Developmental Strategies of Innate Learning in the Early Visual System

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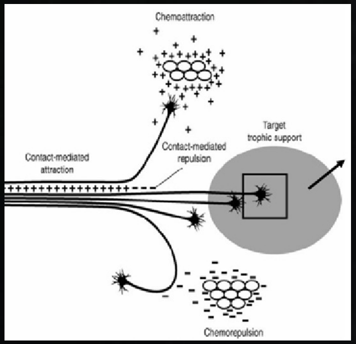


Innate: prior to visual experience

Learned: activity based refinement, as done by natural experience

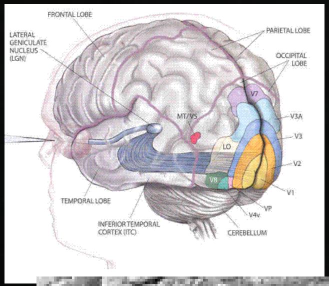
Motivation

The principle of innate learning: spontaneous patterns of neural activity are used to train or refine a sensory system in an analogous way to how the system can adapt based on natural experience.

Main advantage: Parsimony

	Pre eye-opening	Post eye-opening
Neural activity	Spontaneous Activity	Visual experience
Algorithm	Activity-based refinement	Learning
	Activity-based learning (e.g. efficient coding here)	

Outline – Developmental strategies of innate learning...



V1 neurophysiology

- Adult response description
- Developmental timeline
- Role of spontaneous activity

Relevant modeling approaches

- Retinal wave models
- Neural modeling of V1 formation
- Efficient coding of V1, general

Bridging the gap: efficient coding ↔ spontaneous activity

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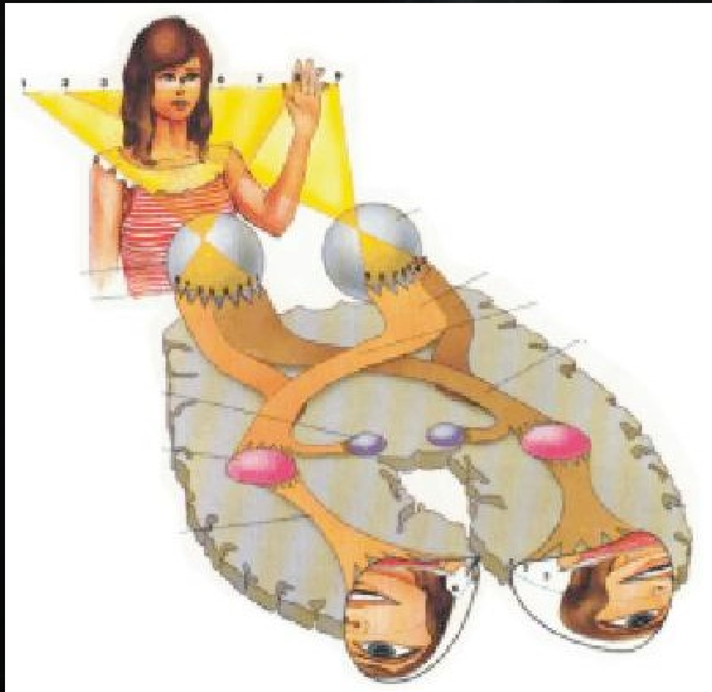
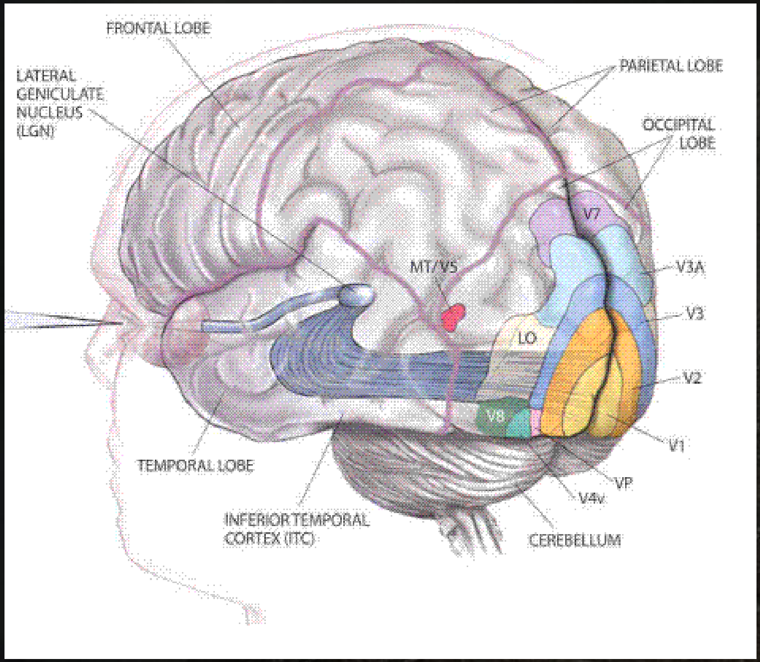
- Binocular model results
- Future work: neurophysiology, neural modeling, and efficient coding

thalamocortical visual pathway



Frisby, 1979



Retina → LGN ⇄ V1

Respective roles

Retina → LGN ⇄ V1

Retina: retinal waves

- Earliest discovered source of visual spontaneous activity (Maffei, Galli-Resta 1990)
- Most widely studied (review in Wong 1999...)
- Physiological models of retinal waves available (Butts et al. 1999, Godfrey & Swindale 2008)

LGN (lateral geniculate nucleus)

- The source of spontaneous activity implicated in V1 development
- V1 Feedback necessary to correlate activity between eye layers (Weliky & Katz 1999)

V1 (primary visual cortex)

- The area innately trained by the LGN/V1 spontaneous activity.
- Primarily interested in “simple cells”

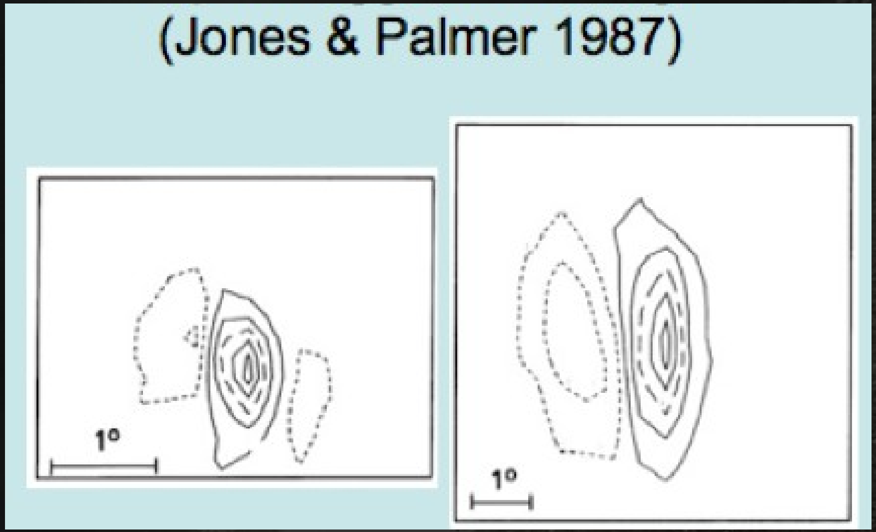
V1 “simple cell” response description

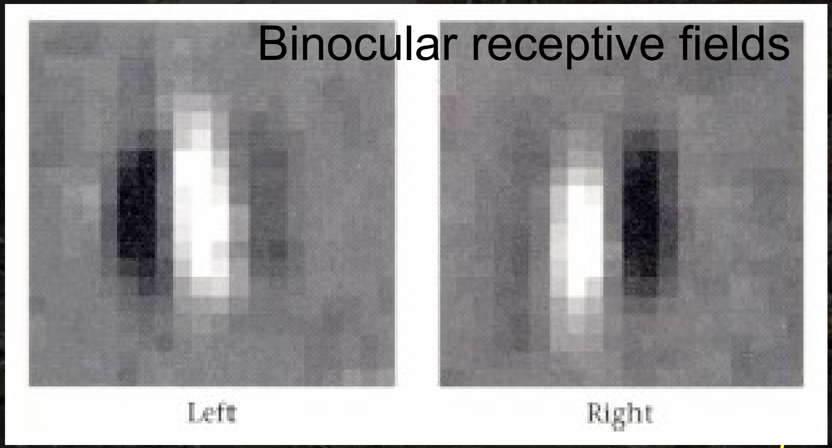
Response described by template matching*

Cells respond when bright and dark areas in the template and viewed image overlap in retinal coordinates

** only for the purposes of this talk. Such descriptions are idealizations - full response descriptions are not so simple.*

Simple cell receptive fields

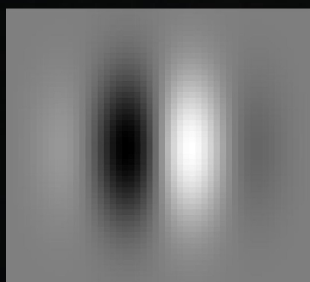




V1 simple cell selectivity

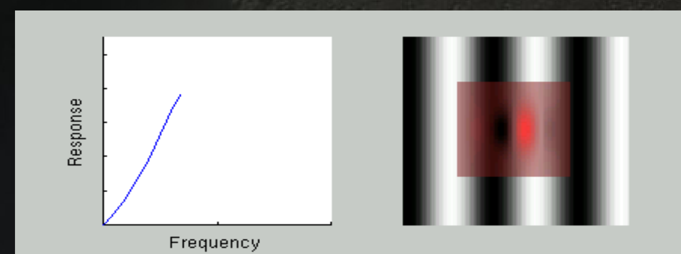
Selective For:

Orientation



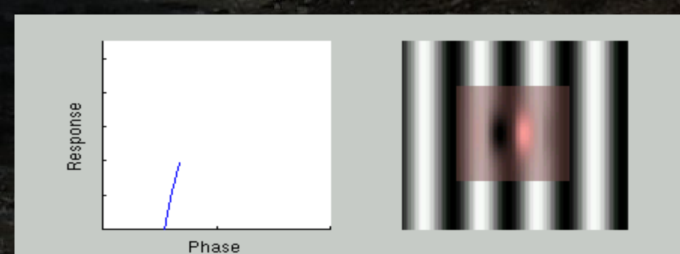
Receptive Field Position

Spatial Frequency



Direction of Motion
(not shown here)

Phase

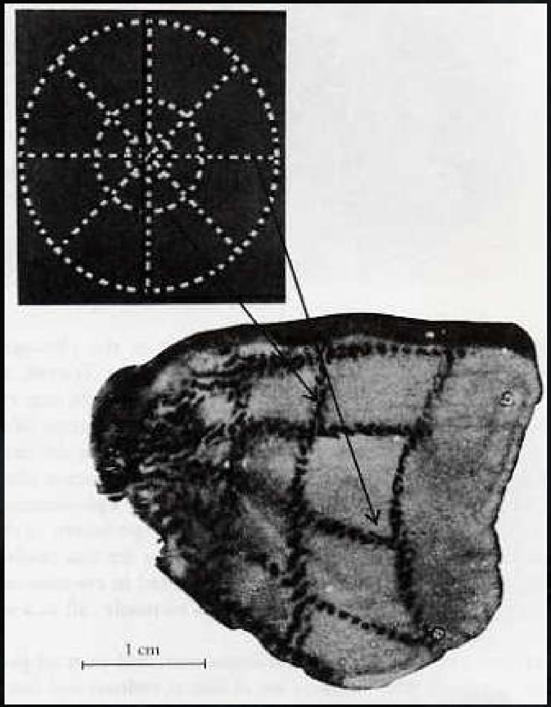


The V1 map

V1 cell responses vary characteristically over the cortical surface

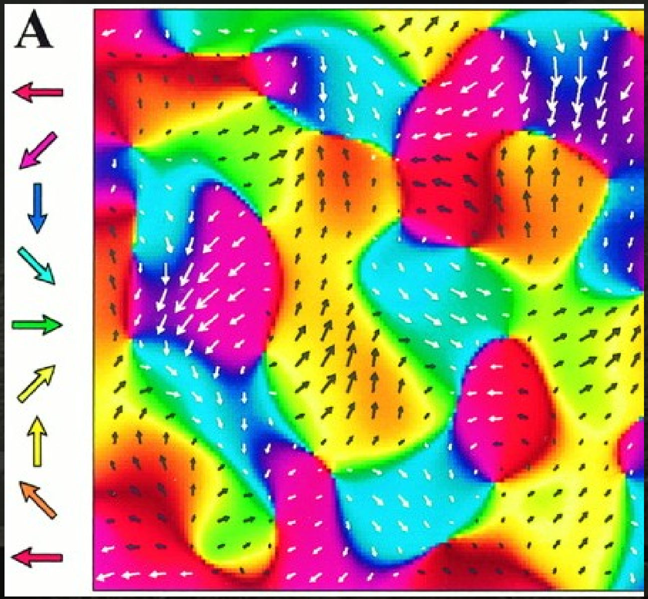
V1 map features

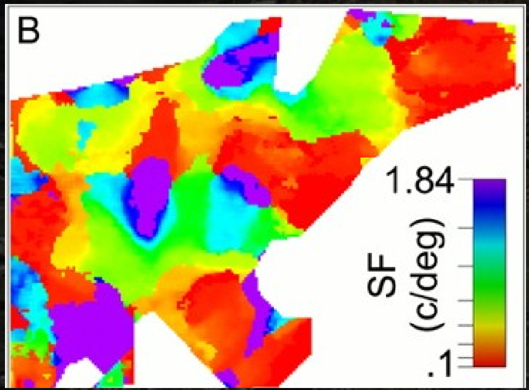
1. Retinotopic location
2. Eye preference
3. Stimulus orientation
4. Direction of Motion
5. Spatial Frequency



(Tootell et al. 1982)
macaque

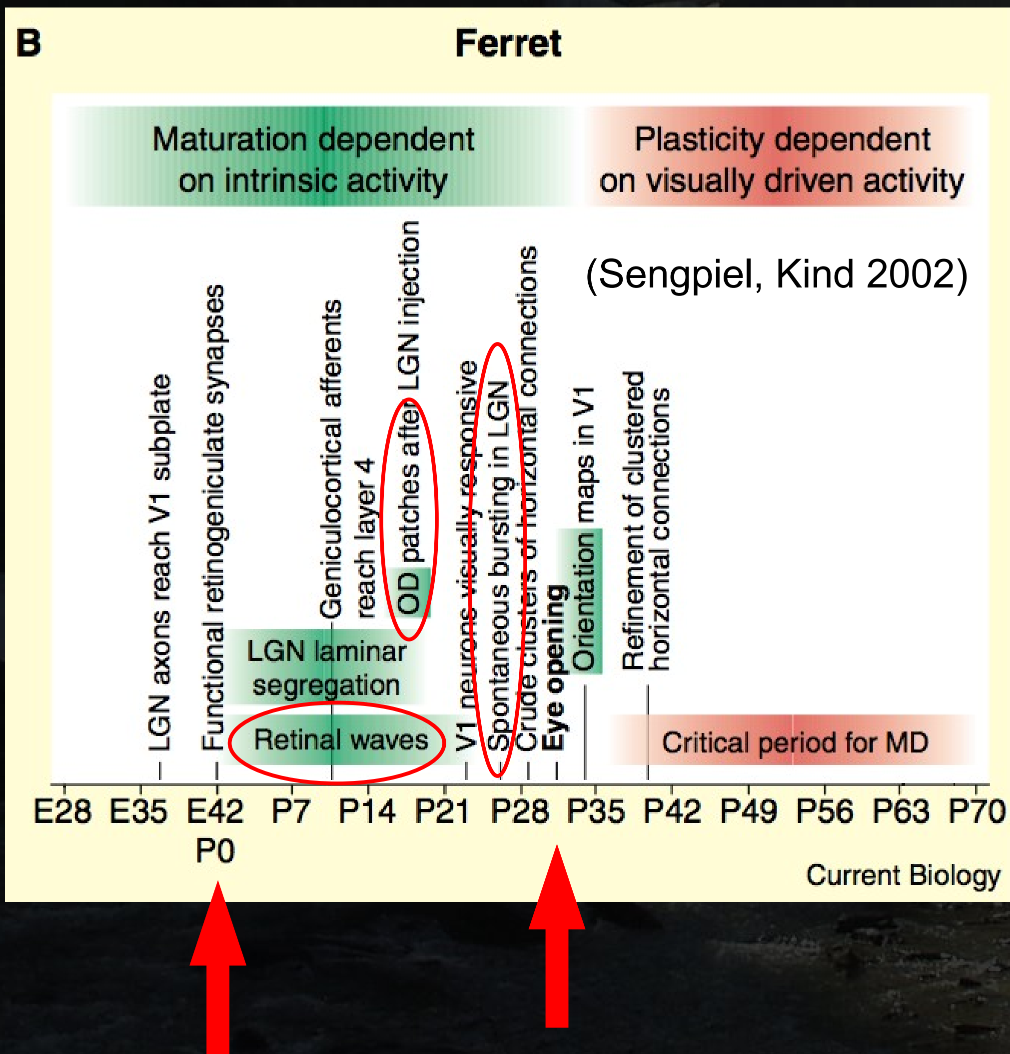
(Shmuel & Grinvald 1996)
cat





(Issa, Trepel, Stryker 2000)
cat

Developmental timeline



P0: Birth

P0-P21 to 25:
Retinal waves (Wong 1993)

P16-P18: ocular dominance patches LGN → V1
(Crowley & Katz 2000)

P23: orientation columns visible (Chapman & Stryker 1993)

P24-27: LGN spont. activity present (Weliky & Katz 1999)

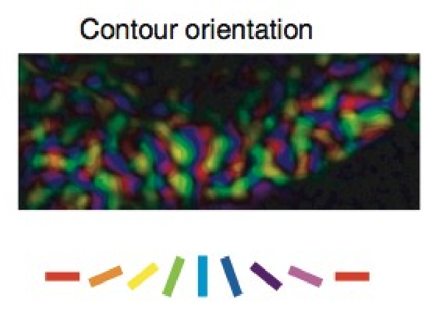
P30-32: Eye opening

~P38: Direction selectivity first visible (Li et al. 2006)

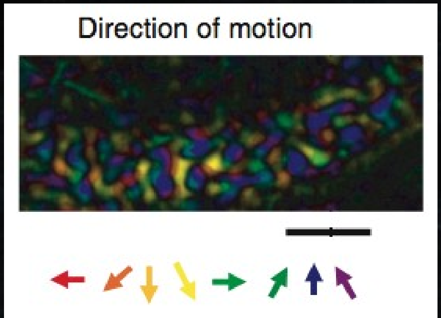
P42: maturation of orientation columns (with or without experience)
(White et al. 2001)

The role of neural activity

Ocular dominance columns form without retinal activity (Chapman et al 1986 cat, Crowley & Katz 2000 ferret...)
• Later imbalanced activity → imbalanced eye representation in cortex: Retinal wave (Chapman et al 1986 cat), lid suture (Wiesel & Hubel 1963, cat)

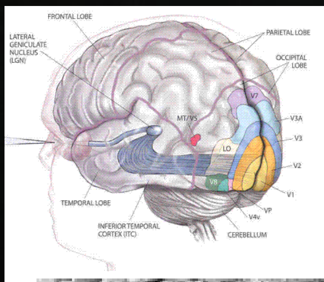


Orientation selective cells are present prior to eye opening, but mature weeks later. (Chapman & Stryker 1993)
• Maturation occurs in the dark, but with more dark rearing they eventually disappear (White et al. 2001)
• Exposure to overabundance of a particular orientation yielded double the cortical area (Sengpiel et al. 1999)



Direction of motion selectivity formation requires experience in ferret (Li et al. 2006)
• Overabundance of an experienced direction yields more cells (Daw et al. 1976, cat)

Outline – Developmental strategies of innate learning...



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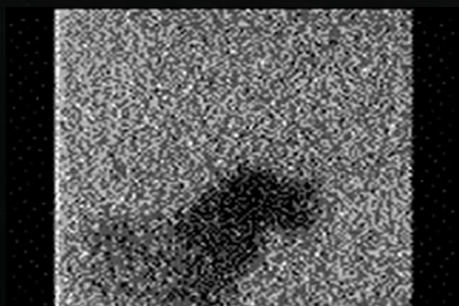
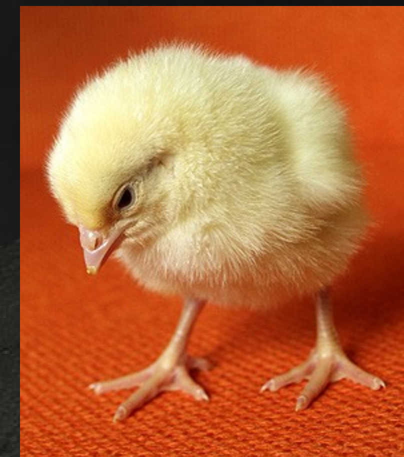
Ubiquity of retinal waves



(Feller et al 1996)

(Galli & Maffei 1988)

(Feller et al. 1996)



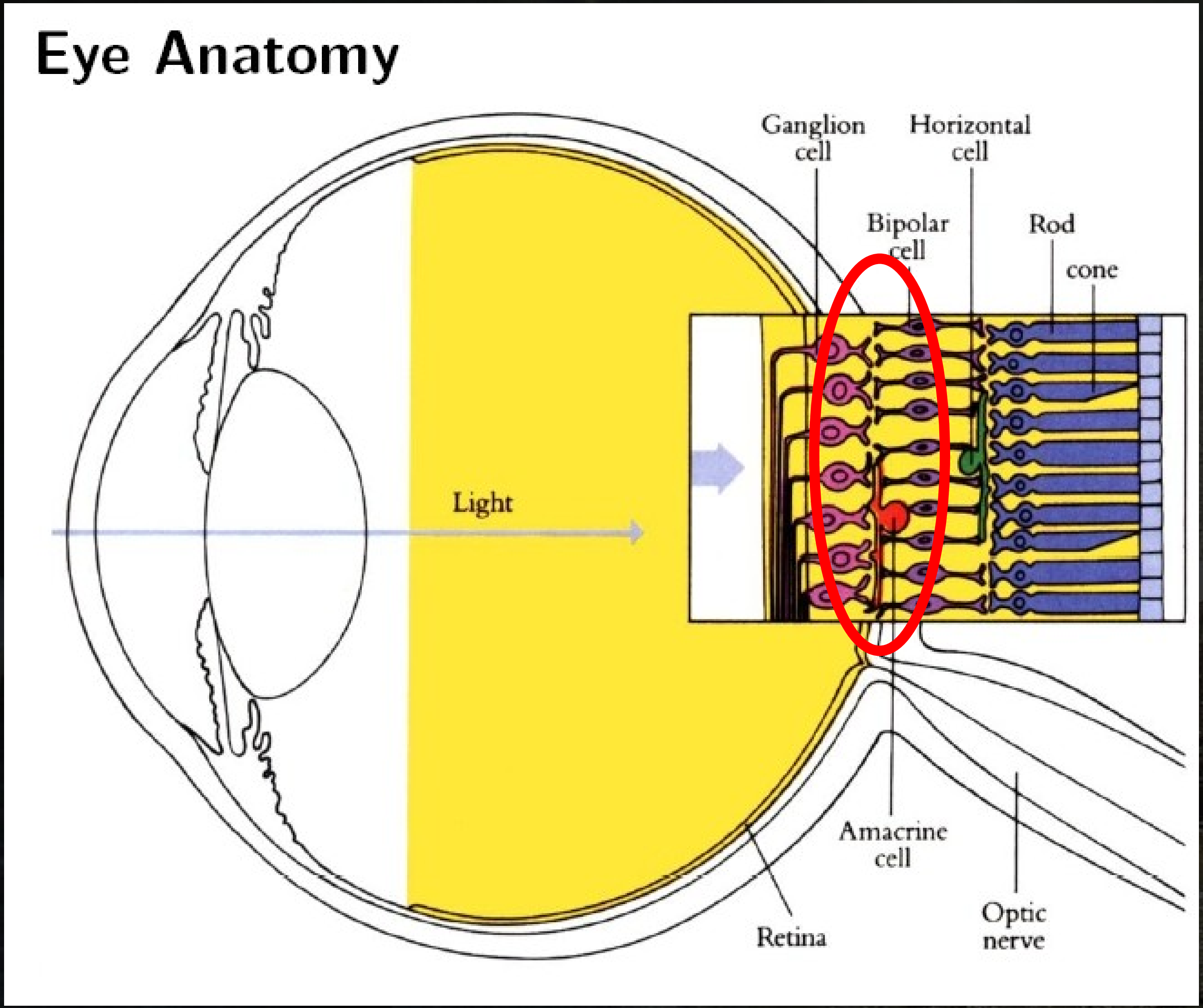
(Catsicas et al. 1998, Wong 1998)

(Warland et al. 2006)

(Meister et al. 1991)

(Sernagor & Grzywacz 1993)

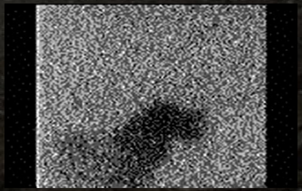
The Retina - biology of retinal waves



Layers:

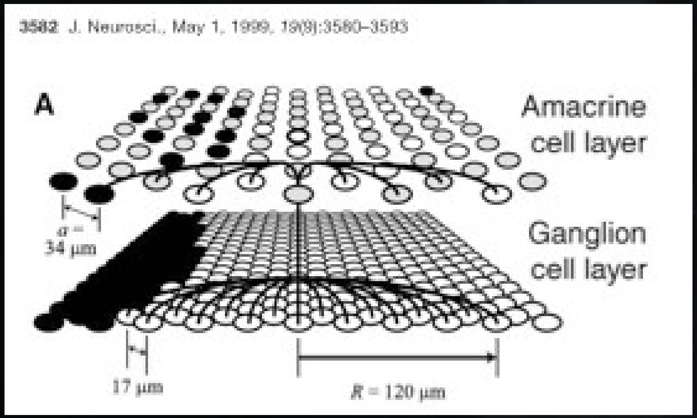
Amacrine Cells

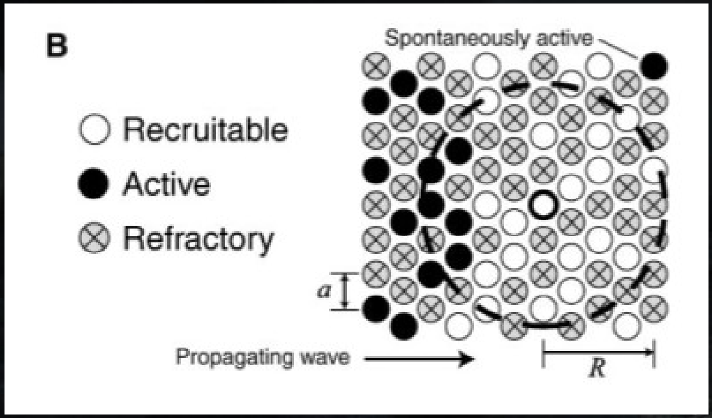
Ganglion Cells



Retinal Wave Model (Butts et al. 1999)

(In red: related parameters in the 3-parameter pattern generation)



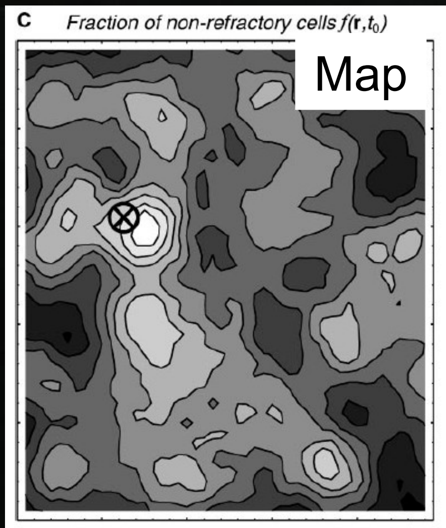


Amacrine cell layer

- Cells in one of three states
- Random, spontaneous firing
- Wave propagation by thresholded local pooling
  - Limited by dendritic field size (like 'r' in our technique)
  - Threshold neighbors for excitation

    (like 't' in our technique)

Retinal Wave Model – fraction of recruitable cells



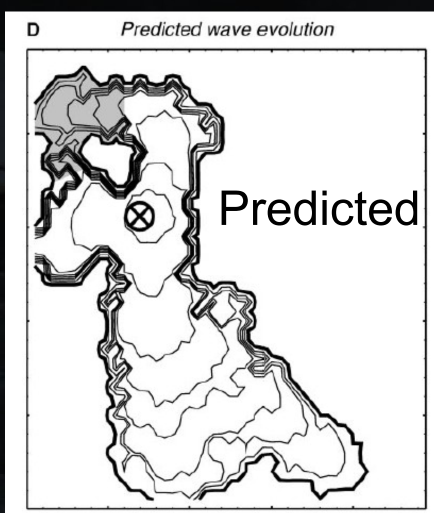
Instantaneous wave propagation depends upon a single parameter:

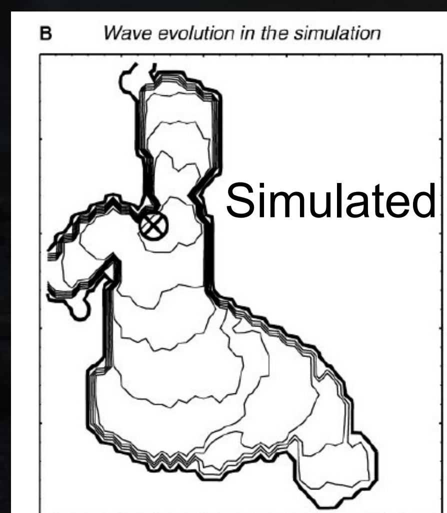
the fraction of recruitable amacrine cells.

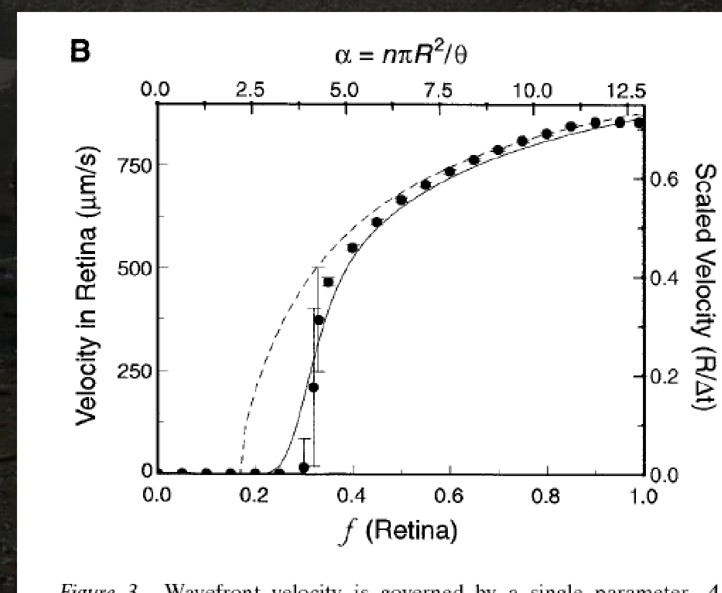
Similar to ‘p’ in our technique

Note: this is a by-product in the Butts model, but a fixed parameter in our generated patterns.

<u>Wave speed vs. “p”</u>







(Butts, Feller, Shatz, Rokhsar 1999)

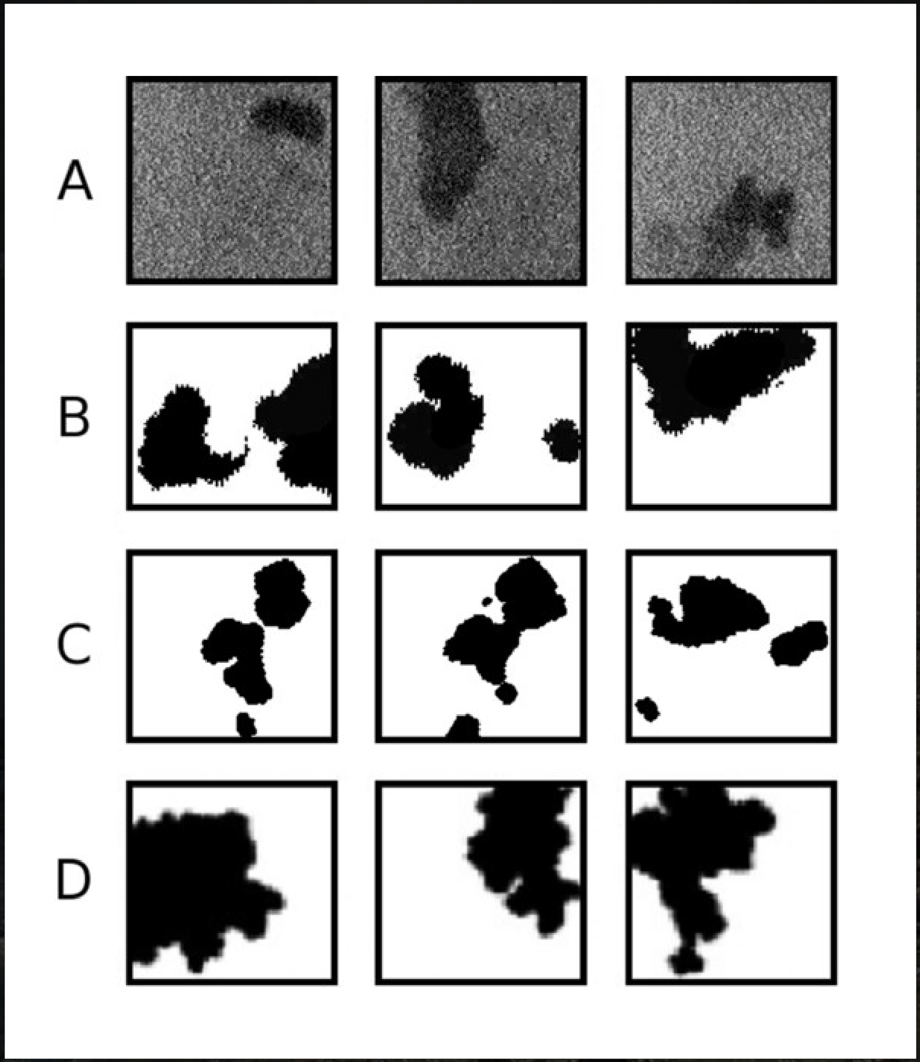
The result: images of spontaneous activity

Experimental waves, ferret
(Feller et al 1996)

Model waves
(Butts et al 1999)

Model wave extent
(Godfrey & Swindale 2007)

Pattern wave extent
(Albert, Schnabel, Field 2008)
($p = 0.55$, $r = 3$, $t = 6$)



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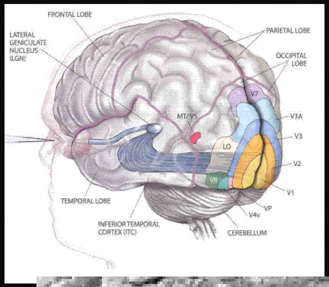

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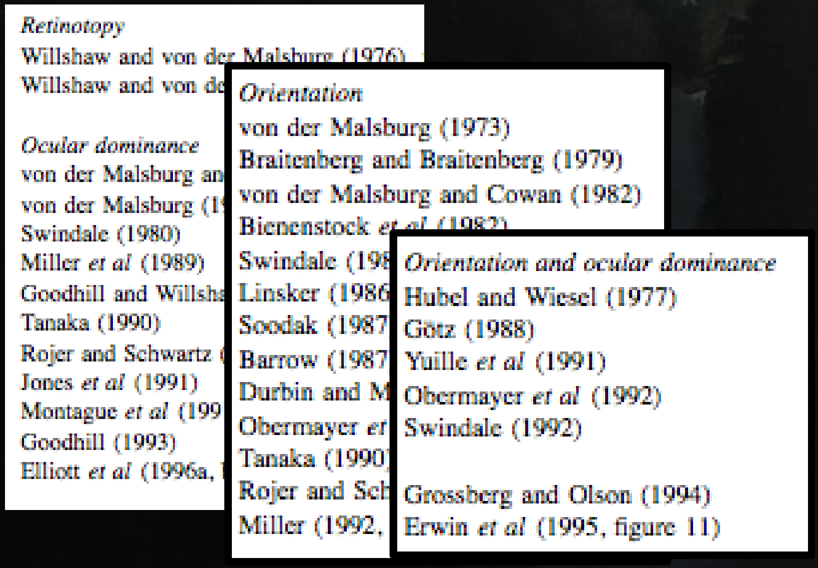
Models of V1 formation

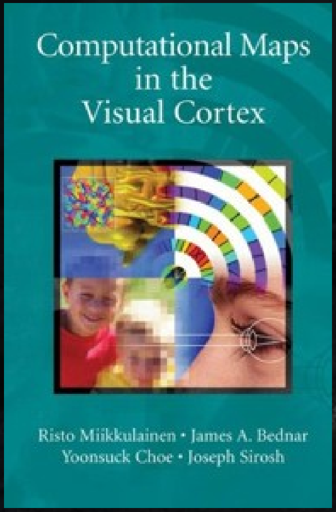


Reviews

(Erwin, Obermeyer, Schulten 1995)

(Swindale 1996)

(Miikkulainen, Bednar, Choe, Sirosh 2005)

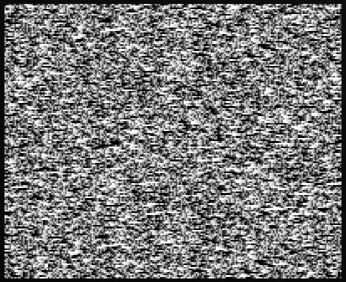


Selected Models

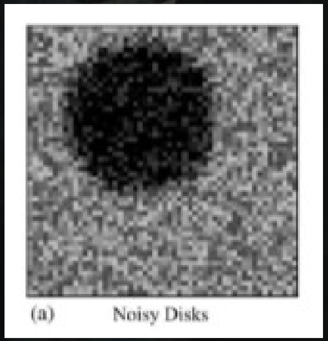
- von der Malsburg (OR, 1973; OR/OC, 1976)
- Linsker (OR, 1986)
- Miller (+Erwin: OR/OC, 1995)
- Goodhill (OD, 1990; +Carriera-Perpinan OR/OC/DR/SF, 2005)
- Bednar & Miikkulainen (OR/DR: 2003, OR/DR/OC, 2006)
- ...

ORientation, OCular dominance, DiRection of Motion, Spatial Frequency

Spontaneous activity ↔ V1 formation



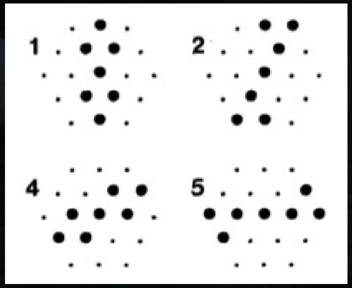
Linsker (1986): uncorrelated noise



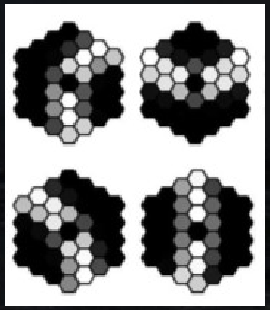
Bednar & Miikkulainen (2004) Circular disks

Inherent tradeoff between constraints in learning model and activity statistics.

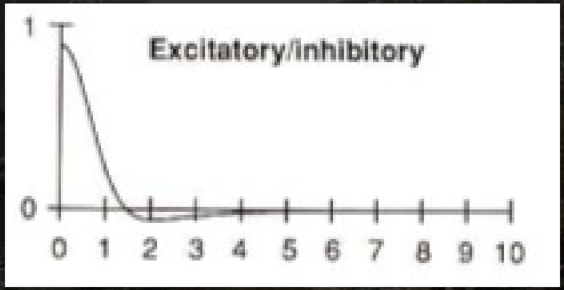
For this reason, the neural map models are less informative about spontaneous activity.



von der Malsburg (1973)



Grabska-Barwinska & Von der Malsburg (2008)



Miller et al. (1989) Defined correlation functions

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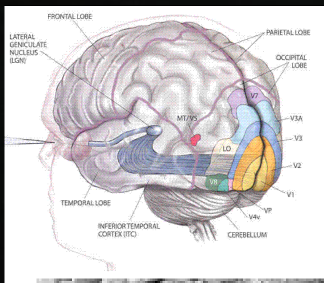

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Efficient coding Hypothesis

The visual system can be understood using different levels of analysis.

Marr's level of analysis:

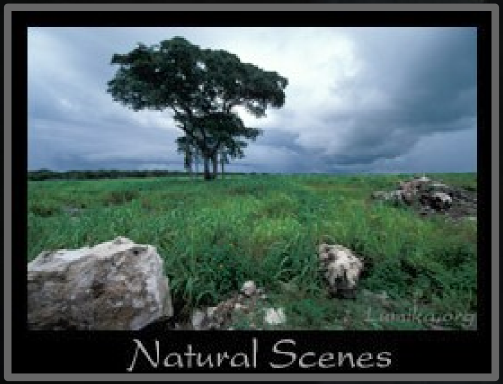
1. Hardware, imlementation
2. Representation, algorithm
3. Computational Theory

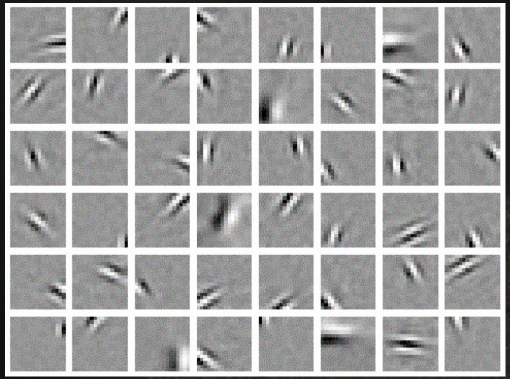
V1 map formation models

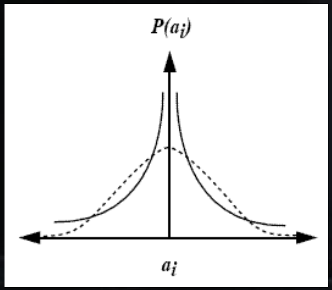
The goal of early sensory systems is to reduce the amount of redundancy in the neural code
(Attneave ‘54, Barlow ‘69)

Efficient coding approaches

<u>Ecological goal</u>: efficiently encode our natural environment, and...







$$p(f_1, f_2) = p(f_1)\, p(f_2)$$

<u>Sparse coding:</u> (Olshausen & Field 1996)

Have fewest neurons highly active at a time (as opposed to compact coding)

<u>Independent Components Analysis:</u> (Bell & Sejnowski 1997)

Make the neural responses as statistically independent as possible

For practical purposes: these approaches are fairly similar

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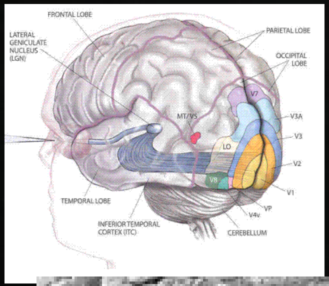

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Recall: images of spontaneous activity

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(Feller et al 1996)

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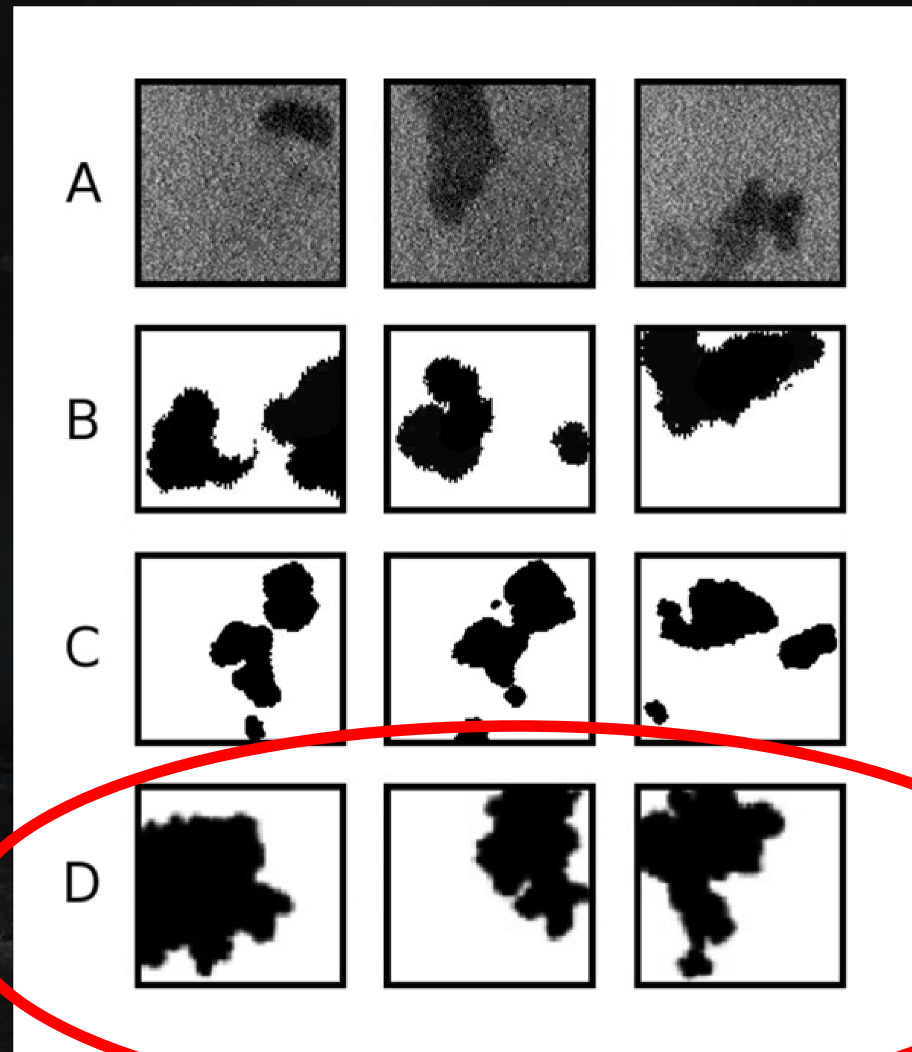
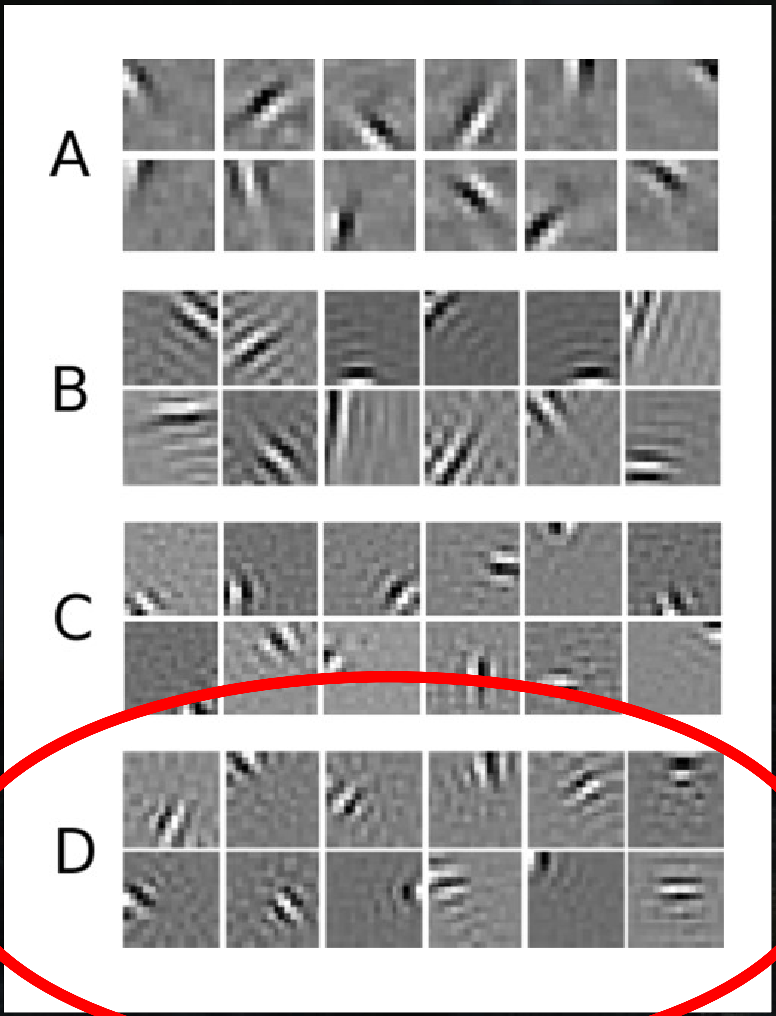
Pattern wave extent
(Albert, Schnabel, Field 2008)
(p = 0.55, r = 3, t = 6)



The patterns have relevant statistical properties for training



Natural images, sparse coding
(Olshausen & Field 1996)

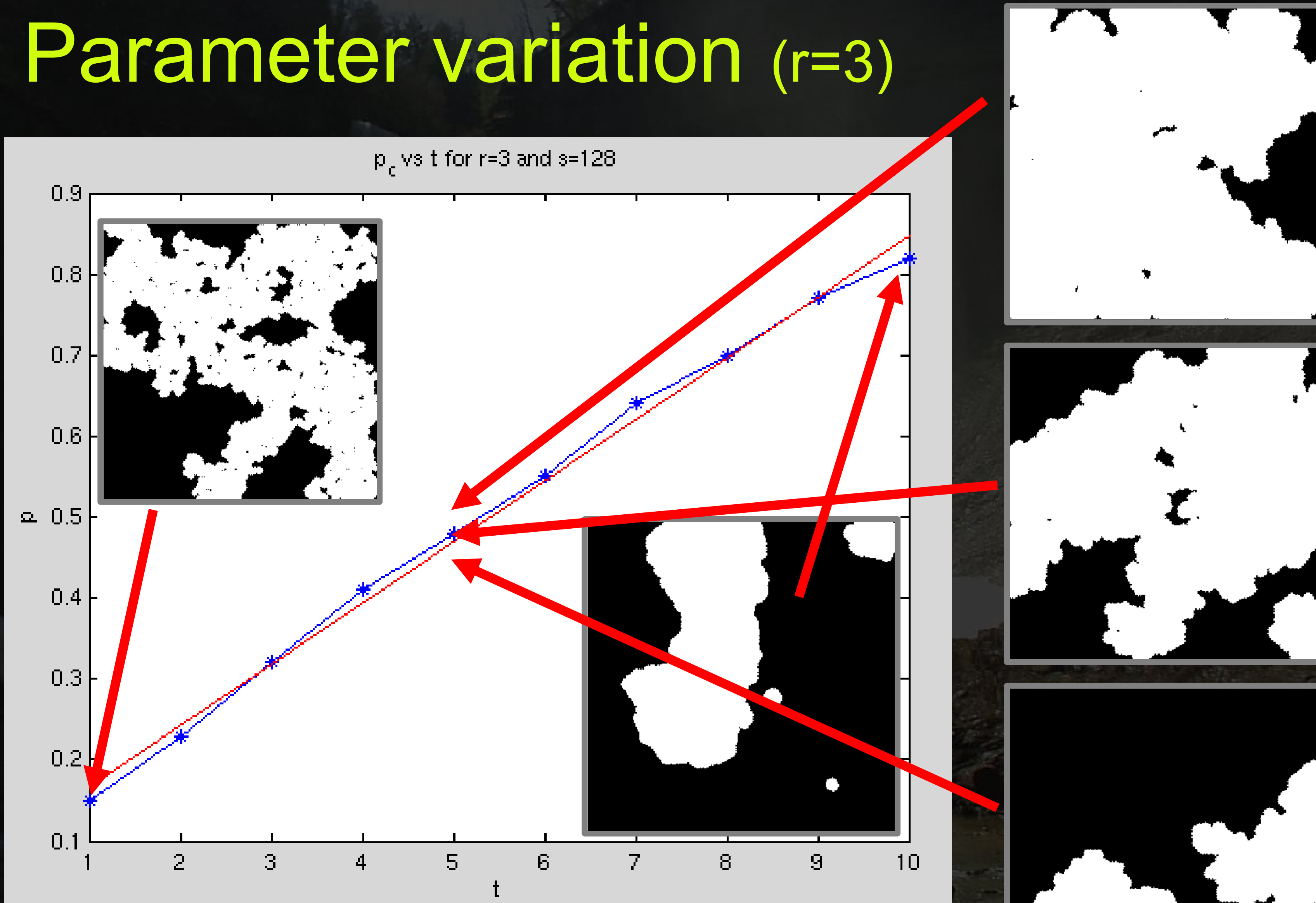
Natural images, ICA
(van Hateren image database)

Retinal wave images, ICA
(Godfrey & Swindale 2007)

3-Parameter model, ICA
(Albert, Schnabel, Field 2008)
(p = 0.7, r = 3, t = 8)

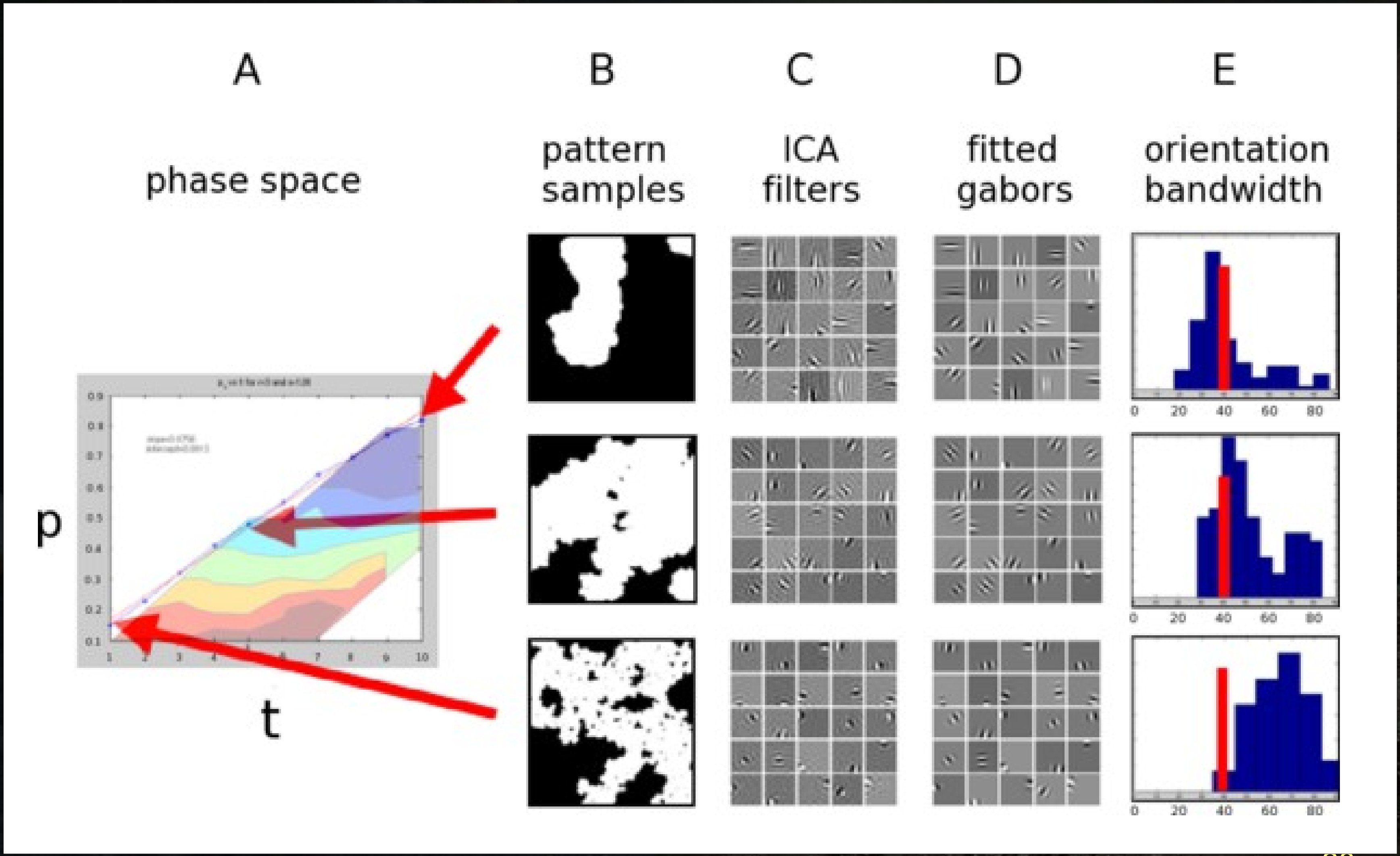
Parameter variation (r=3)

P

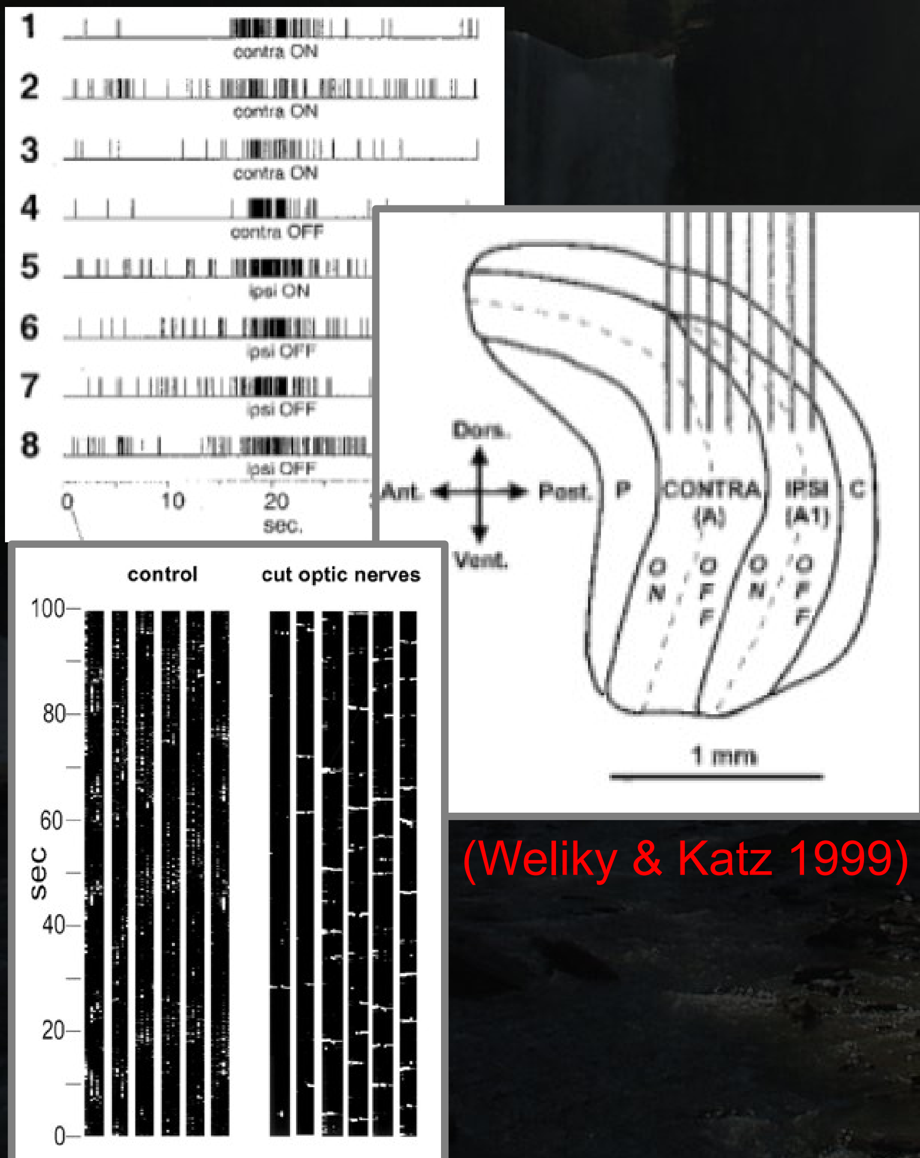


T

Possible statistical variations



The role of LGN/V1 activity



(Weliky & Katz 1999)

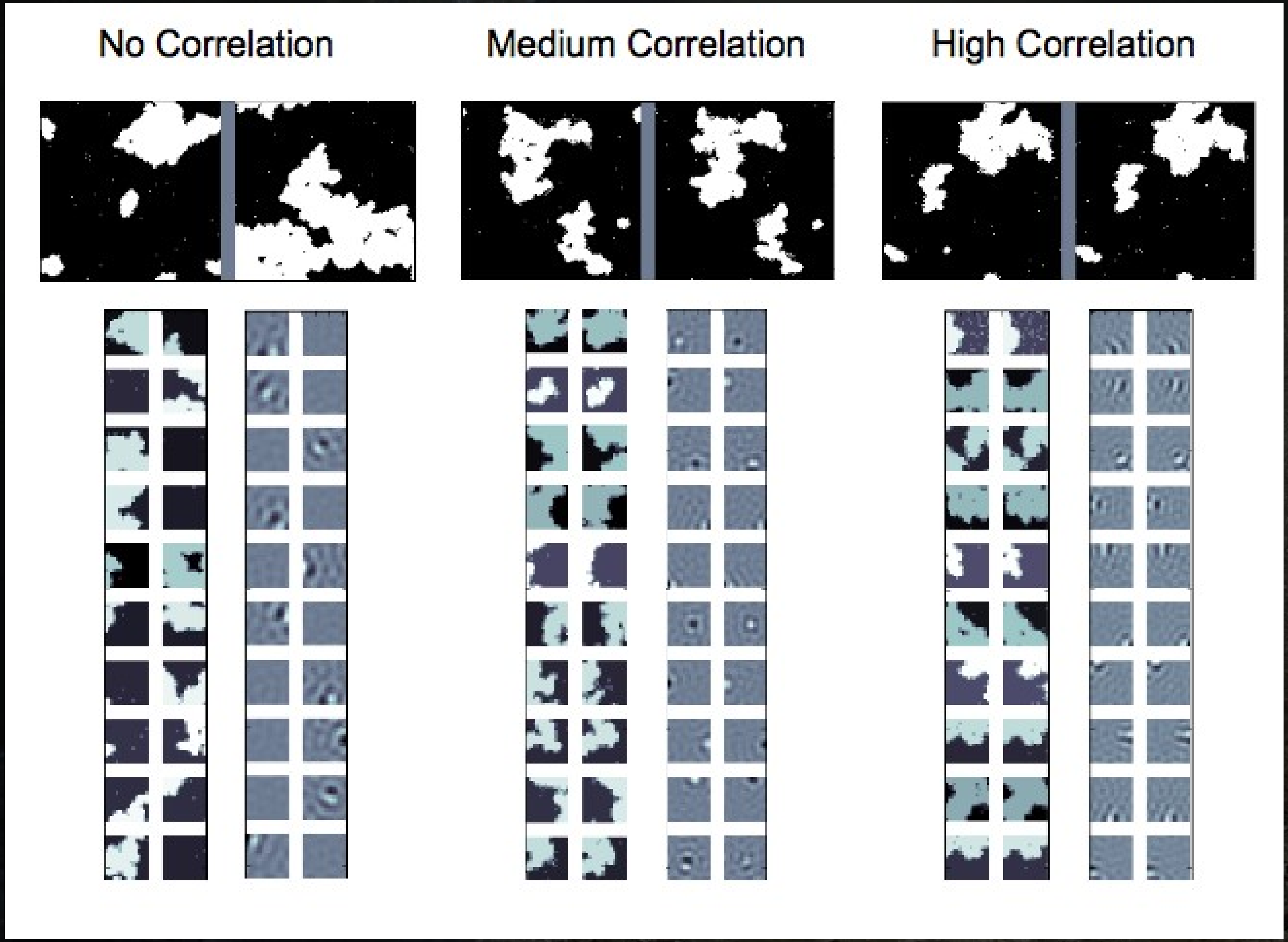
Correlation between eye-specific layers (with V1 feedback)

Silencing experiments: e.g.:

- Binocular enucleation does not prevent ocular dominance column formation (Crowley & Katz 1999)
- TTX in Cortex prevents orientation maturation: (Chapman & Stryker 1993)

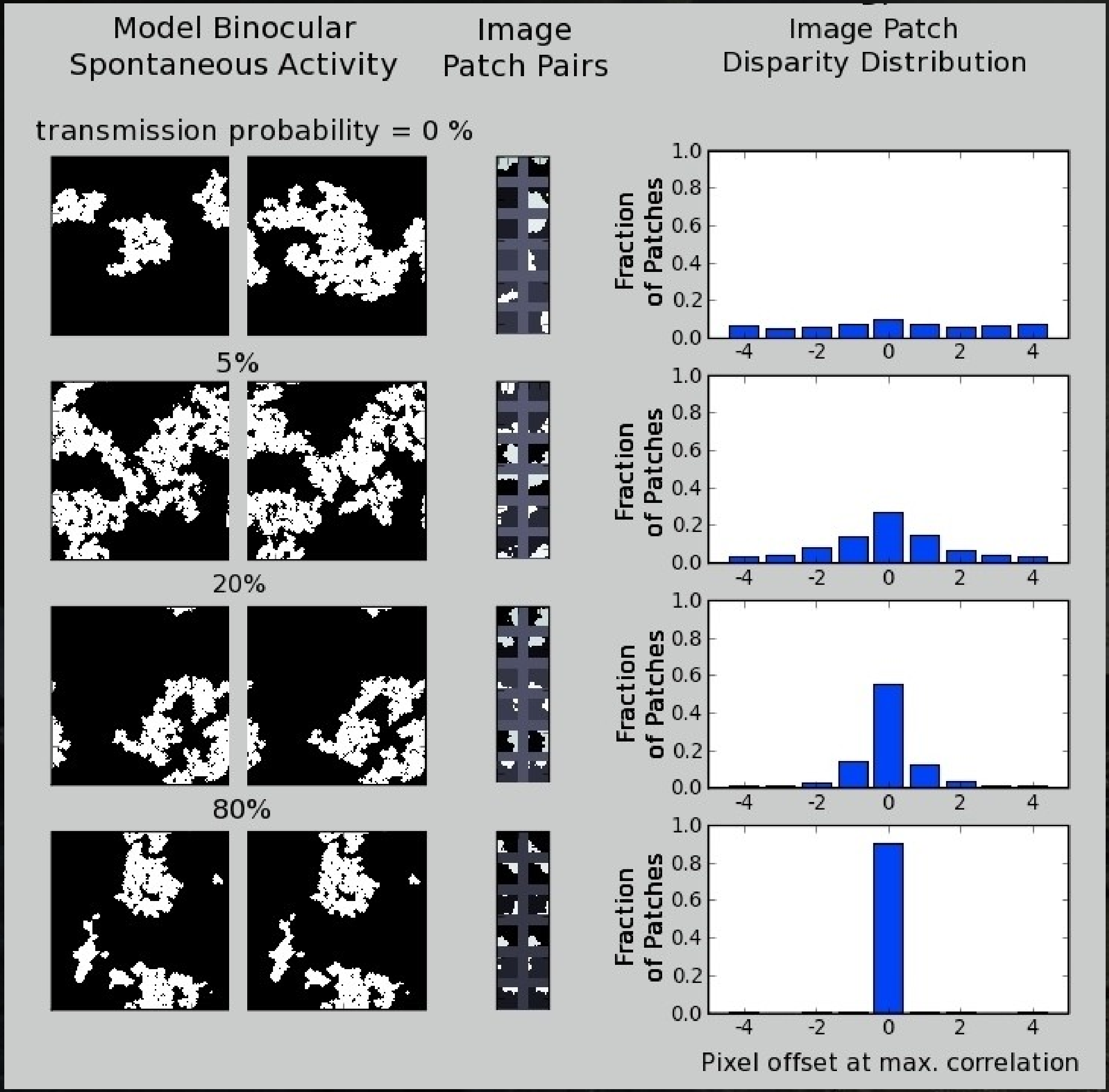
Hypothesized noisy wavefronts of activity

Binocular activity model



LGN/V1 activity simulated with an additional parameter for probability of transmission across eye layers

Adult-like disparity distribution



Adult-like properties near birth occur experimentally:

ocular dominance distributions

(Chino et al. 1997),

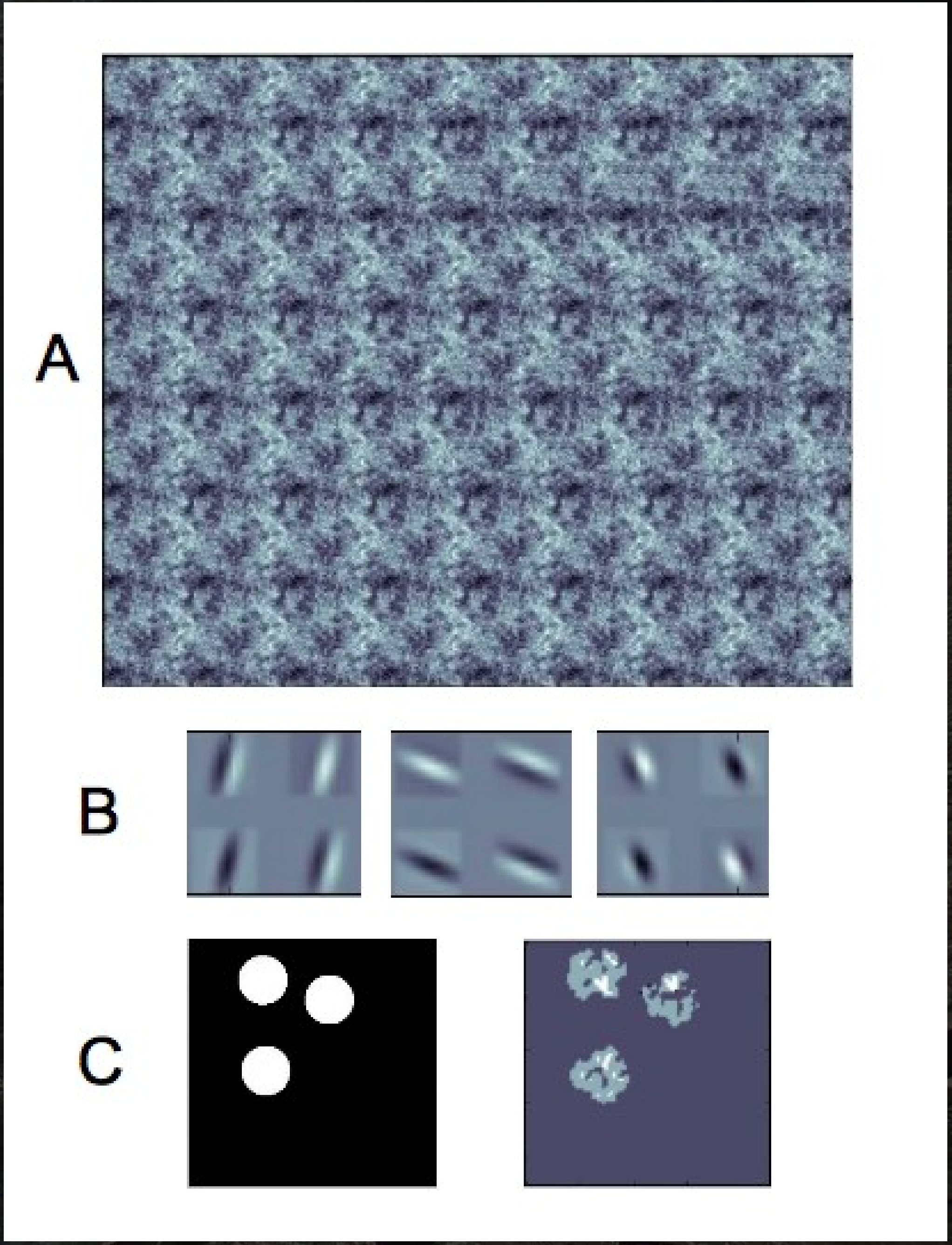
phase-disparity distributions

(Maruko et al. 2008)

Evaluation criteria, depth perception

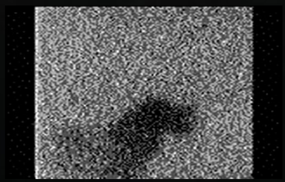
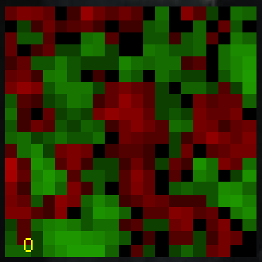
Evaluating innate learning effects can be done by analyzing:

- Receptive field properties
- Code efficiency metrics (e.g. for natural scenes)
- Perceptual effects (e.g. binocular depth perception)

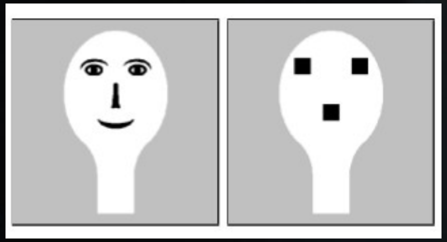
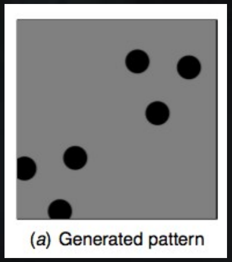


A: autostereogram
B: idealized filters
C: true and deduced depth from B applied to A
Physiologically plausible method (Qian & Zhu 1997)

Additional directions

Spatiotemporal activity and V1 model

Learning an innate face bias

– (e.g. Bednar & Miikkulainen 2003)

Precocial vs. altricial developmental models:

Filter properties depending upon assumption of fixed prior natural experience

Relation to adult spontaneous activity

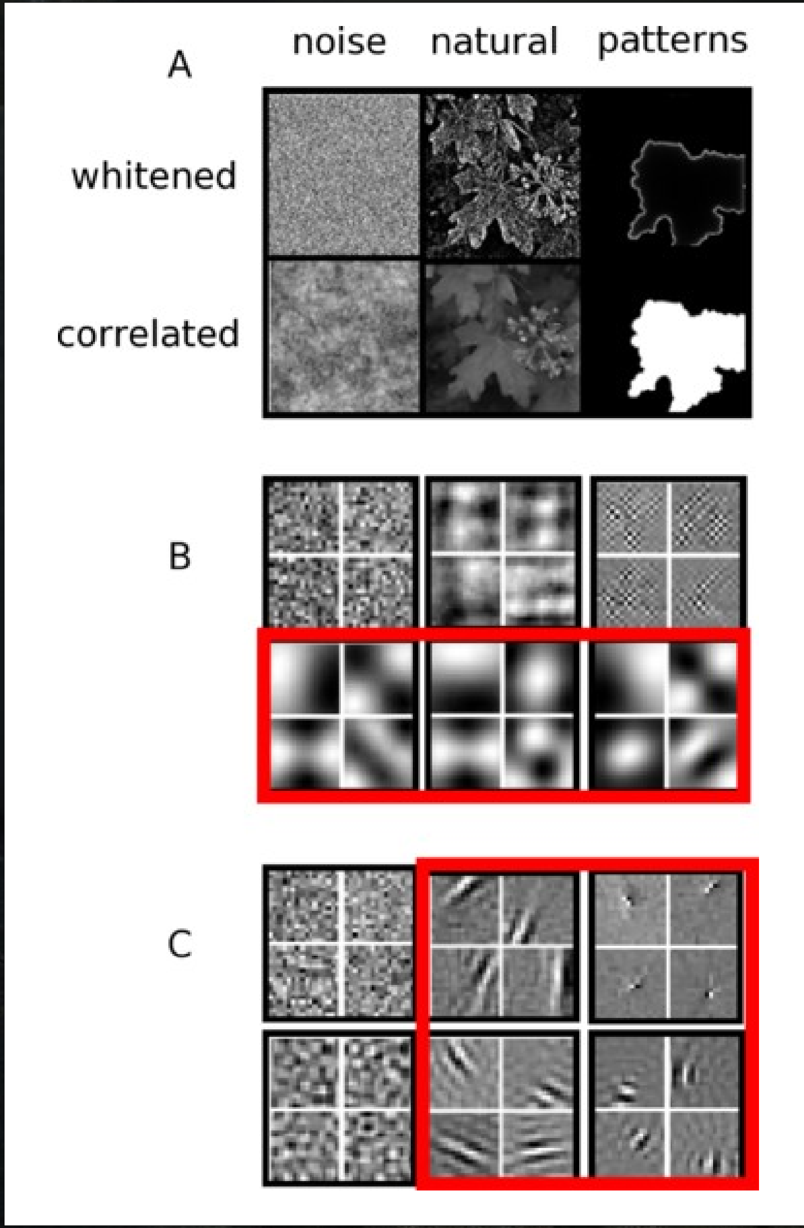
– (e.g. Berkes @ CoSyNe 2009)

Higher-order statistics are critical in development

Adult V1 coding models rely on higher-order statistical structure

The majority of V1 developmental models ignore this structure

The approach here uniquely shows that an efficient coding approach can be effectively applied to understand visual development



A: image classes

B: Correlation-based receptive fields (PCA)

C: Rfs from higher-order statistical approach (ICA)

Conclusions

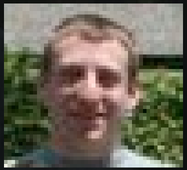
The monocular model uniquely demonstrated that simple patterns of activity can be used to train physiologically relevant cells in an efficient coding paradigm.

The binocular model extended this to include analysis of disparity, relevant to potential tests of perceptual validity by stereoscopic depth.

	Pre eye-opening	Post eye-opening
Neural activity	Spontaneous Activity	Visual experience
Algorithm	Activity-based learning (e.g. efficient coding here)	

The principle of innate learning: spontaneous patterns of neural activity are used to train or refine a sensory system in an analogous way to how the system can adapt based on natural experience.

Acknowledgements



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