Perception as Signal Processing

October 16, 2018

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- provides a mechanistic understanding of observations
- links structure to function
- helps to codify, organise and relate experimental findings

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- provides a mechanistic understanding of observations
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Normative or teleological - why do we see light between 390 to 700 nm?

- provides an understanding of the purpose of function
- only sensible in the context of evolutionary selection

Sensation and Perception

Two dominant ways of thinking about sensory systems and perception.

Signal processing – falls between normative and mechanistic

- a succession of filtering and feature-extraction stages that arrives at a 'detection' or 'recognition' output.
- dominated by feed-forward metaphors
 - temporal processing often limited to integration
 - some theories may incorporate local recurrence and also feedback for feature selection or attention
- behavioural and neural theory is dominated by information-like quantities

Inference – strongly normative

- parse sensory input to work out the configuration of the world
- fundamental roles for lateral interaction, feedback and dynamical state
- behavioural theory is well understood and powerful; neural underpinnings are little understood.

Signal-processing paradigms



Signal-processing paradigms



The eye and retina





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Centre-surround receptive fields



1.5

Centre-surround models

Centre-surround receptive fields are commonly described by one of two equations, giving the scaled response to a point of light shone at the retinal location (x, y). A difference-of-Gaussians (DoG) model:

$$D_{\text{DoG}}(x,y) = \frac{1}{2\pi\sigma_c^2} \exp\left(-\frac{(x-c_x)^2 + (y-c_y)^2}{2\sigma_c^2}\right) - \frac{1}{2\pi\sigma_s^2} \exp\left(-\frac{(x-c_x)^2 + (y-c_y)}{2\sigma_s^2}\right)$$

Centre-surround models

... or a Laplacian-of-Gaussian (LoG) model:

$$D_{\text{LoG}}(x,y) = -\nabla^2 \left[\frac{1}{2\pi\sigma^2} \exp\left(-\frac{(x-c_x)^2 + (y-c_y)^2}{2\sigma^2}\right) \right]$$

Linear receptive fields

The linear-like response apparent in the prototypical experiments can be generalised to give a predicted firing rate in response to an arbitrary stimulus s(x, y):

$$r(c_x, c_y; s(x, y)) = \int dx \, dy \, D_{c_x, c_y}(x, y) s(x, y)$$

The receptive field centres (c_x, c_y) are distributed over visual space.

If we let D() represent the RF function centred at 0, instead of at (c_x, c_y) , we can write:

$$r(c_x, c_y; s(x, y)) = \int dx \, dy \, D(c_x - x, c_y - y) s(x, y)$$

which looks like a convolution.

Transfer functions

Thus a repeated linear receptive field acts like a spatial filter, and can be characterised by its frequency-domain transfer function. (Indeed, much early visual processing is studied in terms of linear systems theory.)

Transfer functions for both DoG and LoG centre-surround models are **bandpass**. Taking 1D versions:



This accentuates mid-range spatial frequencies.

Transfer functions



Edge detection

Bandpass filters emphasise edges:



orginal image



DoG responses



thresholded

Orientation selectivity



Linear receptive fields – simple cells

Linear response encoding:

$$r(t_0, s(x, y, t)) = \int_0^\infty d\tau \int dx \, dy \, s(x, y, t_0 - \tau) D(x, y, \tau)$$

For separable receptive fields:

$$D(x, y, \tau) = D_s(x, y)D_t(\tau)$$

For simple cells:

$$D_s = \exp\left(-rac{(x-c_x)^2}{2\sigma_x^2} - rac{(y-c_y)^2}{2\sigma_y^2}
ight)\cos(kx-\phi)$$

Linear response functions – simple cells



Simple cell orientation selectivity



х

2D Fourier Transforms

Again, the best way to look at a filter is in the frequency domain, but now we need a 2D transform.

$$D(x,y) = \exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right)\cos(kx)$$

$$\widetilde{D}(\omega_x,\omega_y) = \int dx \ dy \ e^{-i\omega_x x} e^{-i\omega_y y} \exp\left(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}\right)\cos(kx - \phi)$$

$$= \int dx \ e^{-i\omega_x x} e^{-x^2/2\sigma_x^2}\cos(kx - \phi) \cdot \int dy \ e^{-i\omega_y y} e^{-y^2/2\sigma_y^2}$$

$$= \sqrt{2\pi}\sigma_x \left[e^{-\sigma_x^2\omega_x^2/2} \circ \pi[\delta(\omega_x - k) + \delta(\omega_x + k)]\right] \sqrt{2\pi}\sigma_y e^{-\sigma_y^2\omega_y^2/2}$$

$$= 2\pi^2\sigma_x\sigma_y \left[e^{-\frac{1}{2}[(\omega_x - k)^2\sigma_x^2 + \omega_y^2\sigma_y^2]} + e^{-\frac{1}{2}[(\omega_x + k)^2\sigma_x^2 + \omega_y^2\sigma_y^2]}\right]$$

Easy to read spatial frequency tuning, bandwidth; orientation tuning and (for homework) bandwidth.

Drifting gratings



$$s(x, y, t) = G + A\cos(kx - \omega t - \phi)$$

Separable and inseparable response functions



Separable: motion sensitive; not direction sensitive

Inseparable: motion sensitive; and direction sensitive

Complex cells

Complex cells are sensitive to orientation, but, supposedly, not phase.

One model might be (neglecting time)

$$r(s(x,y)) = \left[\int dx \, dy \, s(x,y) \exp\left(-\frac{(x-c_x)^2}{2\sigma_x^2} - \frac{(y-c_y)^2}{2\sigma_y^2}\right) \cos(kx) \right]^2 \\ + \left[\int dx \, dy \, s(x,y) \exp\left(-\frac{(x-c_x)^2}{2\sigma_x^2} - \frac{(y-c_y)^2}{2\sigma_y^2}\right) \cos(kx-\pi/2) \right]^2$$

But many cells do have some residual phase sensitivity. Quantified by $(f_1/f_0$ ratio).

Stimulus-response functions (and constructive models) for complex cells are still a matter of debate.

Other V1 responses: surround effects





Other V1 responses

- end-stopping (hypercomplex)
- blobs and colour
- ▶ ...

Signal-processing paradigms



Information

What does a neural response tell us about a stimulus?

Shannon theory:

- Entropy: *bits* needed to specify an exact stimulus.
- Conditional entropy: bits needed to specify the exact stimulus after we see the response.
- (Average mutual) information: the difference (infomation gained from the response)
- ► Mutual information is bounded by the entropy of the response ⇒ maximum entropy encoding and decorrelation.

Discrimination theory:

- How accurately (squared-error) can the stimulus be estimated from the response.
- Cramér-Rao bound relates this to the Fisher Information a differential measure of how much the response distribution changes with the stimulus.
- Fisher information can often be optimised directly.

Linked by rate-distortion theory and by aymptotic (large population) arguments.





If noise is small and "constant" \Rightarrow maximise marginal entropy \Rightarrow maximise $\mathbf{H}\Big[\widetilde{\mathcal{S}}\Big]$

$$\mathbf{I}[\widetilde{S}; R] = \underbrace{\mathbf{H}[R]}_{\text{marginal entropy}} - \underbrace{\mathbf{H}[R|\widetilde{S}]}_{\text{noise entropy}}$$

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

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

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

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

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$$\left[-\frac{1}{2} - r \in [0, r_{\text{max}}] \right]$$

$$p(r) = \left\{ egin{array}{cc} rac{1}{r_{ ext{max}}} & r \in [0, r_{ ext{max}}] \ 0 & ext{otherwise} \end{array}
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= i.

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

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

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Therefore the correlation (covariance) between cells is

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

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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

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

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 $\propto e^{-\alpha |{\bf k}|}.$ So decorrelation requires

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Photodetection introduces noise. Therefore, cascade linear filters:

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

with

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

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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



Tuning curves

We often consider the way that the firing rate of a cell *r* represents a single (possibly multidimensional) stimulus value *s*:

$$r = f(s)$$
.

Even if *s* and *r* are embedded in time-series we assume:

- 1. that coding is instantaneous (with a fixed lag),
- 2. that *r* (and therefore *s*) is constant over a short time Δ .

The function f(s) is known as a tuning curve.

Tuning curves

Commonly assumed mathematical forms for (1D) tuning curves:

• Gaussian
$$r_0 + r_{\max} \exp\left[-\frac{1}{2\sigma^2}(x - x_{\text{pref}})^2\right]$$

- (Thresholded) Ramp $r_0 + \Theta(x x_{thr}) r_{max} \rho \cdot (x x_{thr})$
- Cosine $r_0 + r_{\max} \cos(\theta \theta_{\text{pref}})$

• Wrapped Gaussian
$$r_0 + r_{\max} \sum_n \exp\left[-\frac{1}{2\sigma^2}(\theta - \theta_{\text{pref}} - 2\pi n)^2\right]$$

• von Mises ("circular Gaussian") $r_0 + r_{max}$

$$r_0 + r_{\max} \exp\left[\kappa \cos(\theta - \theta_{\text{pref}})
ight]$$

• periodic (grid) f(s)

$$f(s) = f_1(\sin(2\pi s/\lambda))$$

Decoding - the Cricket cercal system





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$$r_a(s) = r_a^{\max}[\cos(\theta - \theta_a)]_+ = r_a^{\max}[\mathbf{c}_a^{\mathsf{T}}\mathbf{v}]_+ \qquad \qquad \mathbf{c}_1^{\mathsf{T}}\mathbf{c}_2 = 0 \\ \mathbf{c}_3 = -\mathbf{c}_1 \\ \mathbf{c}_4 = -\mathbf{c}_2$$

So, writing $\tilde{r}_a = r_a/r_a^{\text{max}}$:

$$\begin{pmatrix} \tilde{r}_1 - \tilde{r}_3 \\ \tilde{r}_2 - \tilde{r}_4 \end{pmatrix} = \begin{pmatrix} \mathbf{c}_1^{\mathsf{T}} \\ \mathbf{c}_2^{\mathsf{T}} \end{pmatrix} \mathbf{v}$$
$$\mathbf{v} = (\mathbf{c}_1 \mathbf{c}_2) \begin{pmatrix} \tilde{r}_1 - \tilde{r}_3 \\ \tilde{r}_2 - \tilde{r}_4 \end{pmatrix} = \tilde{r}_1 \mathbf{c}_1 - \tilde{r}_3 \mathbf{c}_3 + \tilde{r}_2 \mathbf{c}_2 - \tilde{r}_4 \mathbf{c}_4 = \sum_a \tilde{r}_a \mathbf{c}_a$$

This is called population vector decoding.

Motor cortex (simplified)



Cosine tuning, randomly distributed preferred directions. In general, population vector decoding works for

- cosine tuning
- cartesian or dense (*tight*) directions

But:

- is it optimal?
- does it generalise? (Gaussian tuning curves)
- how accurate is it?

Measuring the potential quality of a representation

Consider a (one dimensional) stimulus that takes on continuous values (e.g. angle).

- contrast
- orientation
- motion direction
- movement speed

Suppose a neuron fires n spikes in response to stimulus s according to some distribution

 $P(n|f(s)\Delta)$

Given an observation of n, how well can we estimate s?

Cramér-Rao bound

Suppose the neural response can be described by a probability distribution P(r|s). The Fisher information measures how this distribution changes with *s*:

$$J(s^*) = -\left\langle \frac{d^2 \log P(r|s)}{ds^2} \Big|_{s^*} \right\rangle_{s^*} = \left\langle \left(\frac{d \log P(r|s)}{ds} \Big|_{s^*} \right)^2 \right\rangle_s$$

The Cramér-Rao bound states that for any *N*, any *unbiased* estimator $\hat{s}(\{n_i\})$ of *s* will have the property that

$$\langle (\hat{\mathbf{s}}(\{n_i\}) - \mathbf{s}^*)^2 \rangle_{n_i \mid \mathbf{s}^*} \geq \frac{1}{J(\mathbf{s}^*)}.$$

Thus, Fisher Information gives a lower bound on the variance of any unbiased estimator.

[For estimators with *bias* $b(s^*) = \langle \hat{s}(\{n_i\}) - s^* \rangle$ the bound is: $\langle (\hat{s}(\{n_i\}) - s^*)^2 \rangle_{n_i | s^*} \ge \frac{(1+b'(s^*))^2}{J(s^*)} + b^2(s^*)$]

The Fisher Information is the most common tool to analyse optimality in populations.

 $n = r\Delta + \text{noise}; \quad r = f(s) \Rightarrow$

$$J(s^*) = \left\langle \left(\frac{d}{ds} \Big|_{s^*} \log P(n|s) \right)^2 \right\rangle_{s^*}$$

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For Poisson neurons

$$P(n|r\Delta) = rac{e^{-r\Delta}}{(r\Delta)^n}n!$$

$$J_{\text{noise}}[r\Delta] = \left\langle \left(\frac{d}{dr\Delta} \Big|_{r^*\Delta} \log P(n|r\Delta) \right)^2 \right\rangle_{s^*}$$

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SO

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$$= \left\langle \left(\frac{d}{dr\Delta} \Big|_{r^*\Delta} - r\Delta + n\log r\Delta - \log n! \right)^2 \right\rangle_{s^*}$$
$$= \left\langle \left((-1 + n/r^*\Delta)^2 \right)_{s^*}$$
$$= \left\langle \frac{(n - r^*\Delta)^2}{(r^*\Delta)^2} \right\rangle_{s^*}$$
$$= \frac{r^*\Delta}{(r^*\Delta)^2} = \frac{1}{r^*\Delta}$$

For Poisson neurons

$$P(n|r\Delta) = \frac{e^{-r\Delta}}{(r\Delta)^n} n!$$

$$J_{\text{noise}}[r\Delta] = \left\langle \left(\frac{d}{dr\Delta} \Big|_{r^*\Delta} \log P(n|r\Delta) \right)^2 \right\rangle_{s^*}$$
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and, referred back to the stimulus value:

$$J[s^*] = f'(s^*)^2 \Delta / f(s^*)$$

Population Fisher Info

Fisher Informations for independent random variates add:

$$J_{\mathbf{n}}(s) = \left\langle -\frac{d^{2}}{ds^{2}} \log P(\mathbf{n}|s) \right\rangle$$
$$= \left\langle -\frac{d^{2}}{ds^{2}} \sum_{a} \log P(n_{a}|s) \right\rangle$$
$$= \sum_{a} \left\langle -\frac{d^{2}}{ds^{2}} \log P(n_{a}|s) \right\rangle = \sum_{a} J_{n_{a}}(s).$$
$$= \Delta \sum_{a} \frac{f'_{a}(s)^{2}}{f_{a}(s)} \quad \text{[for Poisson cells]}$$

A considerable amount of work has been done in recent years on finding optimal properties of tuning curves for rate-based population codes. Here, we reproduce one such argument (from Zhang and Sejnowski, 1999).

Consider a population of cells that codes the value of a *D* dimensional stimulus, **s**. Let the *a*th cell emit *r* spikes in an interval τ with probability distribution that is conditionally independent of the other cells (given **s**) and has the form

$$\mathsf{P}_{a}(r \mid \mathbf{s}, \tau) = S(r, f^{a}(\mathbf{s}), \tau).$$

Also let the tuning curve of the *a*th cell, $f^{a}(\mathbf{s})$, be circularly symmetric:

$$f^{a}(\mathbf{s}) = F \cdot \phi\left((\xi^{a})^{2}
ight); \qquad (\xi^{a})^{2} = \sum_{i}^{D} (\xi^{a}_{i})^{2}; \qquad \xi^{a}_{i} = rac{\mathbf{s}_{i} - c^{a}_{i}}{\sigma},$$

where *F* is a maximal rate and the function ϕ is monotically decreasing. The parameters \mathbf{c}^a and σ give the centre of the *a*th tuning curve and the (common) width.

Now, the (*ij*)th term in the FI matrix for the *a*th cell is (by definition)

$$J_{ij}^{a}(\mathbf{s}) = \mathsf{E}\left[rac{\partial}{\partial s_{i}}\log\mathsf{P}^{a}(r\mid\mathbf{s}, au)rac{\partial}{\partial s_{j}}\log\mathsf{P}^{a}(r\mid\mathbf{s}, au)
ight]$$

Applying the chain rule repeatedly, we find that

$$\begin{split} \frac{\partial}{\partial s_i} \log \mathsf{P}^{\mathsf{a}}(r \mid \mathbf{s}, \tau) &= \frac{1}{S(r, f^{\mathsf{a}}(\mathbf{s}), \tau)} \frac{\partial}{\partial s_i} S(r, f^{\mathsf{a}}(\mathbf{s}), \tau) \\ &= \frac{S^{(2)}(r, f^{\mathsf{a}}(\mathbf{s}), \tau)}{S(r, f^{\mathsf{a}}(\mathbf{s}), \tau)} \frac{\partial}{\partial s_i} f^{\mathsf{a}}(\mathbf{s}) \end{split}$$

(where $S^{(2)}$ indicates differentiation with respect to the second argument)

$$= \frac{S^{(2)}(r, f^{a}(\mathbf{s}), \tau)}{S(r, f^{a}(\mathbf{s}), \tau)} F \phi' \left((\xi^{a})^{2} \right) \frac{\partial}{\partial s_{i}} \sum_{i}^{D} (\xi_{i}^{a})^{2}$$
$$= \frac{S^{(2)}(r, f^{a}(\mathbf{s}), \tau)}{S(r, f^{a}(\mathbf{s}), \tau)} F \phi' \left((\xi^{a})^{2} \right) \frac{2(s_{i} - c_{i}^{a})}{(\sigma_{i}^{a})^{2}}$$

So,

$$\begin{split} J_{ij}^{a}(\mathbf{s}) &= \mathsf{E}\left[\left(\frac{S^{(2)}(r, f^{a}(\mathbf{s}), \tau)}{S(r, f^{a}(\mathbf{s}), \tau)}\right)^{2}\right] 4F^{2} \left(\phi'\left((\xi^{a})^{2}\right)\right)^{2} \frac{(s_{i} - c_{i}^{a})(s_{j} - c_{j}^{a})}{\sigma^{4}} \\ &= \mathsf{A}_{\phi}\left((\xi^{a})^{2}, F, \tau\right) \frac{(s_{i} - c_{i}^{a})(s_{j} - c_{j}^{a})}{\sigma^{4}} \end{split}$$

where the function A_{ϕ} does not depend explicitly on σ .

We assumed neurons were independent \Rightarrow Fisher information adds. Approximate by integral over the tuning curve centres, assuming uniform density η of neurons.

$$\begin{aligned} J_{ij}(\mathbf{s}) &= \sum_{a} J_{ij}^{a}(\mathbf{s}) \\ &\approx \int_{-\infty}^{+\infty} dc_{1}^{a} \cdots \int_{-\infty}^{+\infty} dc_{D}^{a} \eta J_{ij}^{a}(\mathbf{s}) \\ &= \int_{-\infty}^{+\infty} dc_{1}^{a} \cdots \int_{-\infty}^{+\infty} dc_{D}^{a} \eta A_{\phi} \left((\xi^{a})^{2}, F, \tau \right) \frac{(s_{i} - c_{i}^{a})(s_{j} - c_{j}^{a})}{\sigma^{4}} \end{aligned}$$

Change variables: $c_i^a \rightarrow \xi_i^a$

$$= \int_{-\infty}^{+\infty} \sigma d\xi_1^a \cdots \int_{-\infty}^{+\infty} \sigma d\xi_D^a \, \eta A_\phi \left((\xi^a)^2, F, \tau \right) \frac{\xi_i^a \xi_j^a}{\sigma^2} \\ = \frac{\sigma^D}{\sigma^2} \eta \int_{-\infty}^{+\infty} d\xi_1^a \cdots \int_{-\infty}^{+\infty} d\xi_D^a \, A_\phi \left((\xi^a)^2, F, \tau \right) \xi_i^a \xi_j^a$$

Now, if $i \neq j$, integral is odd in both ξ_i^a and ξ_j^a , and thus vanishes. If i = j, then the integral has some value $D \cdot K_{\phi}(F, \tau, D)$, independent of σ . Thus,

$$J_{ii} = \sigma^{D-2} \eta D K_{\phi}(F, \tau, D)$$

and the total Fisher information is proportional to σ^{D-2} .

Thus optimal tuning width depends on the stimulus dimension through the interplay of two effects:

slope:
$$f'(s) \propto \sigma^{-1} \Rightarrow J_a(s) \propto \sigma^{-2}$$
per cellnumber of cells: $N(s) \propto \sigma^D \Rightarrow J(s) \propto \sigma^{D-2}$ population

- ► *D* = 1
 - $\Rightarrow \sigma \rightarrow$ 0 (although a lower limit is encountered when the tuning width falls below the inter-cell spacing)
- ▶ *D* = 2
 - \Rightarrow J independent of σ .
- ▶ D > 2
 - $\Rightarrow \sigma \rightarrow \infty$ (actual limit set by valid stimuli).

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 $\Rightarrow \sigma \rightarrow \infty$ (actual limit set by valid stimuli).

- If circular symmetry is relaxed to allow different scales in each dimension for different cells then solution is a Cartesian code (narrow in one dimension, wide in others).
- Single-bump constraint is essential to analysis. Fisher information cannot address ambiguity between bumps.
- Single coded value analysing multiple values or distributions is more complex.
Signal-processing paradigms



Feature detection and representation



Trained network models



Trained network models

