The Abdus Salam International Centre for Theoretical Physics

2415-10

Winter School on Quantitative Systems Biology

26 November - 7 December, 2011

Topics in Theoretical Neuroscience pt. 2

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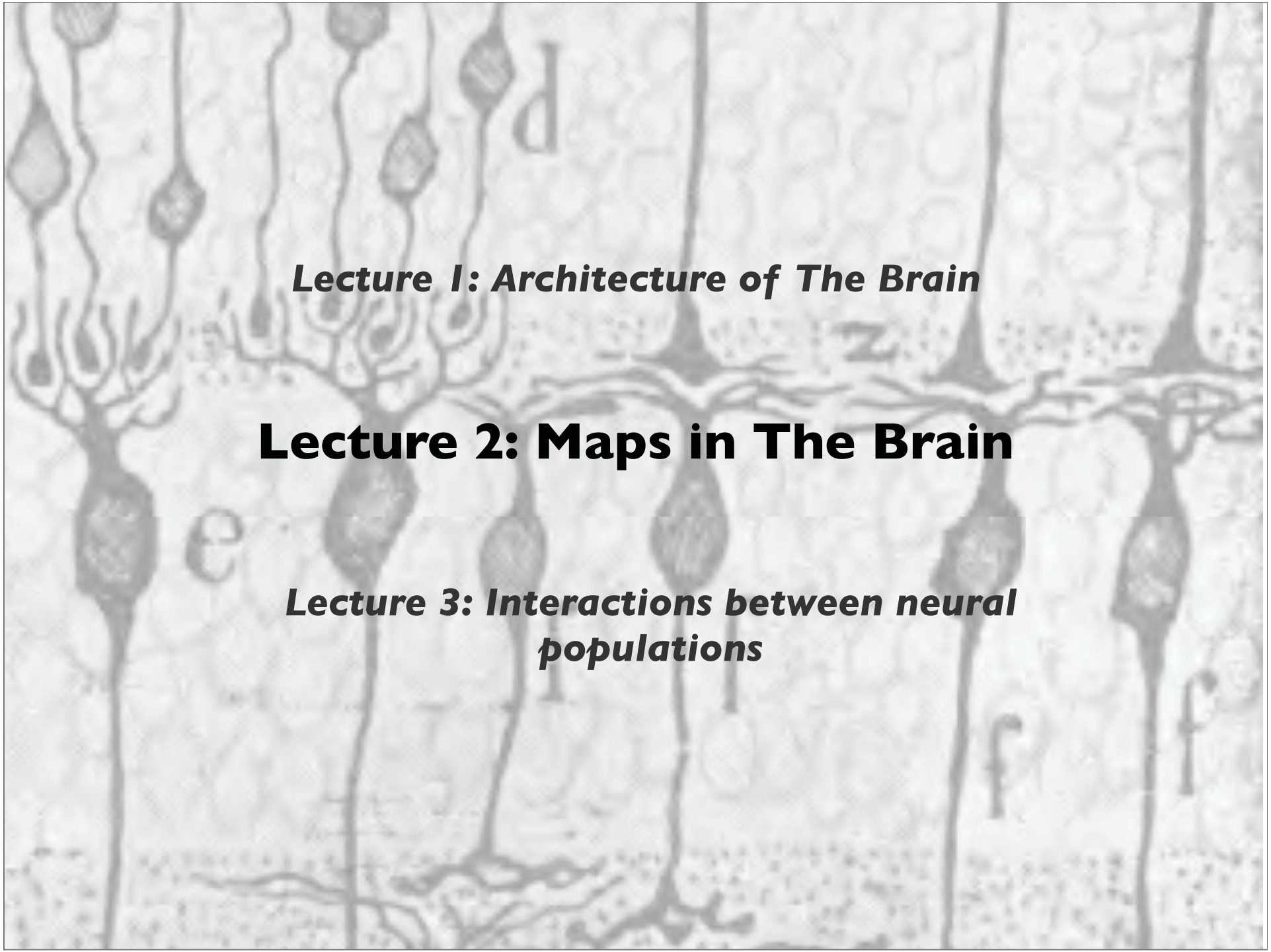


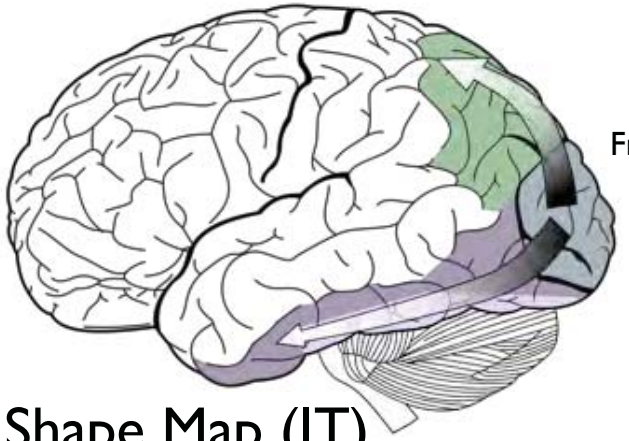
Lecture 1: Architecture of The Brain

Lecture 2: Maps in The Brain

Lecture 3: Interactions between neural populations

Maps in The Brain

Maps are ubiquitous in the brain: orientation map in V1, "shape map" in IT, "place map" in hippocampus map of the body (the homunculus) in motor cortex

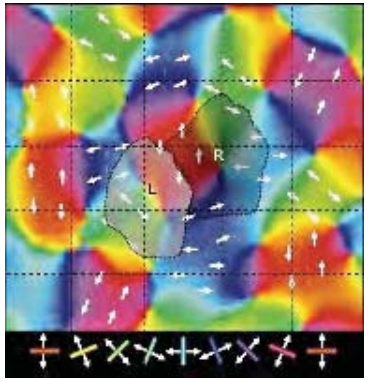


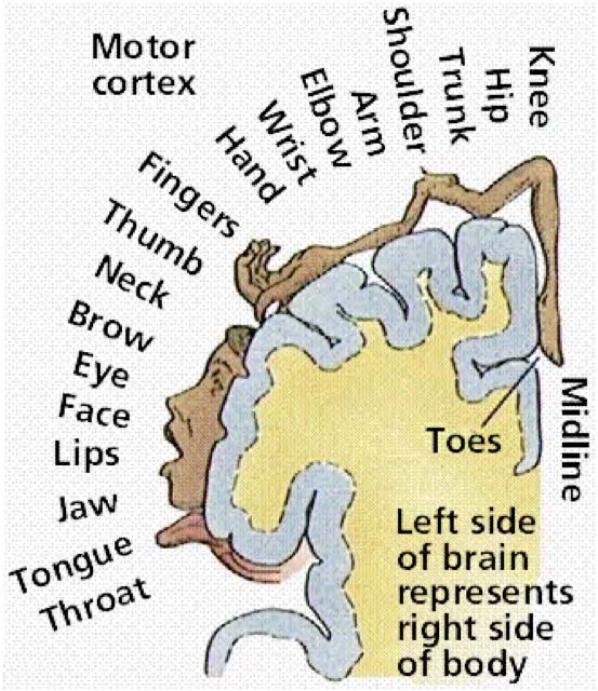
From Wikipedia

Shape Map (IT)

Orientation Map (V1)

Orientation map in visual cortex





From Purves et al., *Life: The Science of Biology*

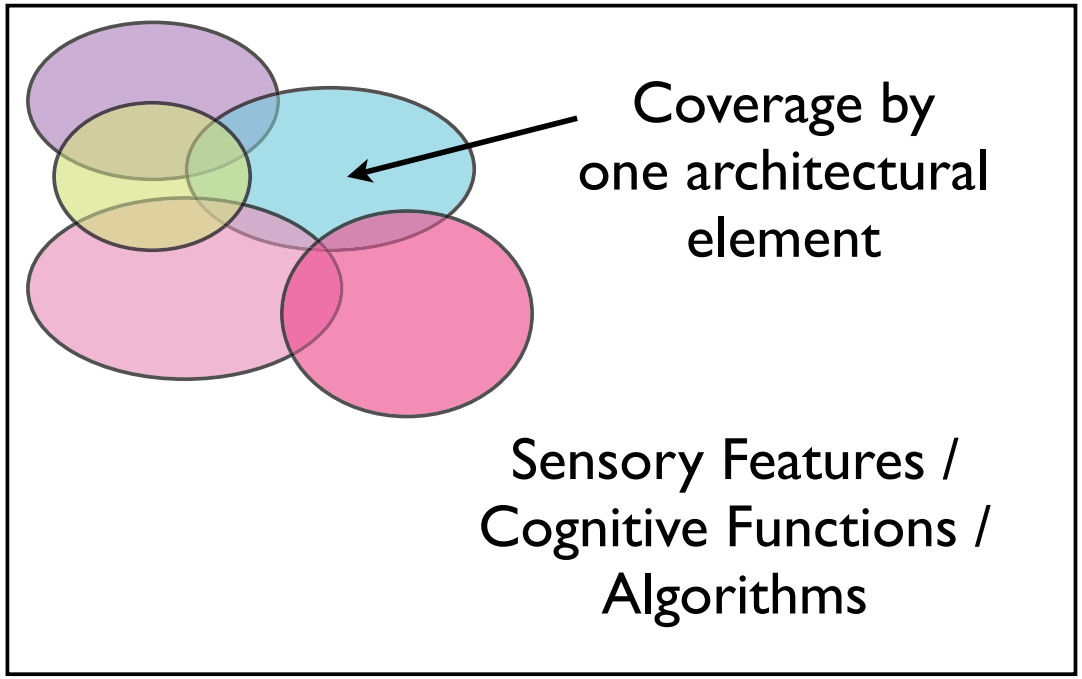
A theory of specialization & complexity?

HYPOTHESIS: Neural populations partition the tasks they perform to minimize resources while maximizing function

e.g Retina
(ganglion cells)

e.g. Entorhinal Cortex
(grid cells)

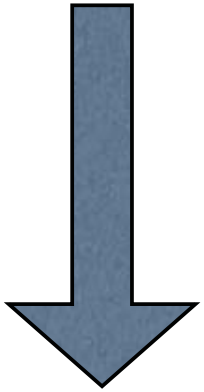
e.g. Whole Brain
(functional areas)



An alternate formulation

Hypothesis: Neural circuits *minimize* the resources (energy, space...) they consume for the functions that they perform, subject to biological constraints.

Can sometimes invert the hypothesis: fix the resources to be as measured, and maximize function



A proxy for the "objective function" of *early vision* is information about "natural scenes"

Hypothesis: Neural circuits *maximize* function (information they convey?) subject to biological constraints.

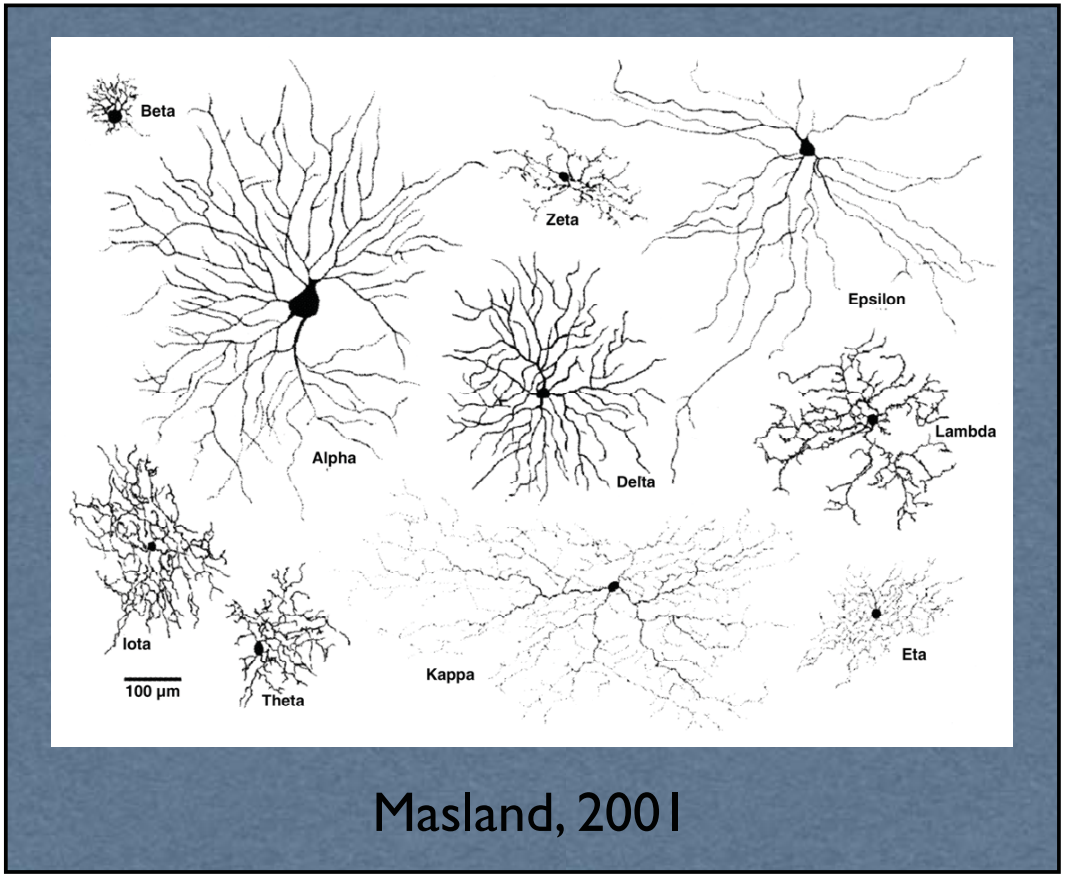
A sensory example: The early visual system

- The relative distribution of red, blue and green photoreceptors
- The shape of ganglion cell receptive fields
- Adaptive changes in retinal ganglion cell responses
- The organization of retinal ganglion cell mosaics
- The balance between OFF cells and ON cells
- The perceptual salience of textures
- The distribution of information traffic in the optic nerve
- The adaptation of pairwise interactions in retinal networks

The Organization of Ganglion Cell Mosaics

Borghuis, Ratliff, Smith, Sterling, VB, J. Neuroscience 2008
(c.f. Liu, Stevens, Sharpee 2009)

Ganglion Cells Measure Local Contrast



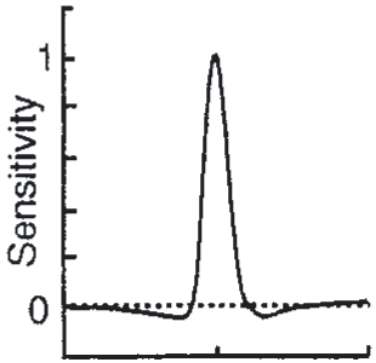
Masland, 2001

The local contrast measured by center-surround receptive fields of retinal ganglion cells reduces redundancy in natural scenes. (Barlow, 1961; Laughlin, 1983; Atick, 1989)

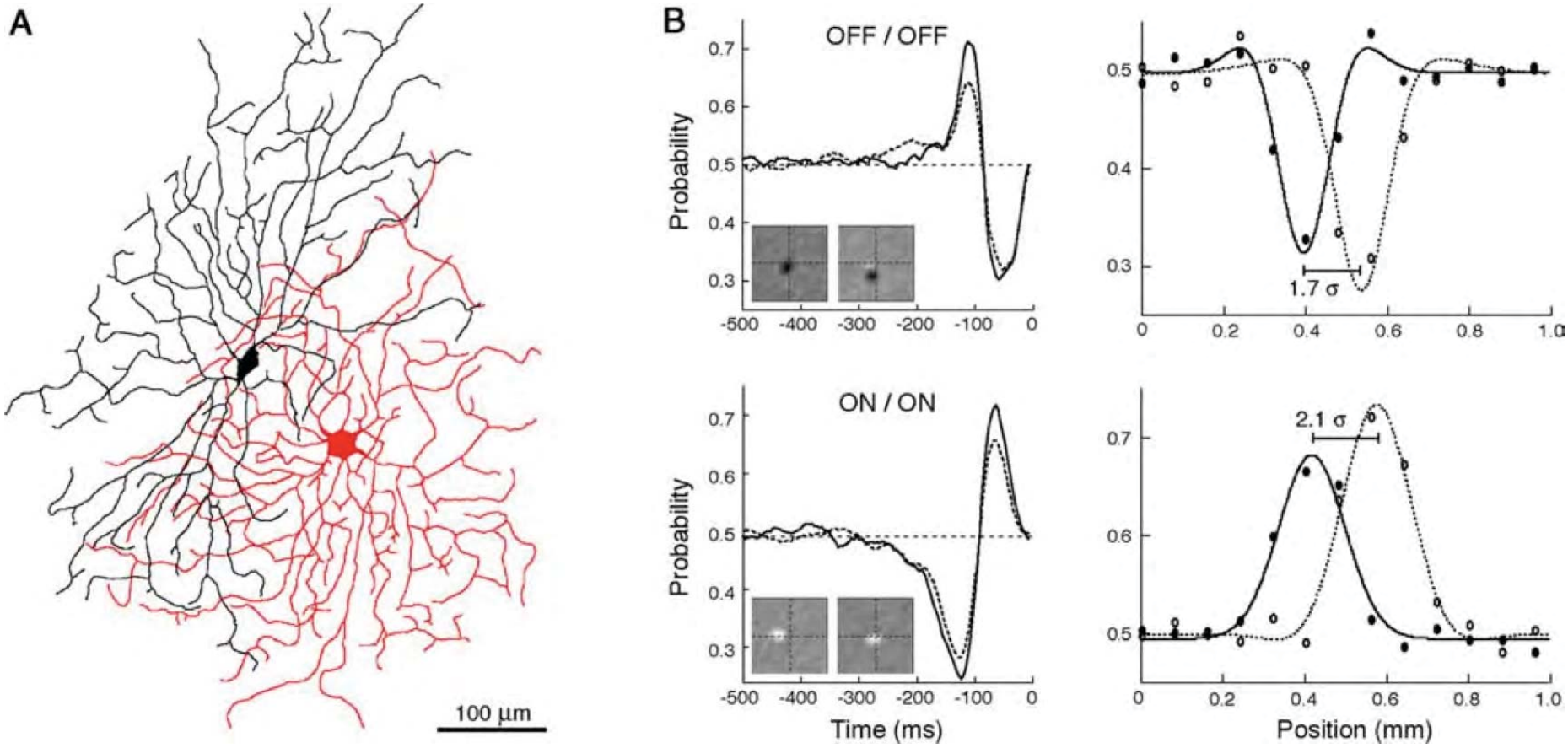
Simple difference of Gaussians model:

$$\text{Contrast}(x,y) = \frac{I_c(x,y) - I_s(x,y)}{I_s(x,y)}$$

Adaptation to local mean luminance



Measurement of mosaics



Linear response filters for recorded ON and OFF cell pairs.
ON cells = light onset / bright spots.
OFF cells = light offset / dark spots

Ganglion cell mosaics tile and have 2 sigma spacing

TABLE 1. *Percentage of recorded cells in retina that fell into each functional class*

Cell Type	Average, %	Range, %	2 σ Spacing
ON BT	10.3	2.7–16.6	+
ON BS	2.5	0–8.3	+
OFF BT	13.2	5.4–31.5	–
OFF BS	9.5	0–20.0	+
OFF delayed	6.6	0–11.1	+
ON η	2.2	0–12.9	+
ON sluggish	3.3	0–9.6	+
OFF sluggish	4	0–10.8	+
LED	5.1	0–18.9	+
ON-OFF DS	30.2	5–48.7	?
ON DS	5.5	0–20.8	?
Unknown	7	0–18.9	

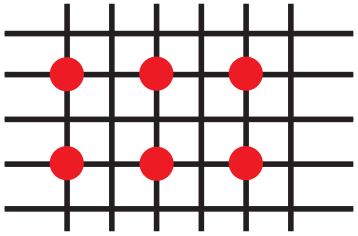
Average values and ranges are shown (total of 272 cells in 9 retinas). BT, brisk transient; BS, brisk sustained; DS, direction sensitive; LED, local edge detector. + Classes for which 2 σ center-center spacing applied. – Spacing did not apply. ? Information about spacing is not available.

de Vries and Baylor, 1997, rabbit; Borghuis et al., J. Neuro, 2008, guinea pig. This design leads to a flat contrast sensitivity surface for the mosaic.

HYPOTHESIS: ~2 sigma spacing maximizes information transfer from natural scenes.

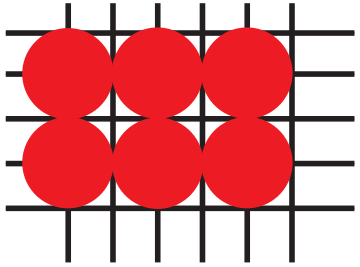
Redundancy vs. SNR

Mosaic of Gaussian receptive field centers at a separation *d*



$\sigma << d$

Smaller receptive fields have less redundant responses.



$\sigma >> d$

Large receptive fields improve SNR by pooling noisy photoreceptor responses

Improvement of SNR by pooling

GIVEN:

- (s/n) = (signal variance/noise variance) of a cone
- a_i = receptive field weight at i^{th} cone
- r_{ij} = correlation coefficient between i^{th} and j^{th} cones

Signal/noise ratio in the cones pooled by a receptive field is:

$$\frac{S}{N} = f^2 \frac{s}{n}$$

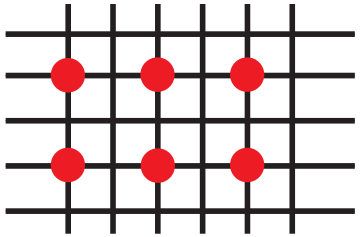
$$f^2 = \frac{\sum_{ij} a_i a_j r_{ij}}{\sum_i a_i^2}$$

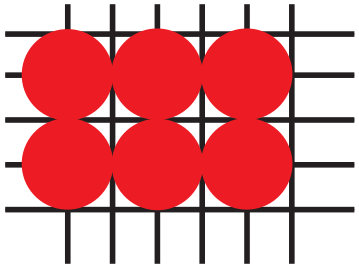
Information in the pooled signal is:

$$I = \frac{1}{2} log_2 \left(1 + \frac{S}{N}\right)$$

Compute the SNR improvement due to pooling photoreceptor responses correlated by natural scene statistics.

Measurement of redundancy





Discretize the receptive field response into *k* levels *commensurate with SNR*. (Account for noise by this discretization.)

The information conveyed by *n* correlated filters with joint distribution $p(x_1, \cdots x_n)$ is:

$$H(x_1, \cdots, x_n) = -\sum_{x_1, \cdots x_n} p(x_1, \cdots x_n) \log p(x_1, \cdots x_n)$$

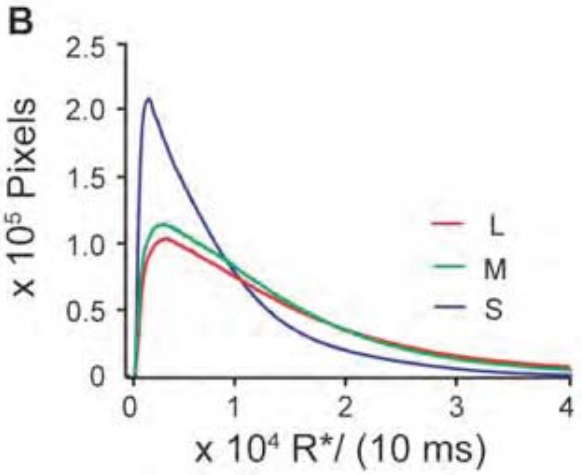
The information conveyed by *n* uncorrelated filters is:

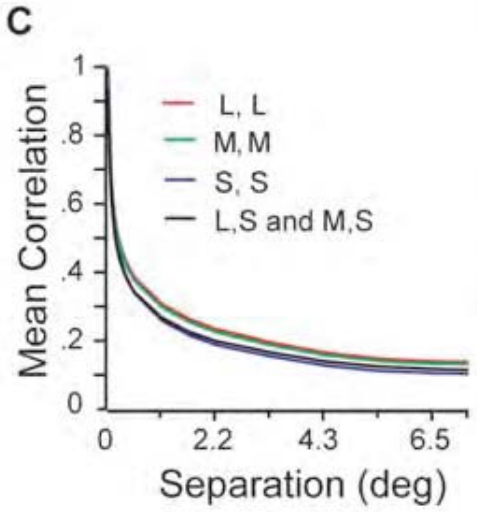
$$n\, H_1 = -n \sum_{x_1} p(x_1) \log p(x_1)$$

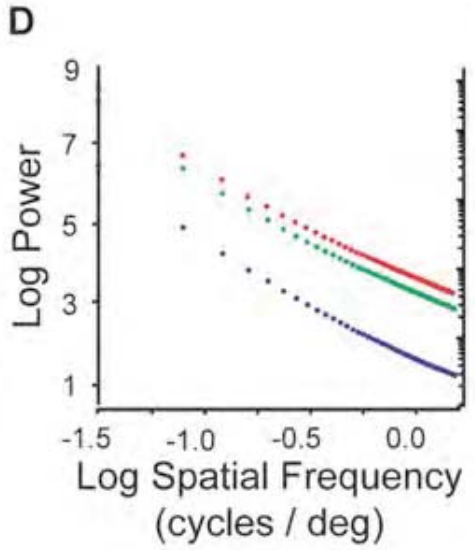
Redundancy: $\boxed{R = \dfrac{H}{nH_1}}$

Statistical structure of natural scenes

Garrigan, Ratliff, Sterling, Brainard, VB (PLoS Comp Bio, 2010)







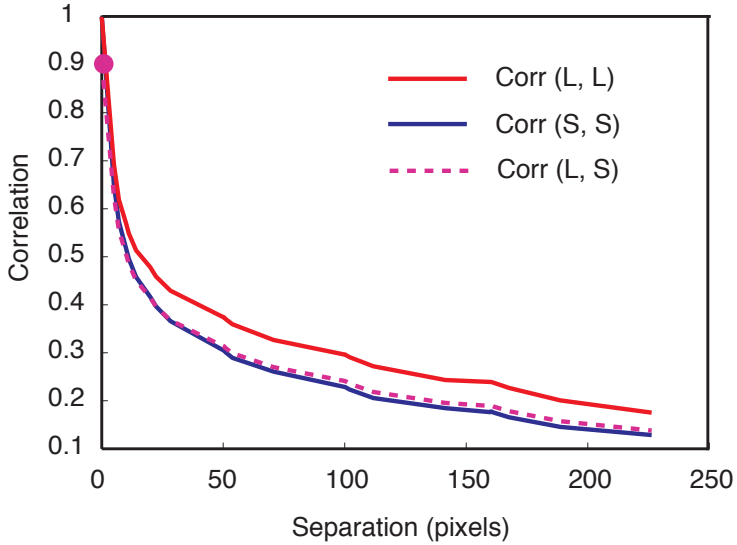
- Low peak, long tail distributions = mean exceeds the median

- Phase averaged power spectrum scales as ~$1/k^2$

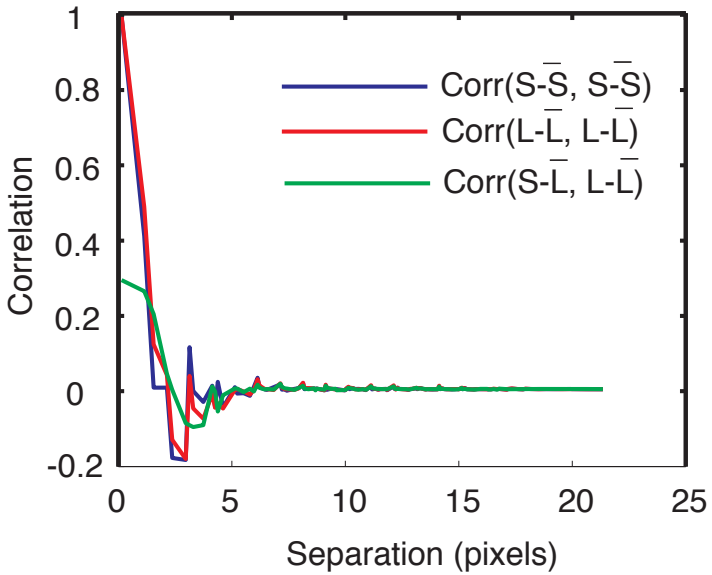
Scale invariant

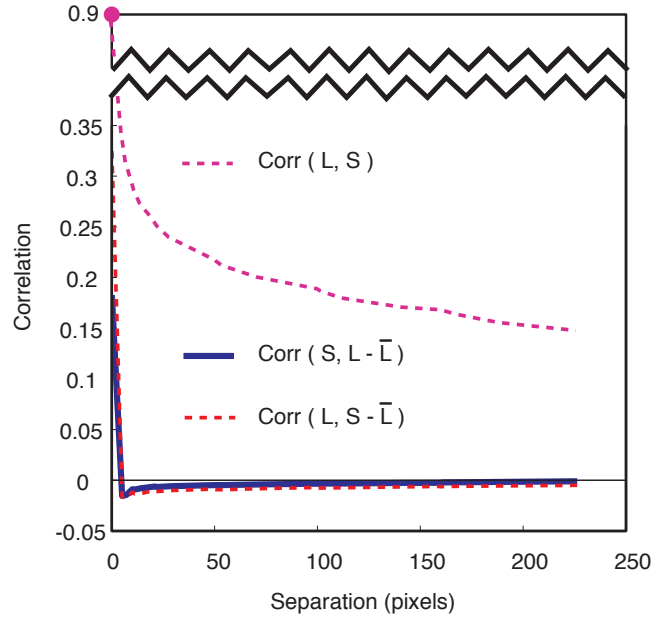
Correlated Luminance - Decorrelated Contrast

Luminance is correlated



Contrast is decorrelated





Luminance is decorrelated from contrast

Here "Contrast" = central luminance - mean luminance in a surround

Redundancy in large arrays

Receptive field is a weighted sum of contrast and luminance:

$$\text{Receptive Field} = C + \alpha\, L$$

Because luminance and contrast are statistically independent:

$$I(C) \leq I_N \leq I(C) + I(L)$$

Luminance has scale invariant correlations:

$$I_N(L) = N I_1(L)(1-\delta)^{\log N} = N^{1-\epsilon} I_i(L)$$

Contrast correlations are short range:

$$I(C) \propto N$$

The information in a large array is mostly about contrast:

$$I(c) \leq I_N \leq I(c) + O(N^{1-\epsilon})$$

Determining Redundancy in a Large Array

Because contrast correlations are short range, redundancy largely arises from shared information between nearest neighbors:

$$I_N = N I_1 - N_{adj}\, M_{adj} - N_{diag}\, M_{diag}$$

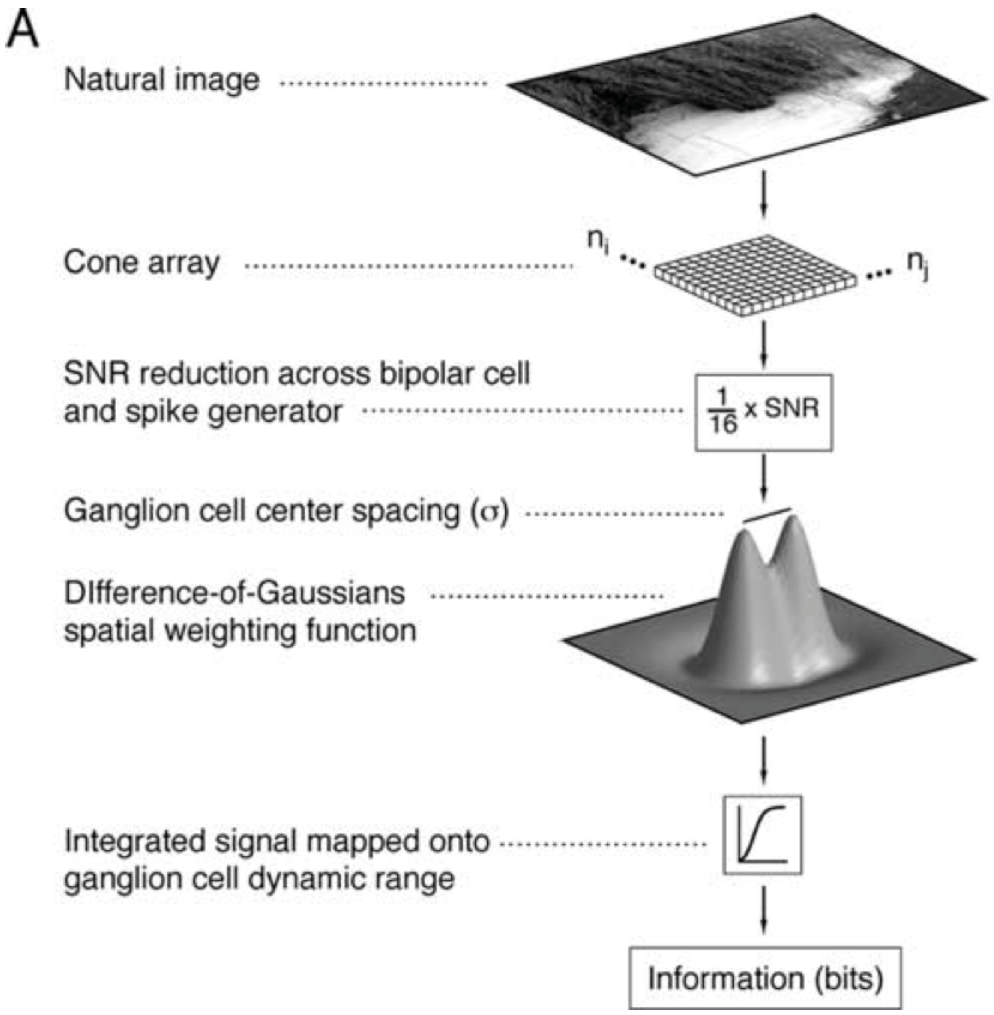
For large arrays, the number of adjacent and diagonal elements can be counted to give:

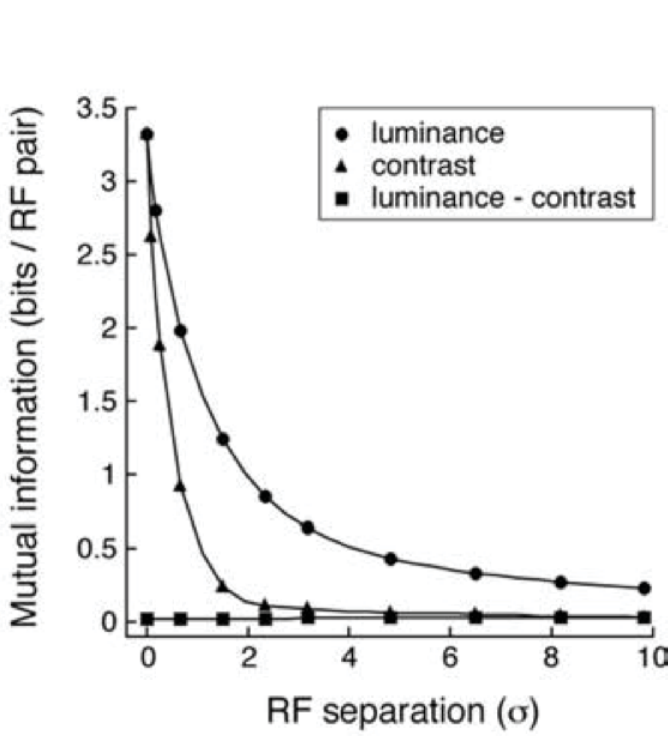
$$I_N \approx N(I_1 - 2\, M_{adj} - 2\, M_{diag})$$

Measuring redundancy

$$R = \frac{I_N}{N\, I_1} \approx 1 - 2\frac{M_{adj} + M_{diag}}{I_1}$$

Summary


A
Natural image
Cone array
n_i
n_j
SNR reduction across bipolar cell and spike generator
$\frac{1}{16}$ x SNR
Ganglion cell center spacing (σ)
DIfference-of-Gaussians spatial weighting function
Integrated signal mapped onto ganglion cell dynamic range
Information (bits)


B
luminance
contrast
luminance - contrast
Mutual information (bits / RF pair)
RF separation (σ)
0
0.5
1
1.5
2
2.5
3
3.5
0
2
4
6
8
10

Finding the optimal center size

Total information in a mosaic of *k* correlated Gaussian receptive fields at a separation *d* and center standard deviation σ is:

$$I = \frac{1}{2} k \, R(\sigma, d) \log \left[1 + f^2(\sigma, d) \left(\frac{s}{n} \right) \right]$$

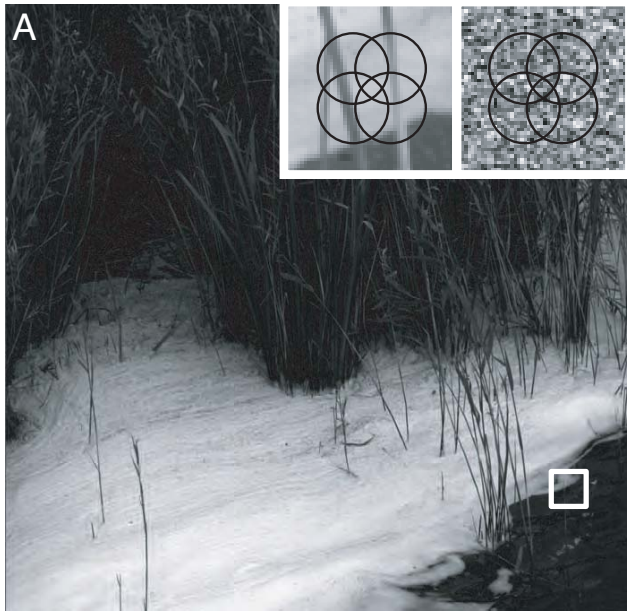
For *guinea pig brisk-transient* (alpha) ganglion cells

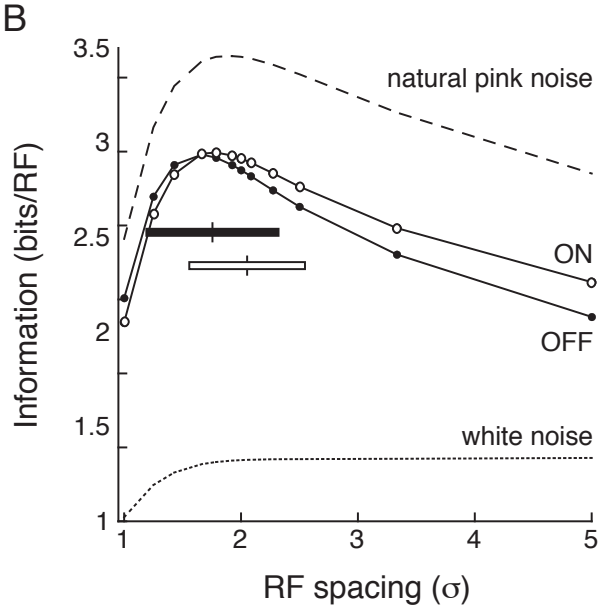
- ON BT Cells (positive contrast): d = 32 pixels
- OFF BT Cells (negative contrast): d = 24 pixels
- Fix center/surround ratio and surround gain to match measurements

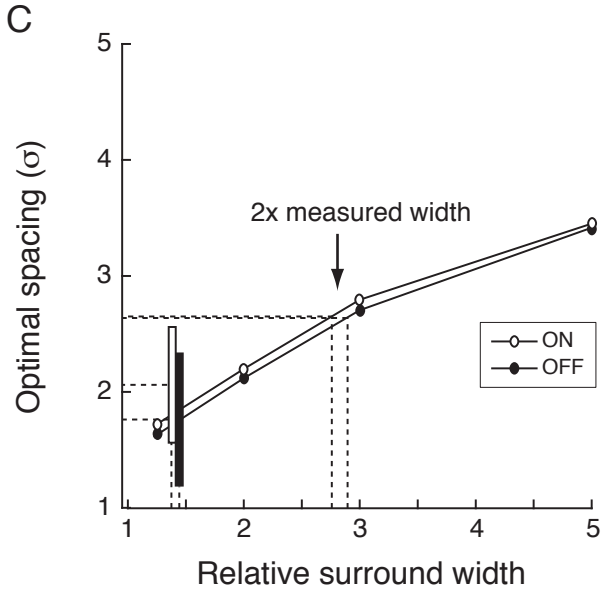
- (s/n) = signal/noise ratio of a cone ~ 10 (Choi et al., 2005)
- r_{ij} = correlation coefficient = natural scene correlation coefficient

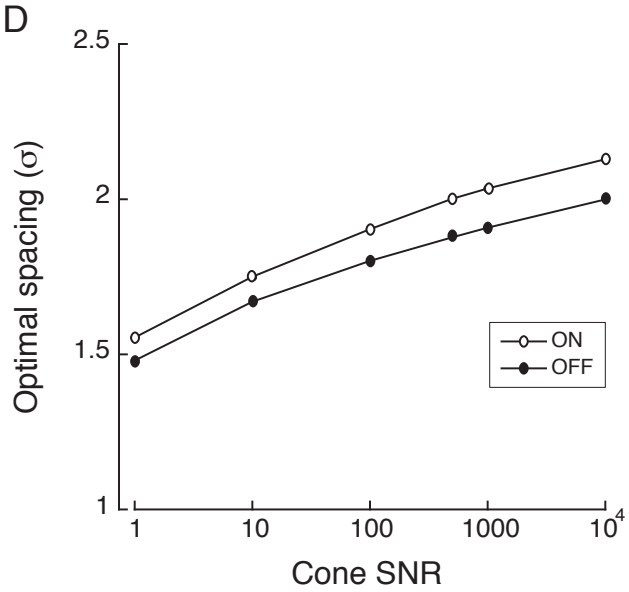
Vary over σ to find optimal center size.

An optimal mosaic has 2 sigma spacing









Measured spacing for BT ganglion cell pairs:

- ON: $2.05 \pm 0.5\ \sigma$
- OFF: $1.76 \pm 0.6\ \sigma$

SUMMARY:

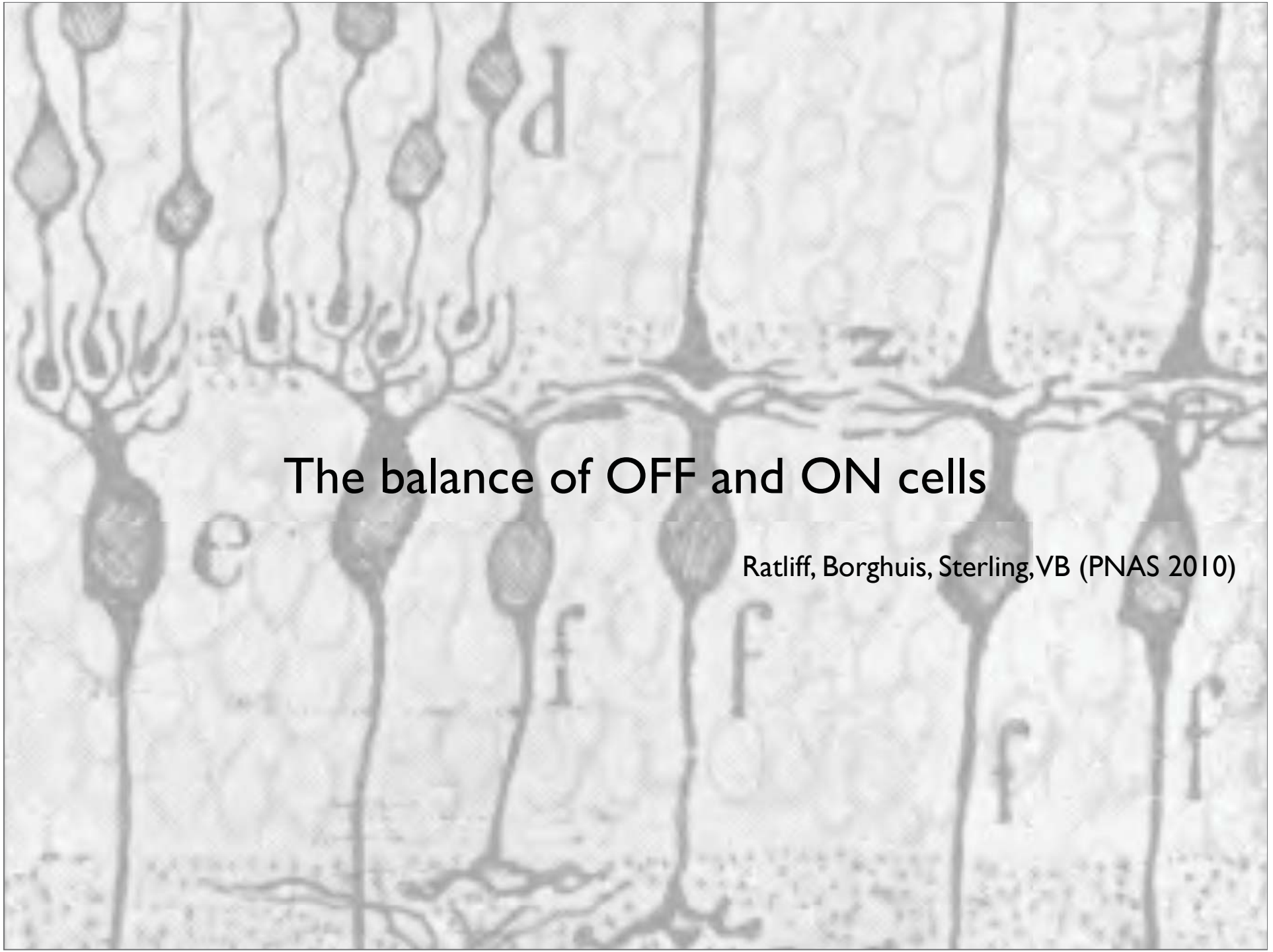
• The principle of efficient coding explains the spatial organization of the retinal mosaic

PREDICTIONS:

• Predicted center size/spacing ratio varies with density of cells and receptive field parameters. Could compare with measurements for different retinas and cell types.

• Specific deficits in visual behavior of mutants with varying ganglion cell overlaps ?

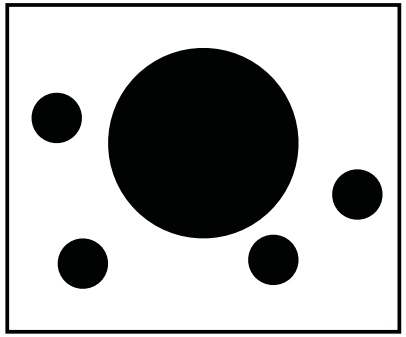
• Irregularities in the ganglion cell mosaic are predicted to be correlated with irregularities in receptive field shape (Liu, Stevens, Sharpee 2009)

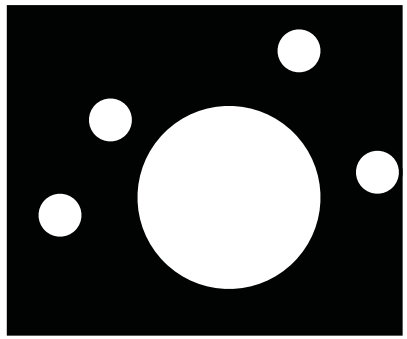


The balance of OFF and ON cells

Ratliff, Borghuis, Sterling, VB (PNAS 2010)

The brain separates light from dark unequally

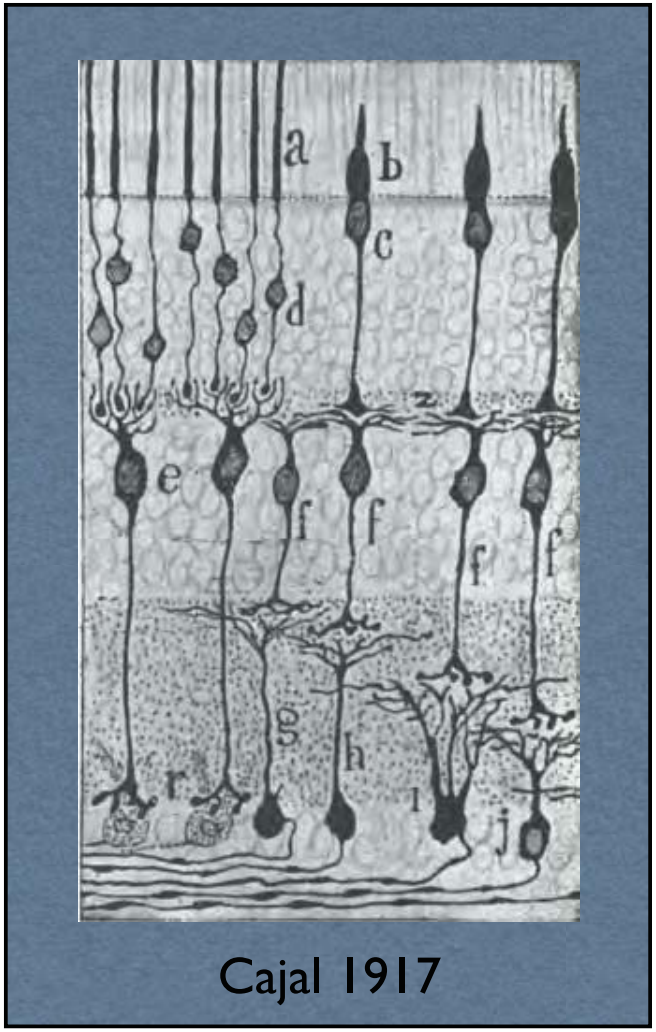




• Psychophysical measurements and visually evoked potentials show greater sensitivity to light decrements and dark spots in images (Zemon et al., '88; Chubb et al., 2004)

• More cortical cells respond to negative that to positive contrasts (Jin et al., 2008)

OFF Bipolars outnumber ON Bipolars

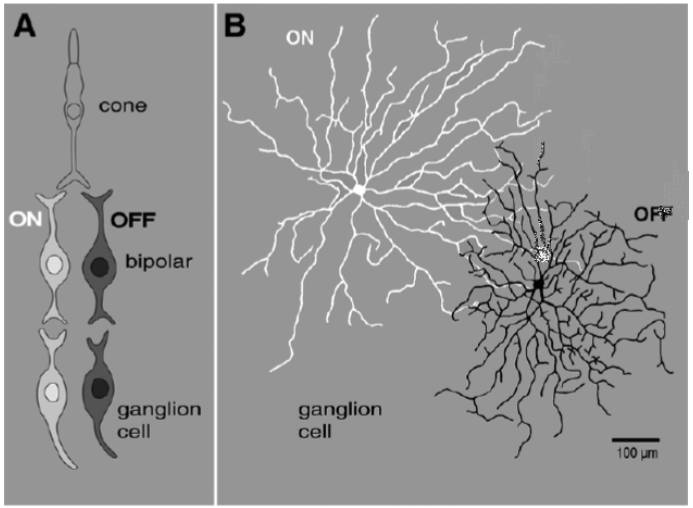


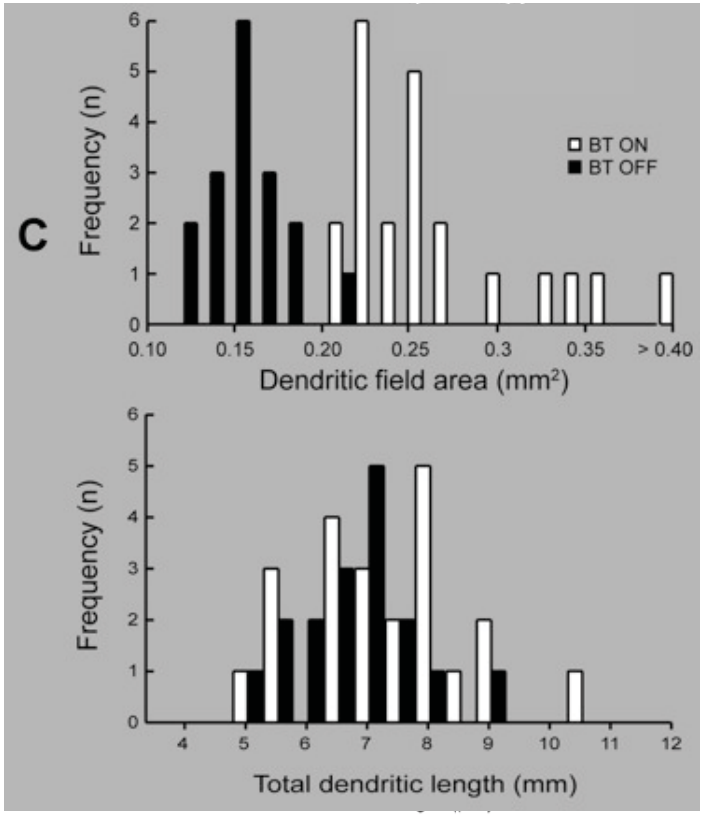
Cajal 1917

The cone-bipolar synapse begins the division into ON vs. OFF pathways separately processing bright vs. dark contrast

Achromatic OFF bipolar cells outnumber ON bipolars by 2:1 (macaque, Ahmad et al., 2003)

Right from the start the retina provides more circuits and devotes more resources to dark contrasts.



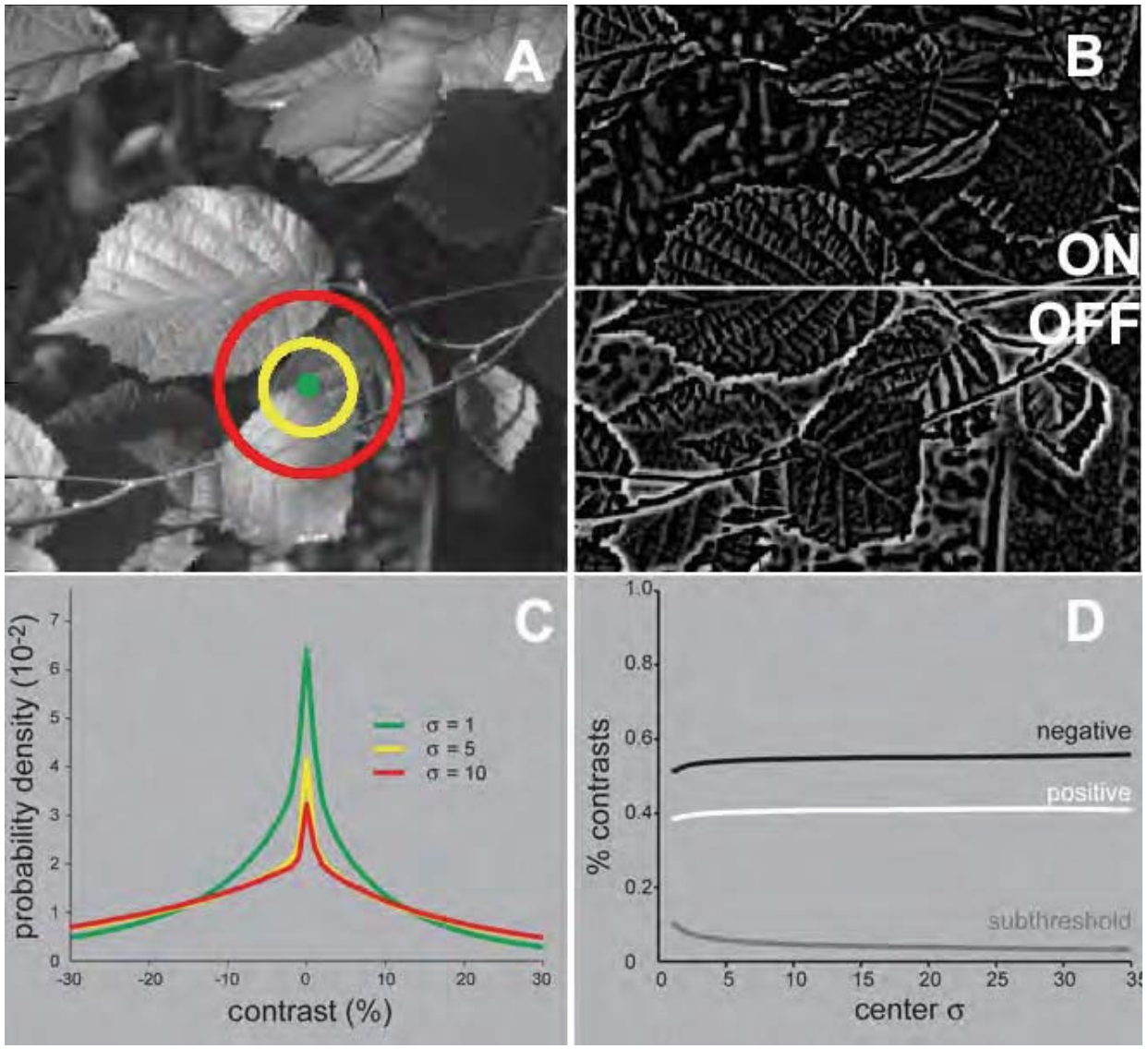


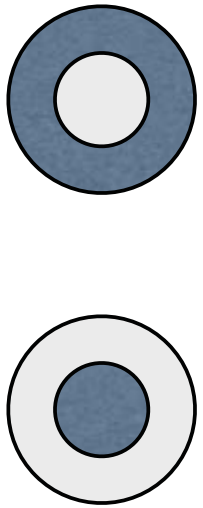
OFF-ON Asymmetries

- OFF cells are ~2 times as numerous as ON
- OFF cells are ~20-50% smaller in area than ON cells
- Total dendritic length of ON and OFF, and thus total number of synapses, is comparable
- Conserved across types and species: guinea pig (Ratliff et al, 2010), rabbit (de Vries & Baylor, 1997), rat (Morigiwa 1989), monkey (Chichilnisky & Kalmar 2002), human (Dacey and Petersen 1992).

HYPOTHESIS: There are more dark regions in natural scenes and information is more densely packed in them.

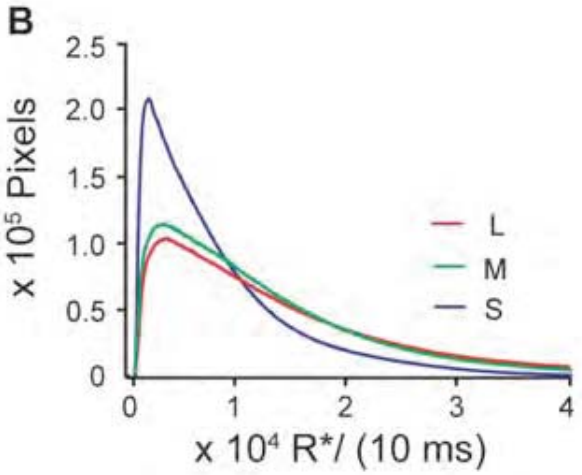
Natural images contain more dark spots

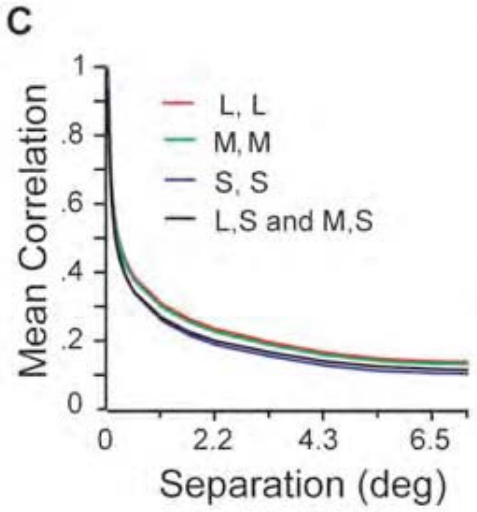


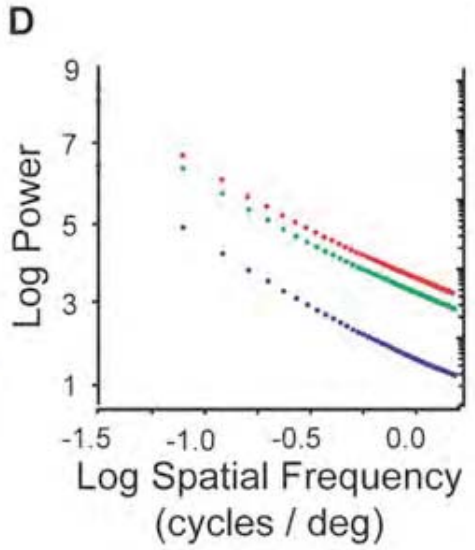


Statistical structure of natural scenes

Garrigan, Ratliff, Sterling, Brainard, VB (PLoS Comp Bio, 2010)







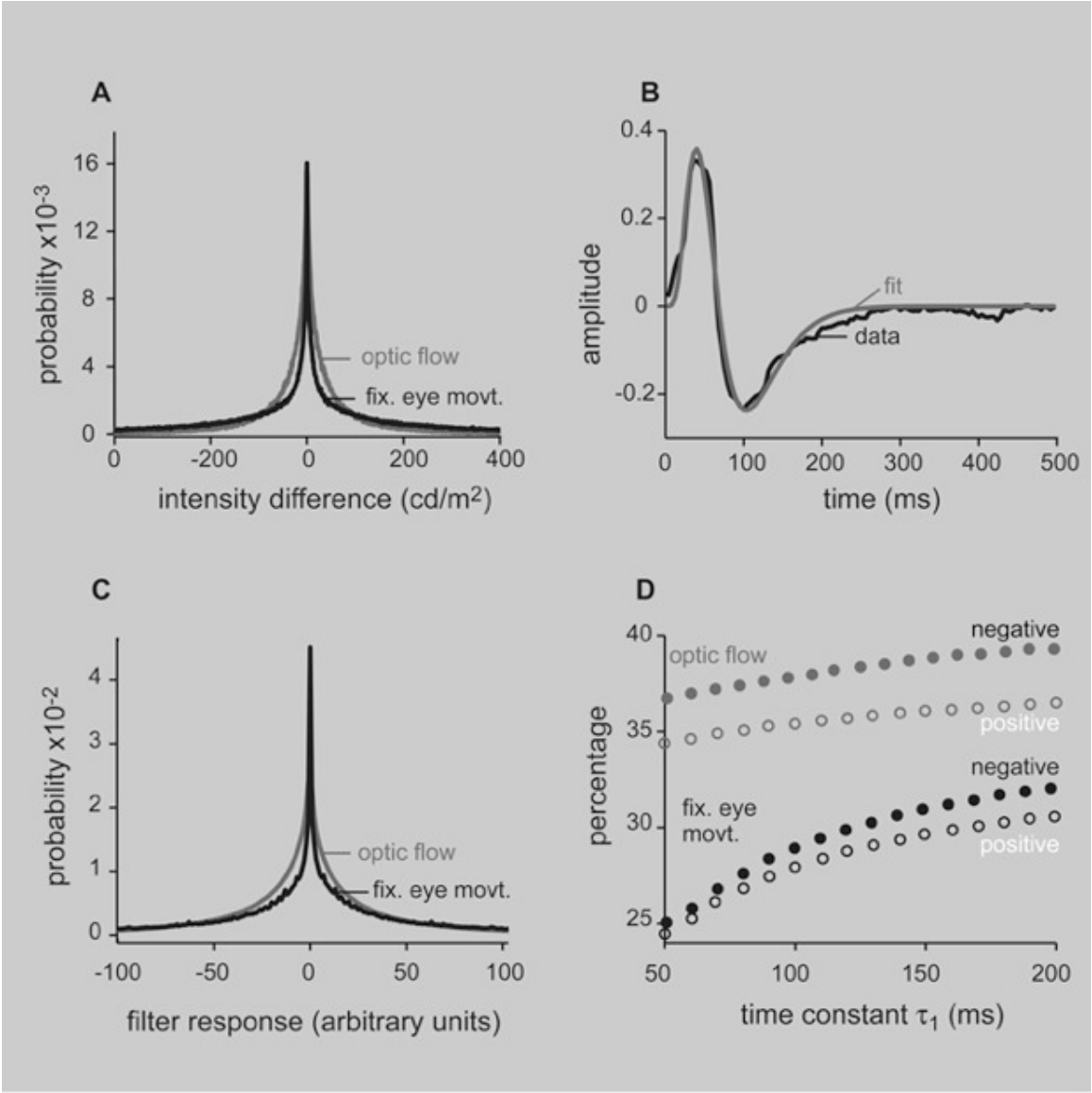
- Low peak, long tail distributions = mean exceeds the median

- Phase averaged power spectrum scales as ~$1/k^2$

Scale invariant

Temporal statistics are ON/OFF symmetric

Distribution of light increments and decrements in natural time series

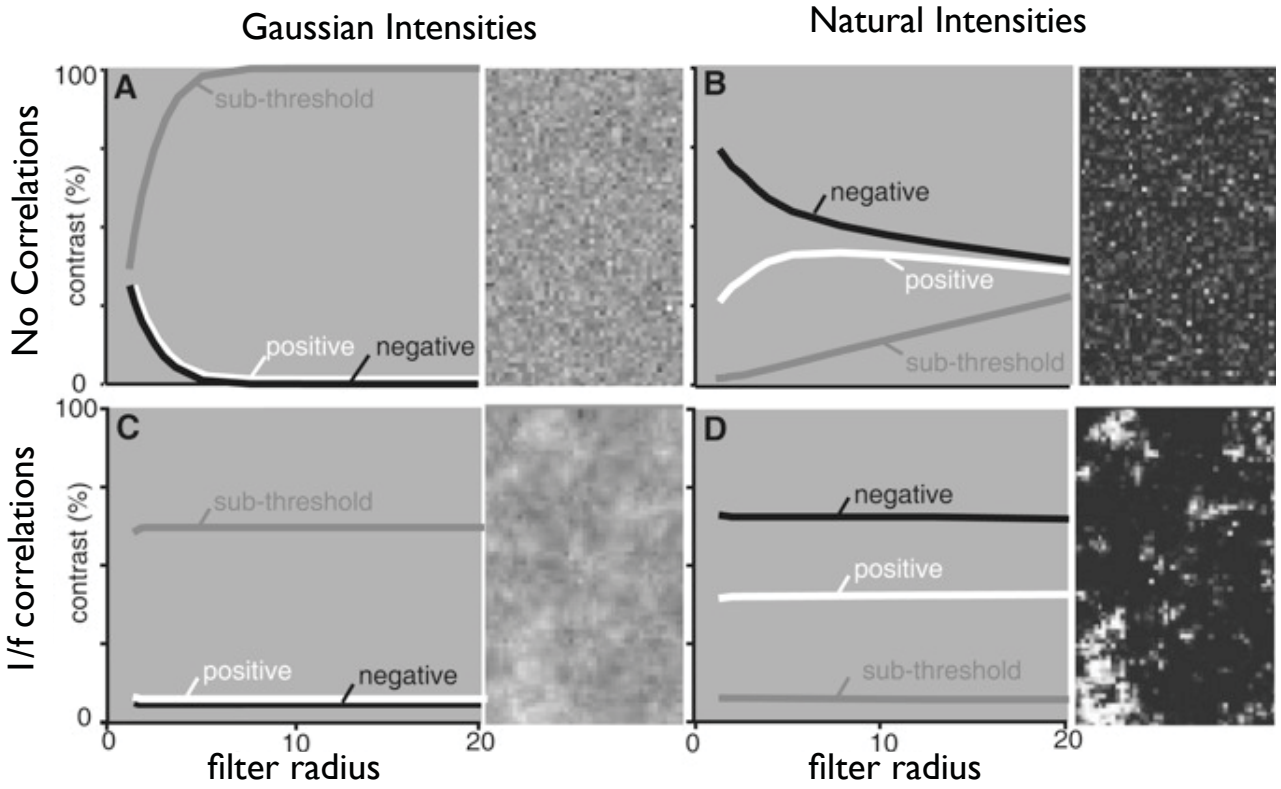


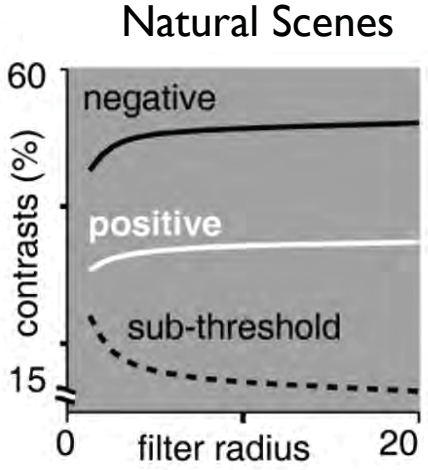
Bandpass fit to retinal ganglion cell temporal filter

Distribution of temporal filter responses natural timeseries

Proportion of positive and negative temporal filter responses for natural time series

What is the origin of the bright/dark asymmetry?



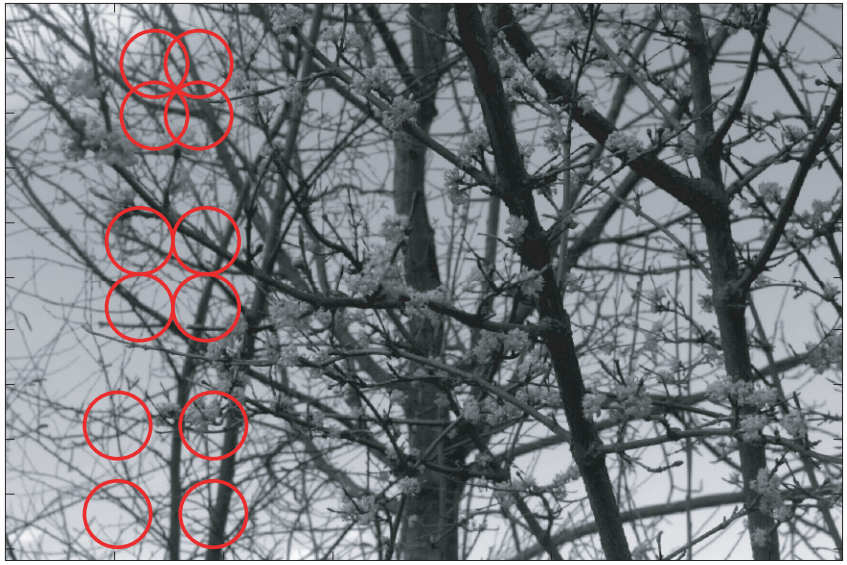


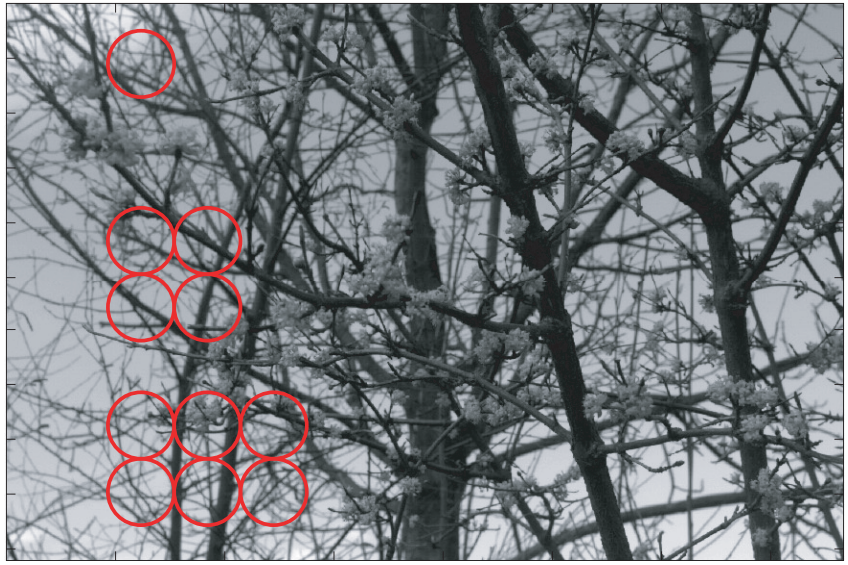
Nature's skewed intensity distribution produces the excess of dark contrasts and the spatial correlations maintain the excess across scales.

Finding the optimal filter mosaic

• Assume that resource constraints require that a particular ON/OFF channel contains N cells. Let $N = N_{OFF} + N_{ON}$.

Given N, find the OFF:ON ratio that maximizes total information.





For N=1 the answer is clear: choose an OFF cell -- it is more likely to respond.

Characterizing the optimal mosaic: simplest model

Total information in the array:

$$I = N_{on}\, I^1_{on} + (N - N_{on})\, I^1_{off}$$

$$\boxed{\frac{\partial I}{\partial N_{on}} = 0}$$

Simple SNR + redundancy approximation of each mosaic:

$$I^1_{on} = N_{on}\, R_{on}\, \tfrac{1}{2}\, \log(1 + f^2_{on}\, SNR)$$

$$I^1_{off} = (N - N_{on})\, R_{off}\, \tfrac{1}{2}\, \log(1 + f^2_{off}\, SNR)$$

Assume 2σ spacing. So R_{on} & R_{off} are independent of N_{on} (scale invariance)

SNR improves with area of receptive field:

$$f^2_{on} = \beta_{on}\, A_{rc} = \beta_{on}\, \frac{A}{N_{on}} \quad \Longrightarrow \quad \frac{\partial I^1_{on}}{N_{on}} \to 0 \text{ for large } N_{on}$$

$$\text{Thus } \frac{\partial I}{\partial N_{on}} \quad \Longrightarrow \quad I^1_{on} = I^1_{off}$$

Information equality in the optimal mosaic.

Characterizing the optimal mosaic

Total information in the array:

$$I = \rho_{ON}\, N_{ON}\, I^1_{ON} + \rho_{OFF}\,(N - N_{ON})\, I^1_{OFF} - M$$

$$\boxed{\frac{\partial I}{\partial N_{on}} = 0}$$

Simple model:

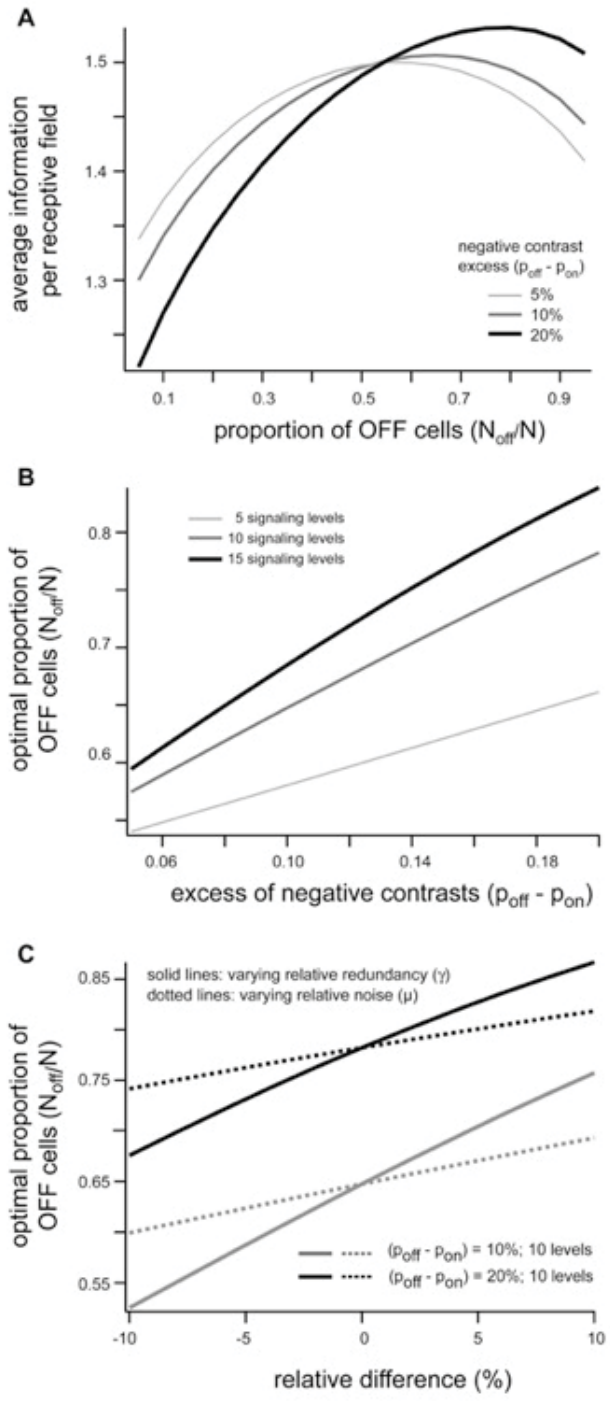
$$I^1_{ON} = -p_{OFF} \log p_{OFF} - \sum_{i=1}^{l_{ON}} \frac{p_{ON}}{l_{ON}} \log \frac{p_{ON}}{l_{ON}}$$

Number of signaling levels improves with area of receptive field:

$$l_{ON} = \beta_{ON} \left(\frac{A}{N_{ON}} \right)^{1/2}$$

Mutual information due to anti-correlation between ON and OFF cells - if an ON cell fails to fire, overlapping OFF cells do fire. Thus the entropy of *non-response* of ON cells is redundant with the OFF responses => drop it

$$\tilde{I}^1_{ON} = p_{ON} \log l_{ON} - p_{ON} \log p_{ON}$$



$$\frac{\partial I}{\partial N_{on}} = 0$$

Assume fixed spacing like real cells.
Thus redundancy is constant.

$$\tilde{I}^1_{OFF} - \tilde{I}^1_{ON} \approx \frac{1}{2}(p_{OFF} - p_{ON})$$

Approximate information equality in the optimal mosaic.

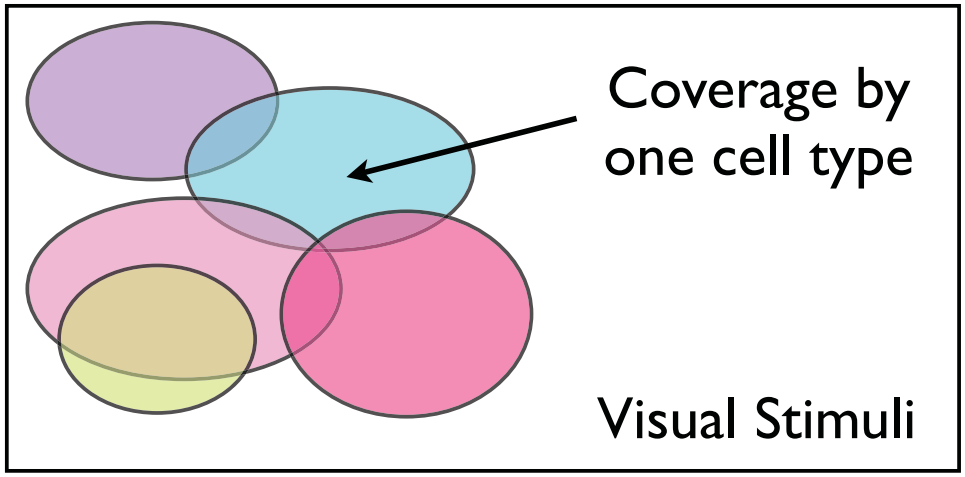
Estimated optimal ratio with model parameters in physiological range

$$\frac{N_{OFF}}{N_{ON}} \approx 1.7$$

Left: Over a wide range of parameters (excess of negative contrasts, relative differences in number of signaling levels, relative differences in redundancy) there is a robust excess of OFF cells in the optimal mosaic

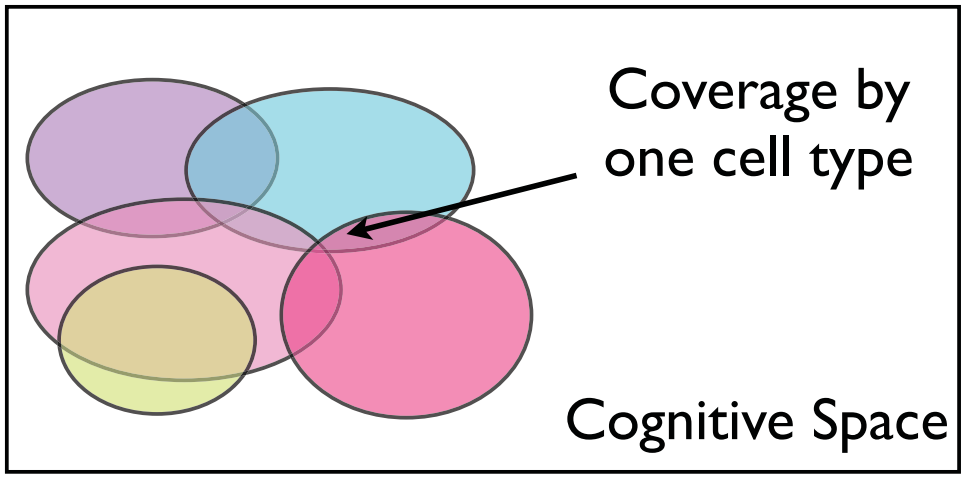
A Fantasy

Can we give an account of *why* and how the early visual system partitions visual stimuli into the observed repertoire of features?



In other words, can we go beyond the division into ON and OFF cells and explain why the visual system breaks up the world into the particular features that it chooses? Or would some other set of features be equally good?

Can this sort of account be extended to the "coverage" of abstract cognitive spaces by neural populations?



Example:

Representation of physical location by grid cells in entorhinal cortex - a "cognitive map" (w/ X. Wei, J. Prentice)

END OF LECTURE 2