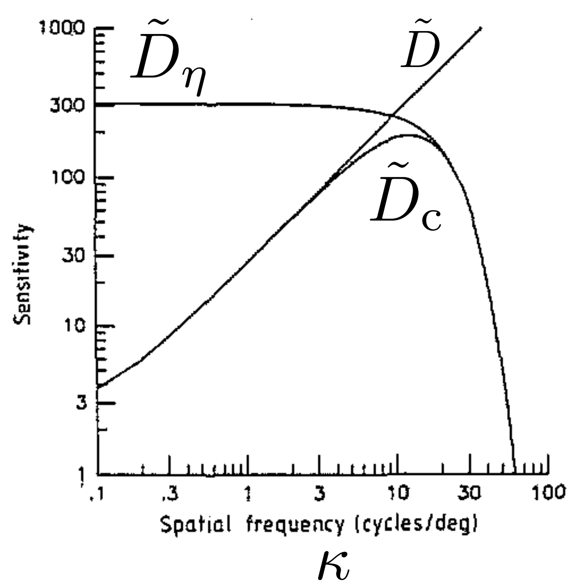
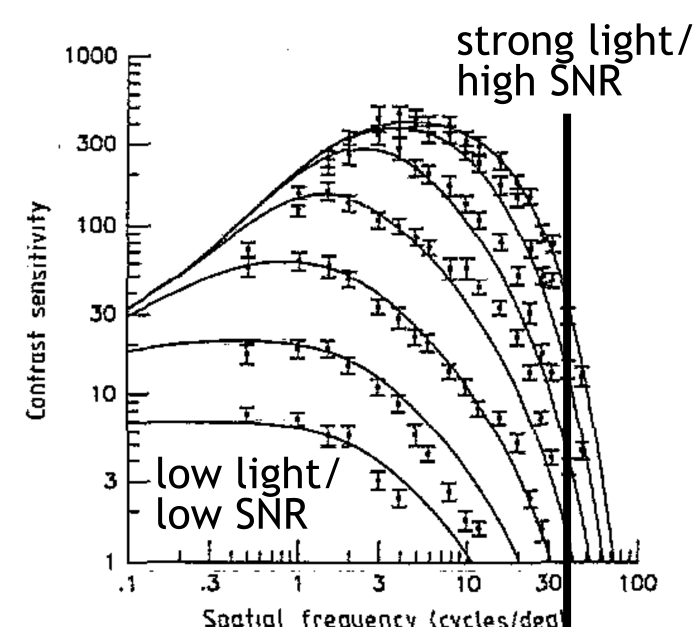
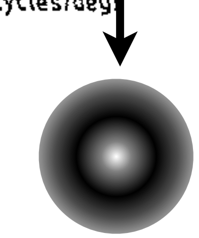
$$\tilde{C}(\boldsymbol{\kappa}) \propto \frac{e^{-\alpha\,|\boldsymbol{\kappa}|}}{|\boldsymbol{\kappa}|^2 + \kappa_0^2}$$

$\leftarrow$ optics of the eye

$\leftarrow$ natural images







centre-surround

WHITENING IN THE RETINA
and denoising

$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

factorial code

$$H_{\mathbf{r}} = \sum_a H_{\mathrm{r}_a} \text{ iff } \mathrm{P}(\mathbf{r}) = \prod_{a=1}^{N} \mathrm{P}(r_a)$$

probability equalisation

$\mathrm{P}(r_a) = \mathrm{P}(r_b)\ \forall a, b$ if constraints are same

$\approx$ decorrelation and variance equalisation

stimulus correlation function

$$Q(\mathbf{a},\mathbf{b}) = \sigma_{\mathrm{r}}^2\, \delta(\mathbf{a}-\mathbf{b}) = \int\!\!\int \mathrm{d}\mathbf{x}\mathrm{d}\mathbf{y}\, D(\mathbf{x}-\mathbf{a})\, D(\mathbf{y}-\mathbf{b})\, C(\mathbf{x}-\mathbf{y})$$

continuous neural field performing filtering

$$r_{\mathbf{a}} = f_{\mathbf{a}}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$$

constraint directly on $f(s)$ rather than on $\mathrm{P_r}(r)$

what is the optimal filter $D(\mathbf{x})$?

white input noise

$$\left.\begin{matrix}\eta \\ s^*\end{matrix}\right\} \rightarrow s_\eta \overbrace{\xrightarrow{D_\eta} s \xrightarrow{D}}^{D_{\mathrm{c}}} r$$

$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

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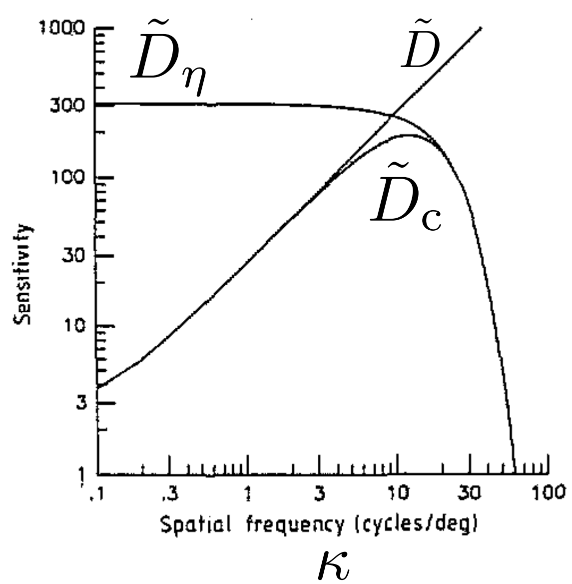
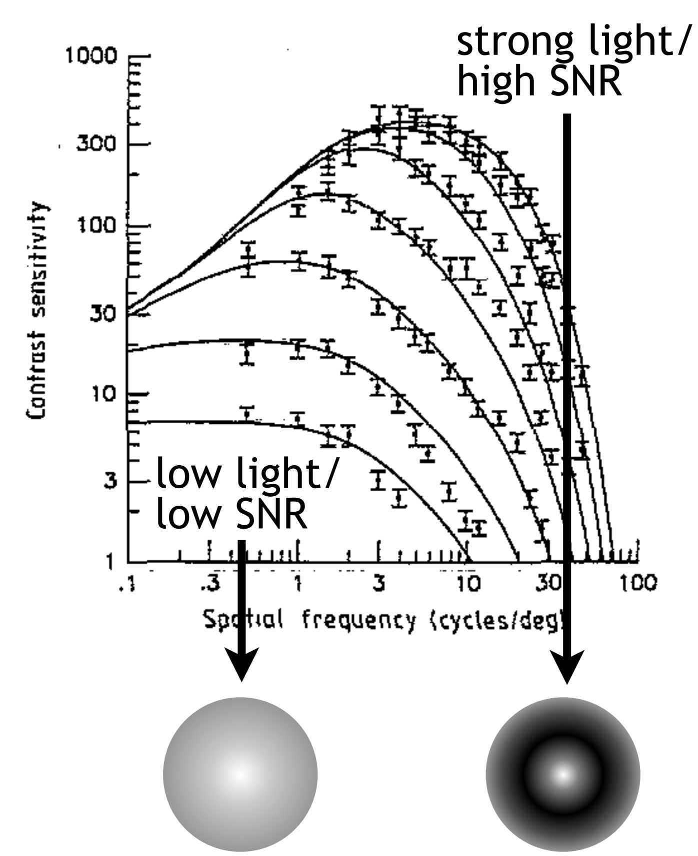
$e^{-\alpha\,|\boldsymbol{\kappa}|}$ ← optics of the eye

$|\boldsymbol{\kappa}|^2 + \kappa_0^2$ ← natural images





centre
no surround

centre-surround

WHITENING IN THE RETINA
and denoising

$$I_{\mathbf{r},\mathbf{s}} = H_{\mathbf{r}} - \cancel{H_{\mathbf{r}|\mathbf{s}}}$$

factorial code $\quad H_{\mathbf{r}} = \sum_a H_{\mathrm{r}_a}$ iff $\mathrm{P}(\mathbf{r}) = \prod_{a=1}^{N} \mathrm{P}(r_a)$

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stimulus correlation function

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continuous neural field performing filtering $\quad r_{\mathbf{a}} = f_{\mathbf{a}}(s) = \int \mathrm{d}\mathbf{x}\, D(\mathbf{x}-\mathbf{a})\ s(\mathbf{x})$

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white input noise

$$\left.\begin{array}{l}\eta \\ s^*\end{array}\right\} \rightarrow s_\eta \overbrace{\xrightarrow{D_\eta} s \xrightarrow{D}}^{D_{\mathrm{c}}} r$$

$$\left|\tilde{D}_\eta(\boldsymbol{\kappa})\right| = \frac{\tilde{C}(\boldsymbol{\kappa})}{\tilde{C}(\boldsymbol{\kappa}) + \tilde{C}_\eta}$$

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$\leftarrow$ optics of the eye

$\leftarrow$ natural images