#### **Modeling the Visual System**

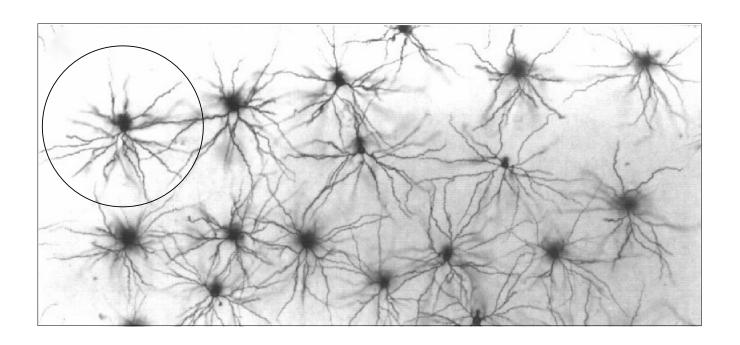
Dr. James A. Bednar

jbednar@inf.ed.ac.uk

http://homepages.inf.ed.ac.uk/jbednar

# **CMVC** figure 3.1a

#### Sample network to model

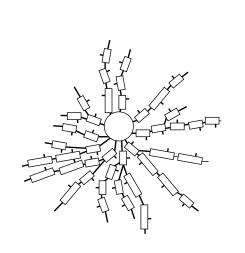


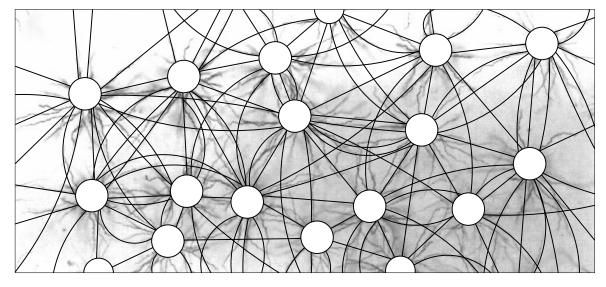
Tangential section with a small subset of neurons labeled

Where do we begin?

# CMVC figure 3.1b,e

#### Modeling approaches





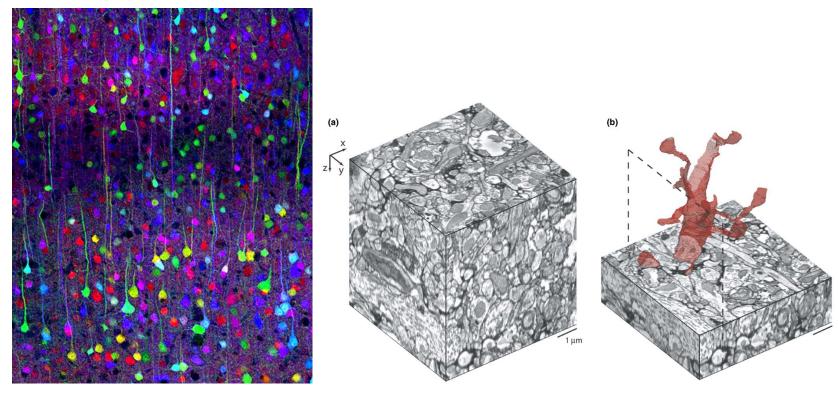
Compartmental neuron model

Integrate-and-fire / firing-rate model of the network

One approach: model single cells extremely well

Our approach: many, many simple single-cell models

#### **Dense connectivity**



Brainbow mouse cortex

Electron microscopy of rat cortex

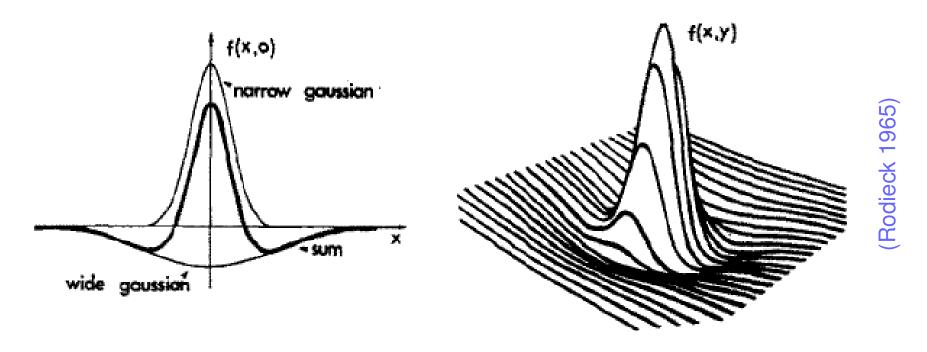
Remember that the actual network is far denser than in the previous slides, with many opportunities for contact between neurons and neurites. (Briggman & Denk 2006)

#### Levels of explanationn

There are many ways to explain the electrophysiological properties (the behavior) of V1 neurons:

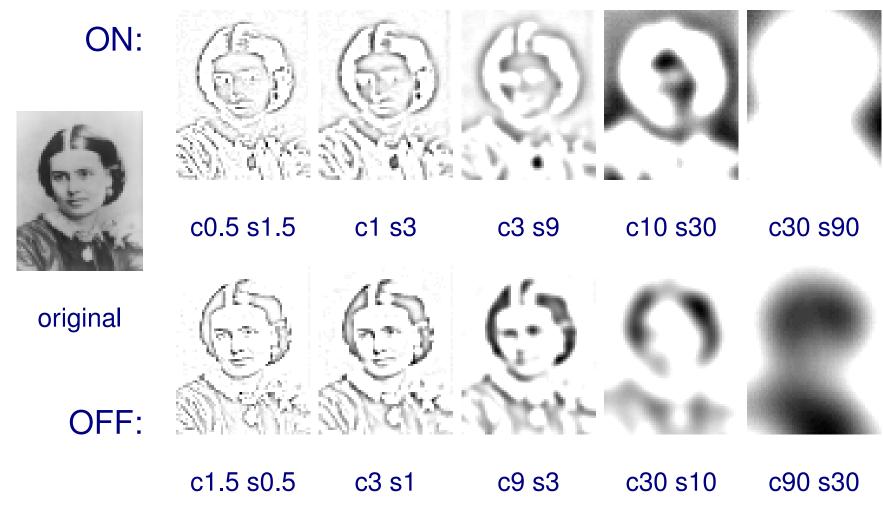
- Phenomenological: Mathematical fit to behavior a good model iff there is a good fit to adults
- 2. **Circuit**: good if a good type 1 model *and* also consistent with known connectivity in adults
- 3. **Developmental**: good if a good type 2 model *and* explains how it comes about, consistent with known data
- 4. **Normative**: good if a good type 1, 2, or 3 model *and* explains why the behavior is useful or appropriate

#### Adult retina and LGN cell models



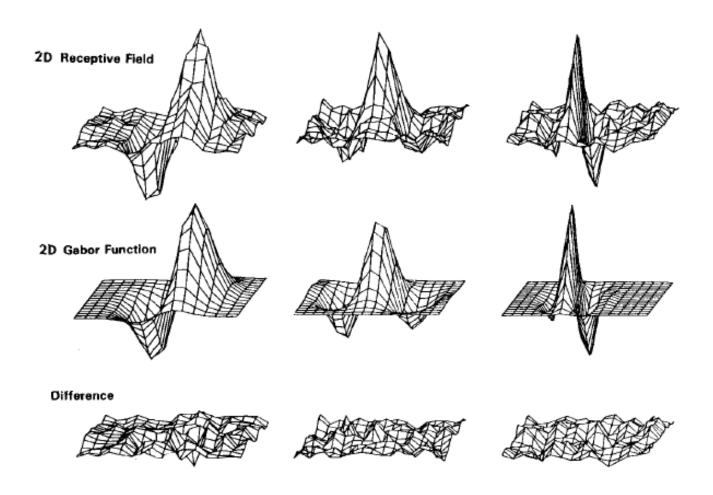
- Standard model of adult RGC or LGN cell activity:
   Difference of Gaussians weight matrix
- Firing rate: dot product of weight and input matrices
- Can be tuned for quantitative match to firing rate
- Can add temporal component (transient+sustained)

#### **Effect of DoG**



Each DoG, if convolved with the image, performs edge detection at a certain size scale (spatial frequency band)

#### Adult V1 cell model: Gabor



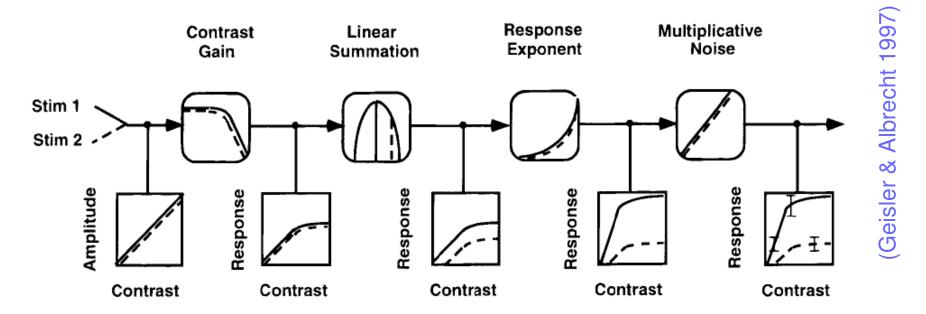
(Adult cat; Daugman 1988)

Standard model of adult V1 simple cell spatial preferences:

Gabor (Gaussian times sine grating) (Daugman 1980)

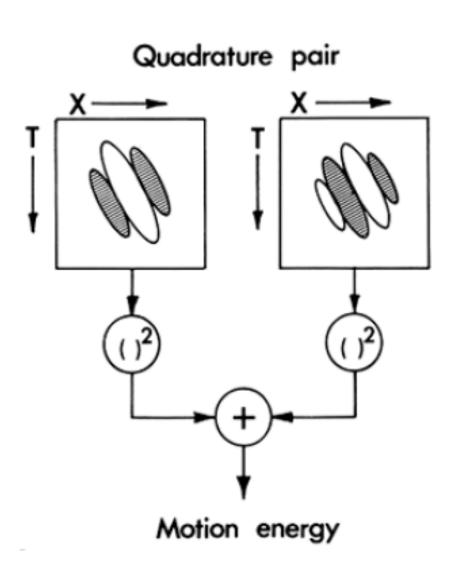
#### Adult V1 cell model: CGE

Contrast-Gain Exponent (CGE) Model



- Gabor model fits spatial preferences
- Simple response function: dot product
- To match observations: need to add numerous nonlinearities
- Examples: CGE model (Geisler & Albrecht 1997); LN model

#### Adult V1 cell model: Energy



 Spatiotemporal energy:
 Standard model of complex direction cell

(Adelson & Bergen 1985)

- Combines inputs from a quadrature pair (two simple cell motion models out of phase)
- Achieves phase invariance, direction selectivity

#### Retina/LGN development models

Relatively rare, but more in recent years:

Retinal wave generation

```
(e.g. Feller et al. 1997; Godfrey & Swindale 2007; Hennig et al. 2009)
```

RGC development based on retinal waves

```
(e.g. Eglen & Willshaw 2002)
```

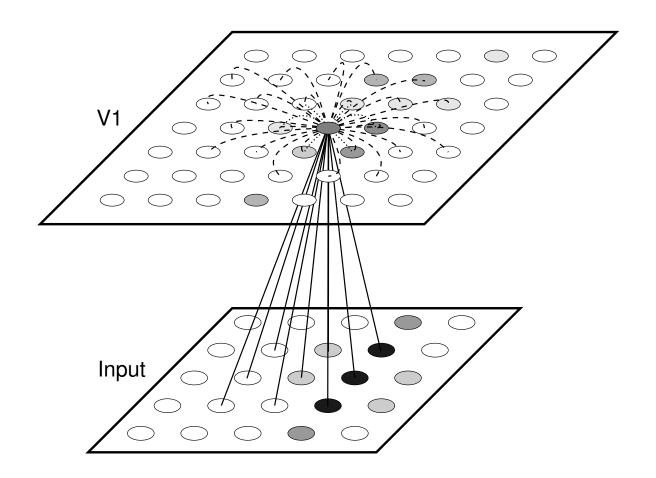
Retinogeniculate pathway based on retinal waves

```
(e.g. Eglen 1999; Haith 1998)
```

Because of the wealth of data from the retina, such models can now become quite detailed.

## CMVC figure 3.3

#### Our focus: Cortical map models



Basic architecture: input surface mapped to cortical surface + some form of lateral interaction

#### Kohonen SOM: Feedforward

Popular computationally tractable map model (Kohonen 1982)

Feedforward activity of unit (i, j):

$$\eta_{ij} = \|\vec{V} - \vec{W}_{ij}\| \tag{1}$$

(distance between input vector  $ec{V}$  and weight vector  $ec{W}$ )

Not particularly biologically plausible, but easy to compute, widely implemented, and has some nice properties.

Note: Activation function is not typically a dot product; the CMVC book is confusing about that.

#### Kohonen SOM: Lateral

Abstract model of lateral interactions:

- Pick winner (r, s)
- Assign it activity  $\eta_{\max}$
- Assume that activity of unit (i, j) can be described by a neighborhood function, such as a Gaussian:

$$h_{rs,ij} = \eta_{\text{max}} \exp\left(-\frac{(r-i)^2 + (s-j)^2}{\sigma_{\text{h}}^2}\right), \tag{2}$$

Models lateral interactions that depend only on distance from winning unit.

#### Kohonen SOM: Learning

Inspired by basic Hebbian rule (Hebb 1949):

$$w' = w + \alpha \eta \chi \tag{3}$$

where the weight increases in proportion to the product of the input and output activities.

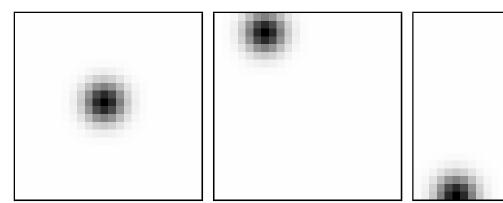
In SOM, the weight vector is shifted toward the input vector based on the Euclidean difference:

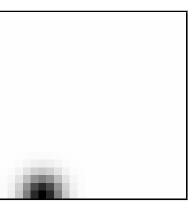
$$w'_{k,ij} = w_{k,ij} + \alpha(\chi_k - w_{k,ij}) h_{rs,ij}.$$
 (4)

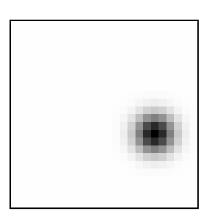
Hebb-like, but depending on distance from winning unit

# CMVC figure 3.4

#### **SOM example: Input**

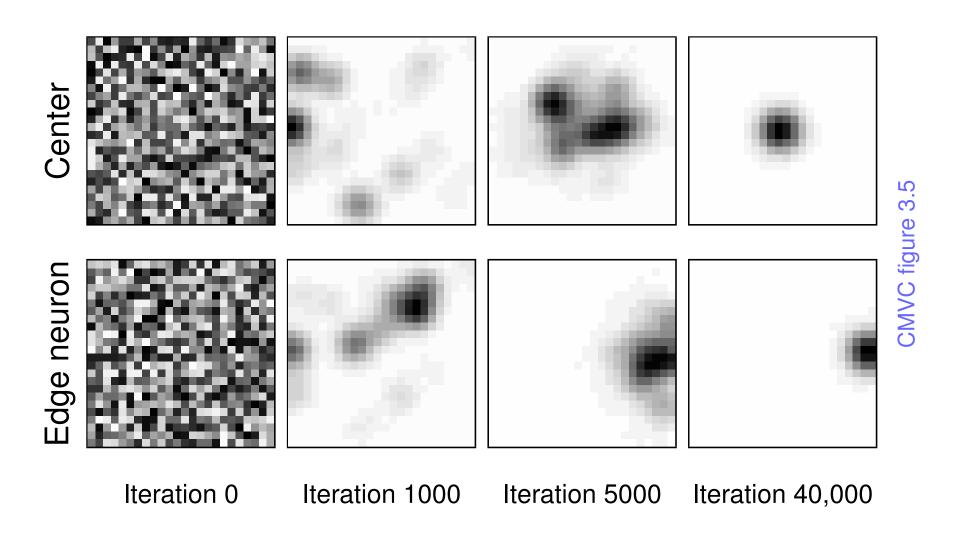






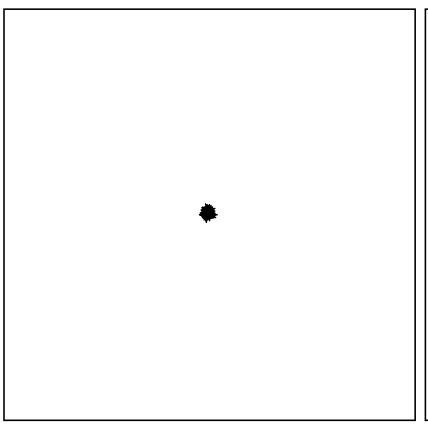
- SOM will be trained with unoriented Gaussian activity patterns
- Random (x, y) positions anywhere on retina
- 576-dimensional input, but the x and y locations are the only source of variance

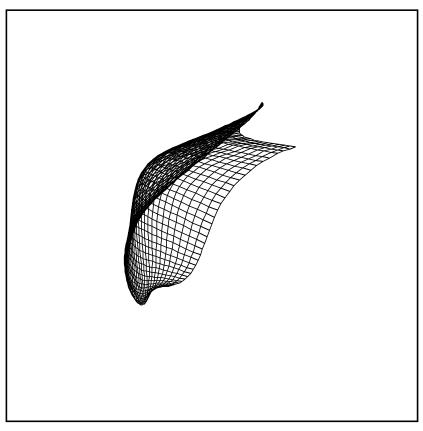
#### **SOM: Weight vector self-org**



Combination of input patterns; eventually settles to an exemplar

#### **SOM: Retinotopy self-org**





CMVC figure 3.6a-b

Iteration 0: Initial

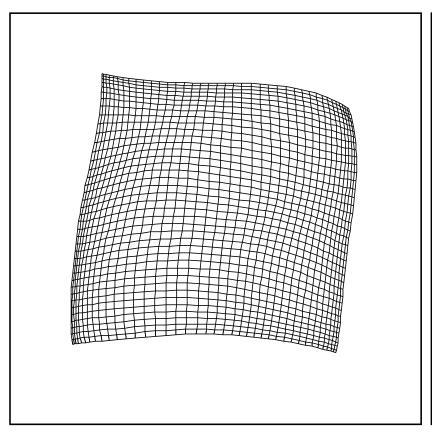
Iteration 1000: Unfolding

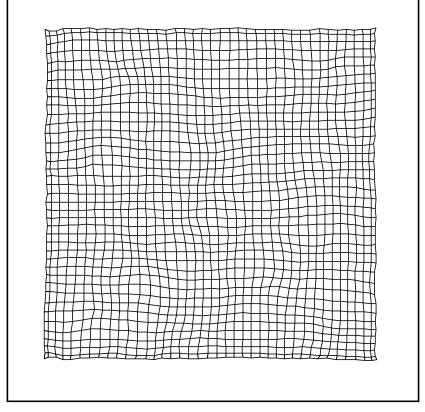
Initially bunched (all average to zero)

Unfolds as neurons differentiate

# CMVC figure 3.6c-d

#### **SOM: Retinotopy self-org**



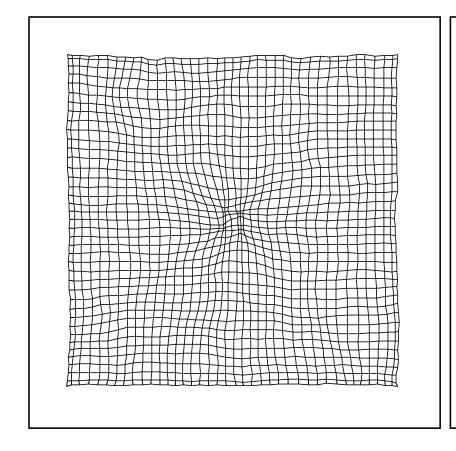


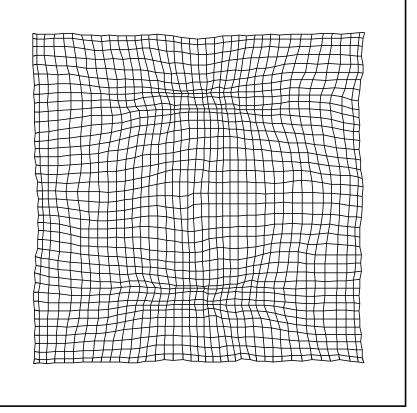
Iteration 5000: Expanding Iteration 40,000: Final

Expands to cover usable portion of input space.

## CMVC figure 3.7

#### Magnification of dense input areas



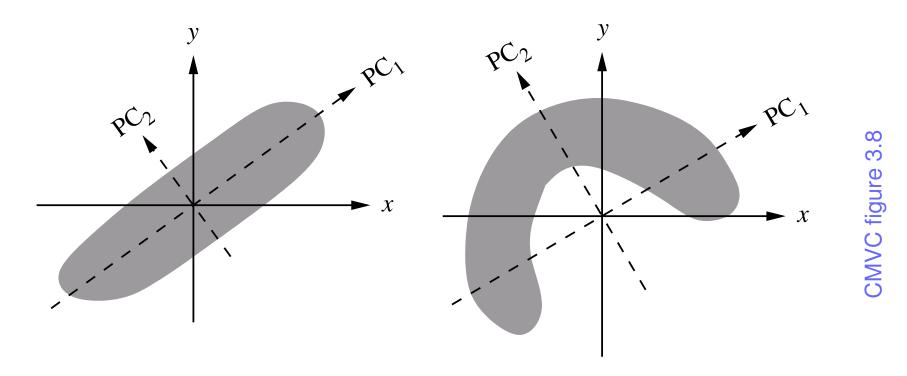


Gaussian distribution Two long Gaussians

Density of units receiving input from a particular region

depends on input pattern statistics

## Principal components of data distributions



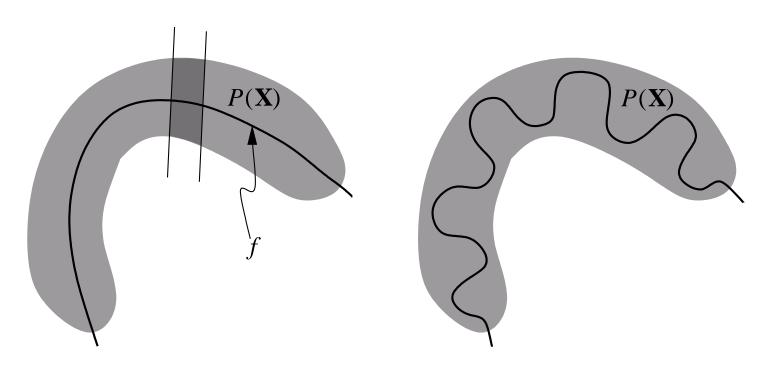
(a) Linear distribution

(b) Nonlinear distribution

PCA: linear approximation, good for linear data

# CMVC figure 3.9

### Nonlinear distributions: principal curves, folding



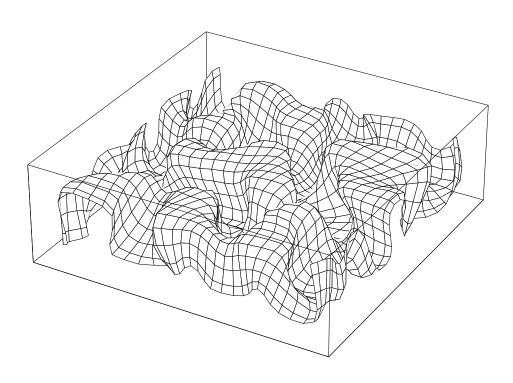
Principal curve

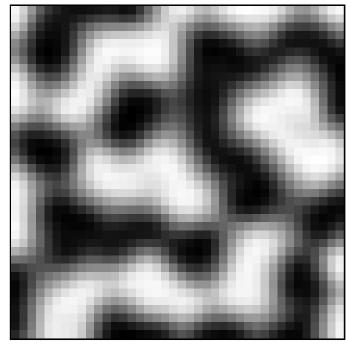
Folded curve

Generalization of idea of PCA to pick best-fit curve(s)

Multiple possible curves

### Three-dimensional model of ocular dominance





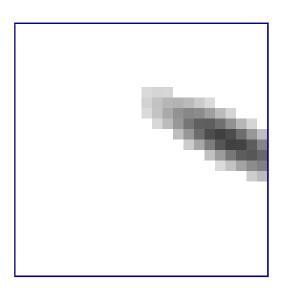
CMVC figure 3.10

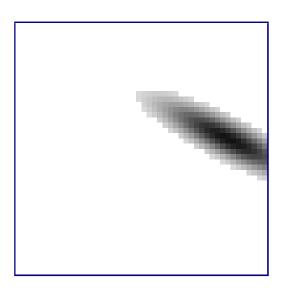
Representing the third dimension by folding

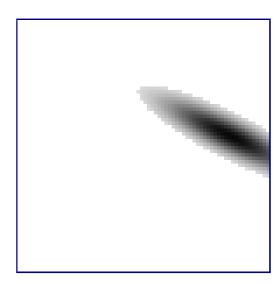
Visualization of ocular dominance

Feature maps: Discrete approximations to principal surfaces?

#### Role of density of input sheet







- Gaussian inputs are nearly band-limited (since Fourier transform is also Gaussian)
- Density of input sampling unimportant, if it's greater than 2X highest frequency in input (Nyquist theorem)

#### Role of density of SOM sheet

SOM sheet acts as a discrete approximation to a two-dimensional surface.

How many units are needed for the SOM depends on how nonlinear the input distribution is — a smoothly varying input distribution requires fewer units to represent the shape.

Only loosely related to the input density – input density limits how quickly the input varies across space, but only for wideband stimuli.

#### Other relevant models

ICA Independent Component Analysis yields realistic RFs (Olshausen & Field 1996); also can be applied to maps (Hyvärinen & Hoyer 2001).

InfoMax Information maximization can lead to RFs (Linsker 1986b,c) and basic maps (Kozloski et al. 2007; Linsker 1986a)

Elastic net Achieving good coverage and continuity leads to realistic feature maps (Carreira-Perpiñán et al. 2005; Goodhill & Cimponeriu 2000)

This course focuses on mechanistic circuit models, not normative models (ICA, Infomax, PCA, principal surfaces) or feature space models (elastic net), both of which are hard to relate directly to the underlying biological systems.

#### **Summary**

- Basic intro to visual modeling
- Adult models are well established, but vision-specific
- SOM: maps multiple dimensions down to two
- Feature maps: Principal surfaces?

#### References

- Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, *2*, 284–299.
- Briggman, K. L., & Denk, W. (2006). Towards neural circuit reconstruction with volume electron microscopy techniques. *Current Opinion in Neurobiology*, *16* (5), 562–570.
- Carreira-Perpiñán, M. A., Lister, R. J., & Goodhill, G. J. (2005). A computational model for the development of multiple maps in primary visual cortex. *Cerebral Cortex*, *15* (8), 1222–1233.
- Daugman, J. G. (1980). Two-dimensional spectral analysis of cortical receptive field profiles. *Vision Research*, *20*, 847–856.

- Daugman, J. G. (1988). Complete discrete 2-D Gabor transforms by neural networks for image analysis and compression. *IEEE Transactions on Acoustics, Speech, and Signal Processing*, *36* (7).
- Eglen, S. J. (1999). The role of retinal waves and synaptic normalization in retinogeniculate development. *Philosophical Transactions of the Royal Society of London Series B*, *354* (1382), 497–506.
- Eglen, S. J., & Willshaw, D. J. (2002). Influence of cell fate mechanisms upon retinal mosaic formation: A modelling study. *Development*, *129* (23), 5399–5408.
- Feller, M. B., Butts, D. A., Aaron, H. L., Rokhsar, D. S., & Shatz, C. J. (1997). Dynamic processes shape spatiotemporal properties of retinal waves. *Neuron*, *19*, 293–306.

- Geisler, W. S., & Albrecht, D. G. (1997). Visual cortex neurons in monkeys and cats: Detection, discrimination, and identification. *Visual Neuroscience*, *14* (5), 897–919.
- Godfrey, K. B., & Swindale, N. V. (2007). Retinal wave behavior through activity-dependent refractory periods. *PLoS Computational Biology*, *3* (11), e245.
- Goodhill, G. J., & Cimponeriu, A. (2000). Analysis of the elastic net model applied to the formation of ocular dominance and orientation columns. *Network: Computation in Neural Systems*, *11*, 153–168.
- Haith, G. L. (1998). *Modeling Activity-Dependent Development in the Retino*geniculate Projection. Doctoral Dissertation, Department of Psychology, Stanford University, Palo Alto, CA.

- Hebb, D. O. (1949). *The Organization of Behavior: A Neuropsychological Theory*. Hoboken, NJ: Wiley.
- Hennig, M. H., Adams, C., Willshaw, D., & Sernagor, E. (2009). Early-stage retinal waves arise close to a critical state between local and global functional network connectivity. *The Journal of Neuroscience*, *29*, 1077–1086.
- Hyvärinen, A., & Hoyer, P. O. (2001). A two-layer sparse coding model learns simple and complex cell receptive fields and topography from natural images. *Vision Research*, *41* (18), 2413–2423.
- Kohonen, T. (1982). Self-organized formation of topologically correct feature maps. *Biological Cybernetics*, *43*, 59–69.
- Kozloski, J., Cecchi, G., Peck, C., & Rao, A. R. (2007). Topographic infomax in a neural multigrid. In Liu, D. e. a. (Ed.), *Advances in Neural Networks*

- ISSN 2007 (Lecture Notes in Computer Science4492, pp. 500–509).
   Berlin: Springer.
- Linsker, R. (1986a). From basic network principles to neural architecture: Emergence of orientation columns. *Proceedings of the National Academy of Sciences, USA*, *83*, 8779–8783.
- Linsker, R. (1986b). From basic network principles to neural architecture: Emergence of orientation-selective cells. *Proceedings of the National Academy of Sciences, USA*, 83, 8390–8394.
- Linsker, R. (1986c). From basic network principles to neural architecture: Emergence of spatial-opponent cells. *Proceedings of the National Academy of Sciences, USA*, 83, 7508–7512.
- Livet, J., Weissman, T. A., Kang, H., Draft, R. W., Lu, J., Bennis, R. A., Sanes,

- J. R., & Lichtman, J. W. (2007). Transgenic strategies for combinatorial expression of fluorescent proteins in the nervous system. *Nature*, *450*, 56–62.
- Olshausen, B. A., & Field, D. J. (1996). Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, *381*, 607–609.
- Rodieck, R. W. (1965). Quantitative analysis of cat retinal ganglion cell response to visual stimuli. *Vision Research*, *5* (11), 583–601.