Pattern Formation in the Developing Visual Cortex

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Pattern formation in the developing visual cortex

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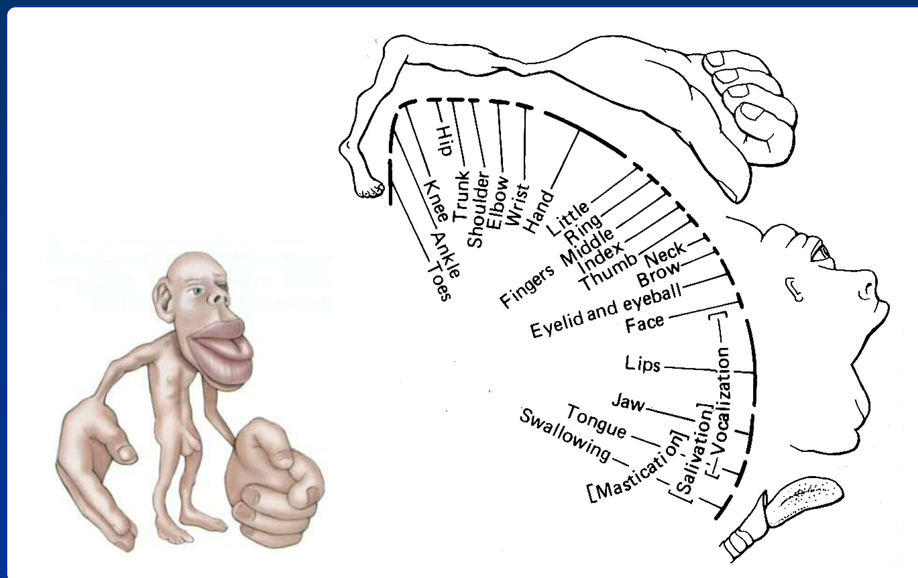
Somato-Sensory Map



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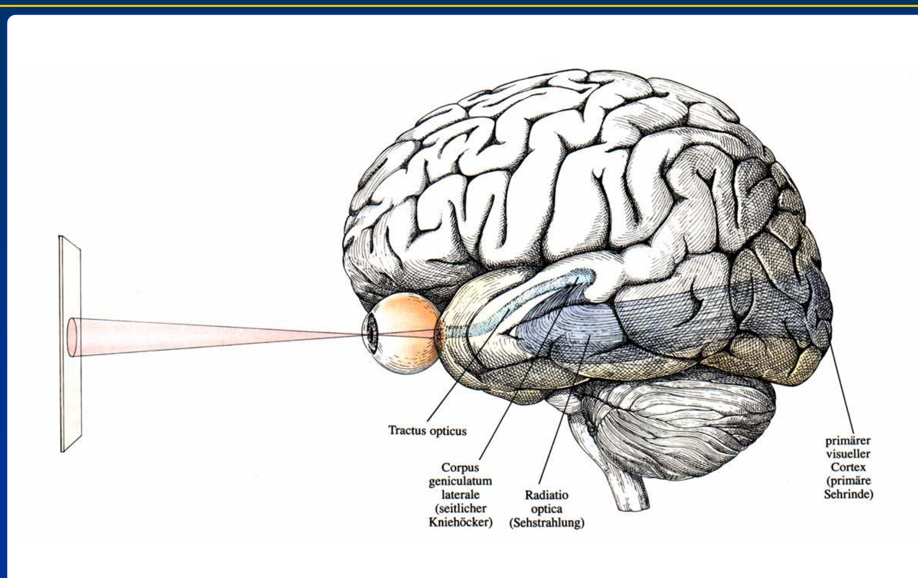
Visual System



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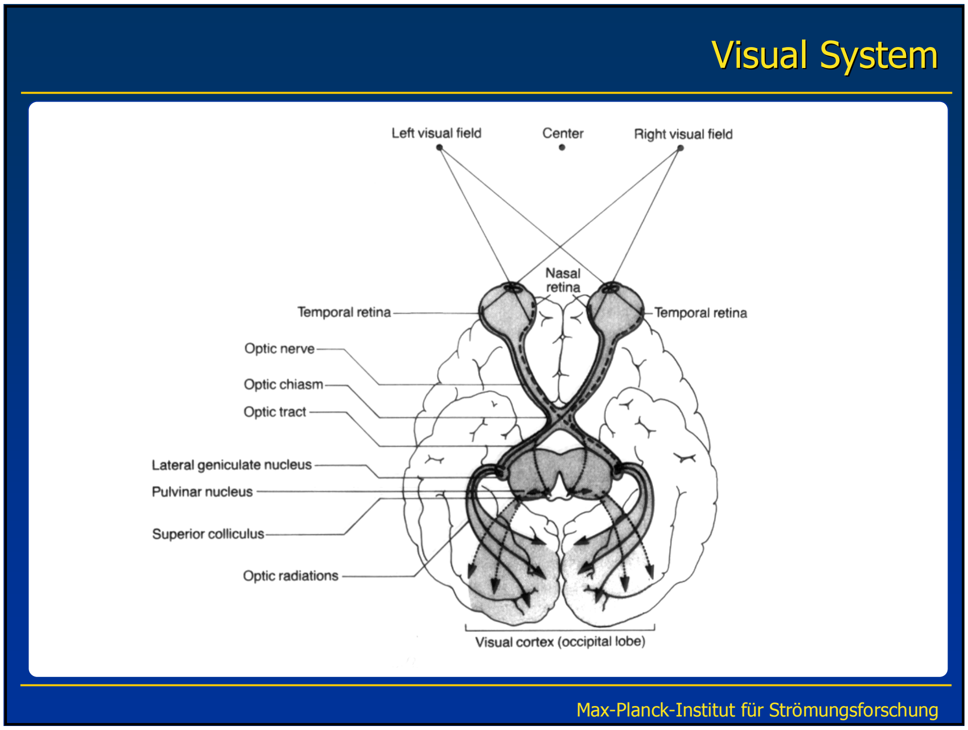
Visual System
Left visual field
Center
Right visual field
Nasal retina
Temporal retina
Temporal retina
Optic nerve
Optic chiasm
Optic tract
Lateral geniculate nucleus
Pulvinar nucleus
Superior colliculus
Optic radiations
Visual cortex (occipital lobe)
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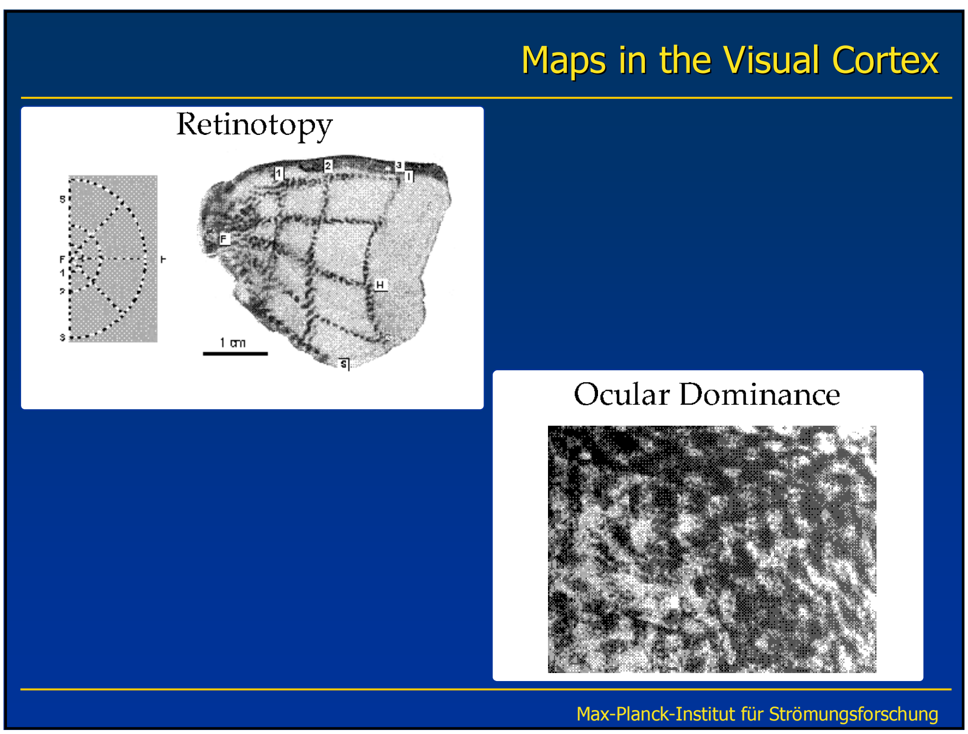
Maps in the Visual Cortex
Retinotopy
1 cm
Ocular Dominance
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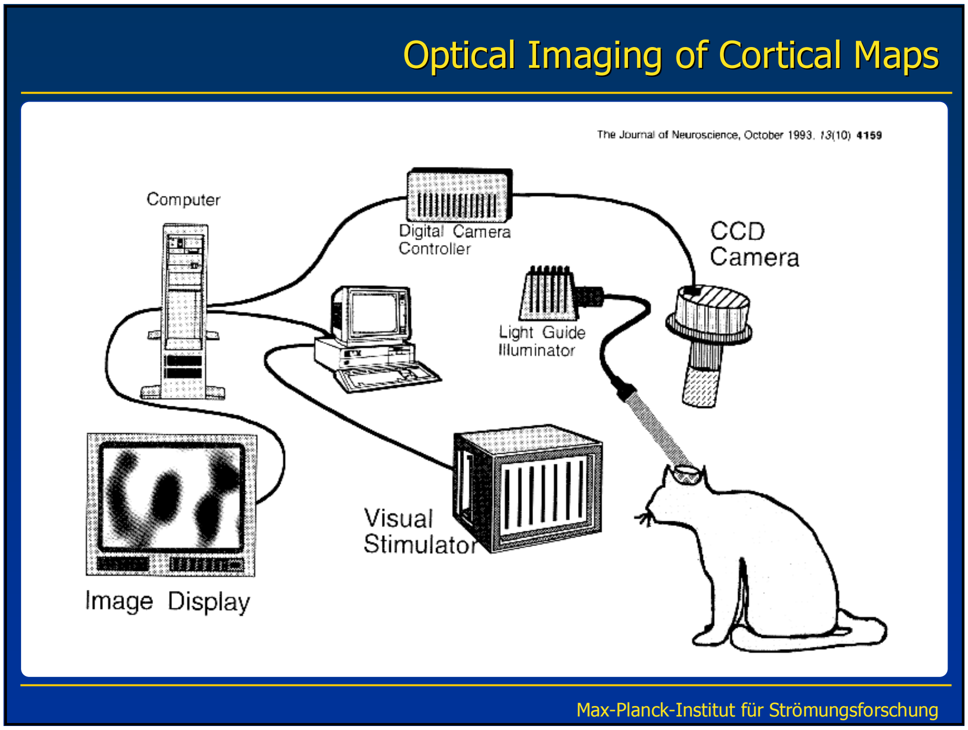
Optical Imaging of Cortical Maps
The Journal of Neuroscience, October 1993, 13(10) 4159
Computer
Digital Camera Controller
CCD Camera
Light Guide Illuminator
Visual Stimulator
Image Display
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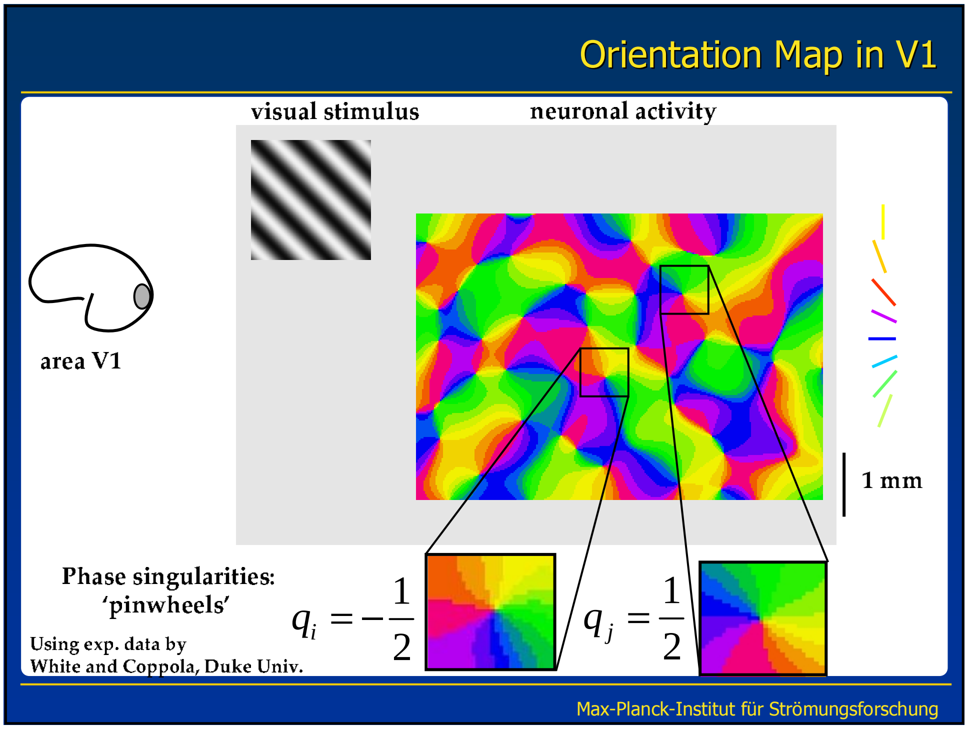
Orientation Map in V1
visual stimulus
neuronal activity
area V1
1 mm
Phase singularities: 'pinwheels'
$q_i = -\frac{1}{2}$
$q_j = \frac{1}{2}$
Using exp. data by
White and Coppola, Duke Univ.
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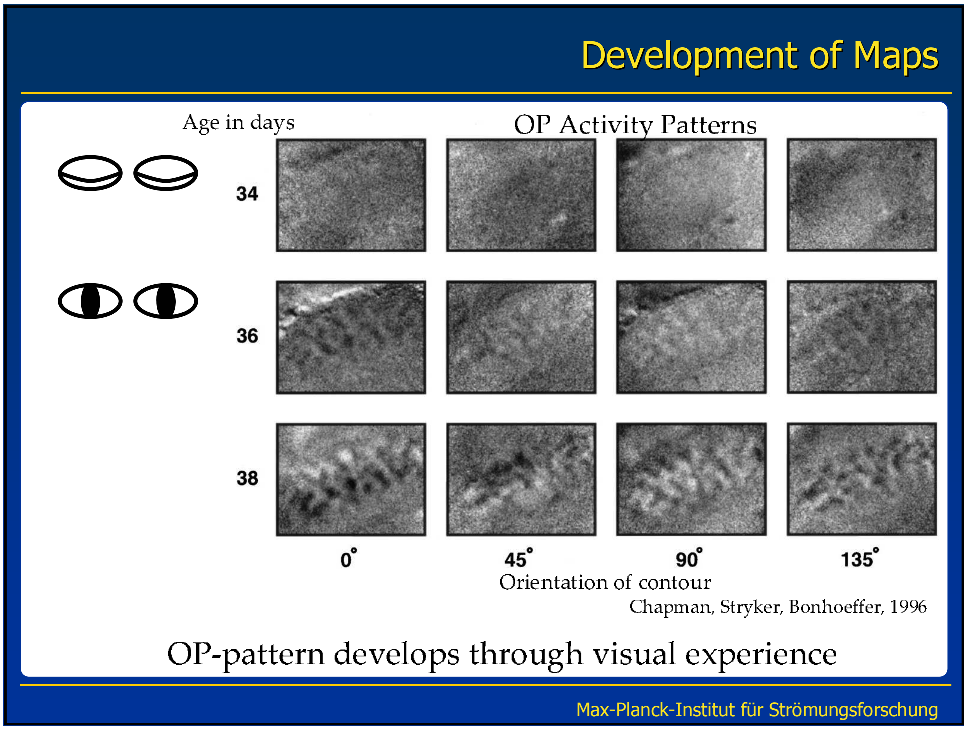
Development of Maps
Age in days
OP Activity Patterns
34
36
38
0°
45°
90°
135°
Orientation of contour
Chapman, Stryker, Bonhoeffer, 1996
OP-pattern develops through visual experience
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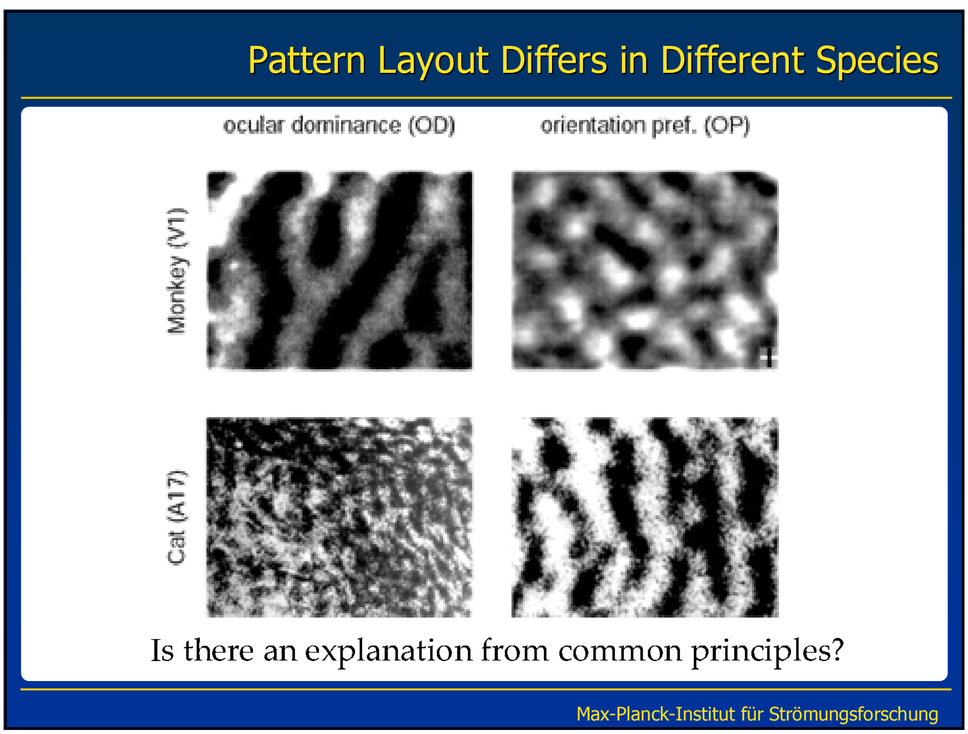
Pattern Layout Differs in Different Species
ocular dominance (OD)
orientation pref. (OP)
Monkey (V1)
Cat (A17)
Is there an explanation from common principles?
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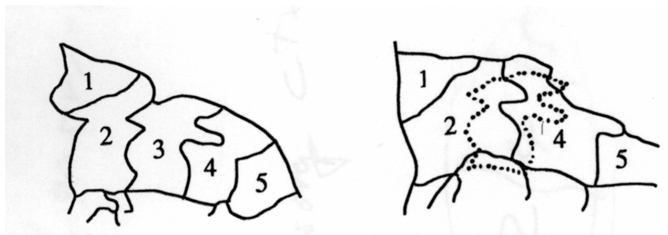
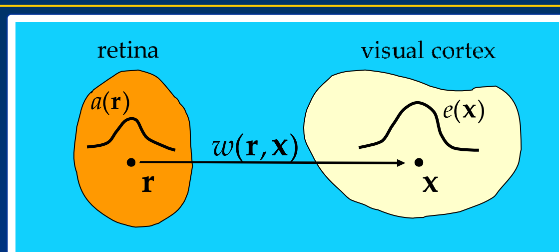
Plasticity and Hebbian Learning

Example: hand representation somatosensory cortex



Fox, 1984

Dynamics of Learning



Competitive Hebbian plasticity:

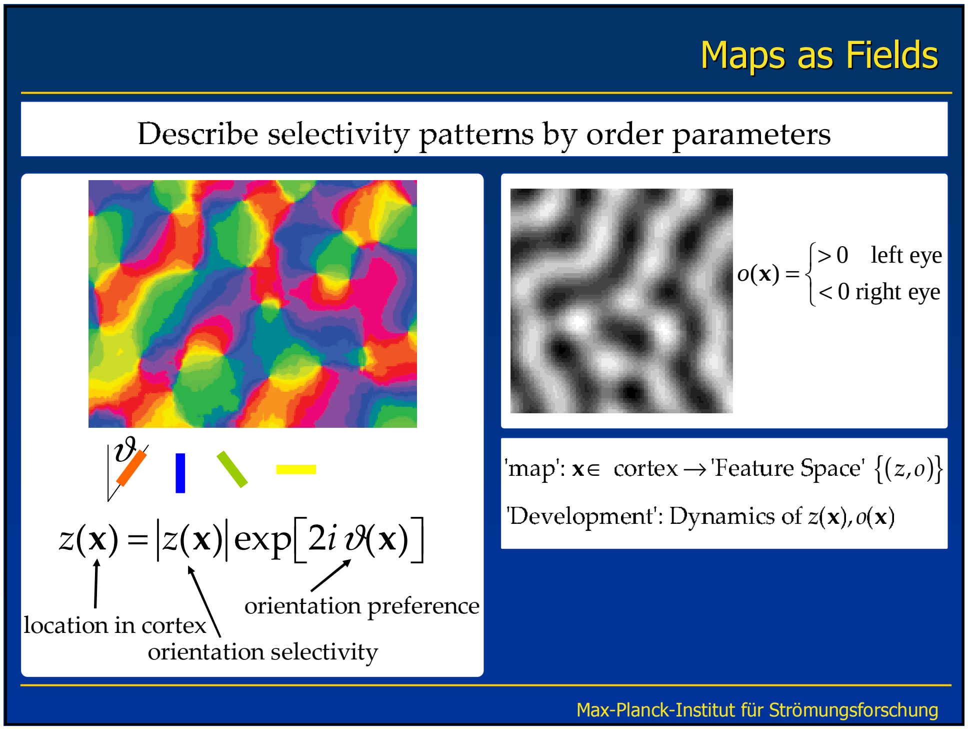
$$\delta w(\mathbf{r},\mathbf{x}) = \varepsilon\left[a(\mathbf{r})e(\mathbf{x}) - w(\mathbf{r},\mathbf{x})e(\mathbf{x})\right]$$

Hebb ↗ ↖ decay

Simplifying assumption:

$$e(\mathbf{x}) \propto \exp\left(\frac{-\left|\mathbf{x}-\mathbf{x}^*\right|^2}{2\sigma^2}\right)$$

Learning → stationary state


Maps as Fields
Describe selectivity patterns by order parameters
ϑ
$z(\mathbf{x}) = |z(\mathbf{x})| \exp[2i\,\vartheta(\mathbf{x})]$
location in cortex
orientation preference
orientation selectivity
$o(\mathbf{x}) = \begin{cases} >0 & \text{left eye} \\ <0 & \text{right eye} \end{cases}$
'map': $\mathbf{x} \in$ cortex $\rightarrow$ 'Feature Space' $\{(z, o)\}$
'Development': Dynamics of $z(\mathbf{x}), o(\mathbf{x})$
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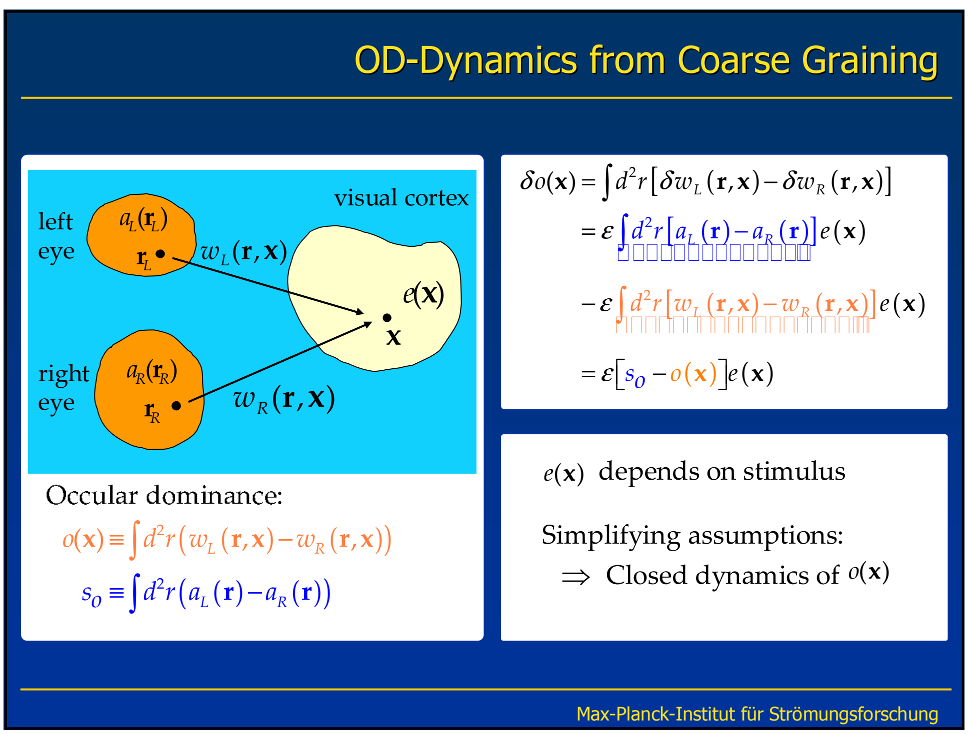
OD-Dynamics from Coarse Graining
left eye
$a_L(\mathbf{r}_L)$
$\mathbf{r}_L$
right eye
$a_R(\mathbf{r}_R)$
$\mathbf{r}_R$
visual cortex
$w_L(\mathbf{r},\mathbf{x})$
$w_R(\mathbf{r},\mathbf{x})$
$e(\mathbf{x})$
$\mathbf{x}$
Occular dominance:
$o(\mathbf{x}) \equiv \int d^2r \left(w_L(\mathbf{r},\mathbf{x}) - w_R(\mathbf{r},\mathbf{x}) \right)$
$s_0 \equiv \int d^2r \left(a_L(\mathbf{r}) - a_R(\mathbf{r}) \right)$
$\delta o(\mathbf{x}) = \int d^2r \left[\delta w_L(\mathbf{r},\mathbf{x}) - \delta w_R(\mathbf{r},\mathbf{x}) \right]$
$= \varepsilon \int d^2r \left[a_L(\mathbf{r}) - a_R(\mathbf{r}) \right] e(\mathbf{x})$
$- \varepsilon \int d^2r \left[w_L(\mathbf{r},\mathbf{x}) - w_R(\mathbf{r},\mathbf{x}) \right] e(\mathbf{x})$
$= \varepsilon \left[s_0 - o(\mathbf{x}) \right] e(\mathbf{x})$
$e(\mathbf{x})$ depends on stimulus
Simplifying assumptions:
$\Rightarrow$ Closed dynamics of $o(\mathbf{x})$
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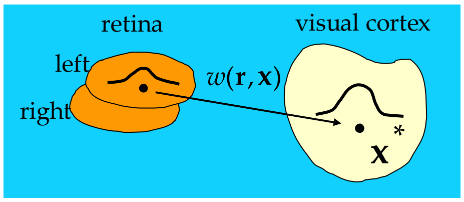
Retinotopy



Stereotyped activity patterns in visual cortex:

$$e(\mathbf{x}) = \exp\left(-\frac{|\mathbf{x}-\mathbf{x}^*|^2}{2\sigma^2}\right)$$

Stimulus center of mass:

$$\mathbf{s_R} = \frac{1}{\text{Norm}} \int d^2r\, \mathbf{r}\left(a_L(\mathbf{r}) + a_R(\mathbf{r})\right)$$

Receptive field (RF) centers:

$$R(\mathbf{x}) = \frac{1}{\text{Norm}} \int d^2r\, \mathbf{r}\left(w_L(\mathbf{r},\mathbf{x}) + w_R(\mathbf{r},\mathbf{x})\right)$$

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Simplifying Assumptions, Closure of O-Dynamics

$$\delta o(\mathbf{x}) = \varepsilon\left(s_0 - o(\mathbf{x})\right)e(\mathbf{x})$$

$$\rightarrow \partial_t o(\mathbf{x}) = \left\langle \left(s_0 - o(\mathbf{x})\right)e(\mathbf{x})\right\rangle_{\mathbf{s_R}, s_O}$$

$$e(\mathbf{x}) = \exp\left(-\frac{|\mathbf{x}-\mathbf{x}^*|^2}{2\sigma^2}\right)$$

Closure:

$$\mathbf{x}^* = \mathbf{x}^*\left(\mathbf{s_R}, s_O, \mathbf{R}(\mathbf{x}), o(\mathbf{x})\right)$$

$$\mathbf{x}^*: \quad \left(\left|\mathbf{s_R} - \mathbf{R}(\mathbf{x}^*)\right|^2 + \left|s_O - o(\mathbf{x}^*)\right|^2\right) = \min$$

$\rightarrow$ Nonlinear Dynamics of $o(\mathbf{x})$

OD-Pattern?
$\rightarrow$ Stability analysis

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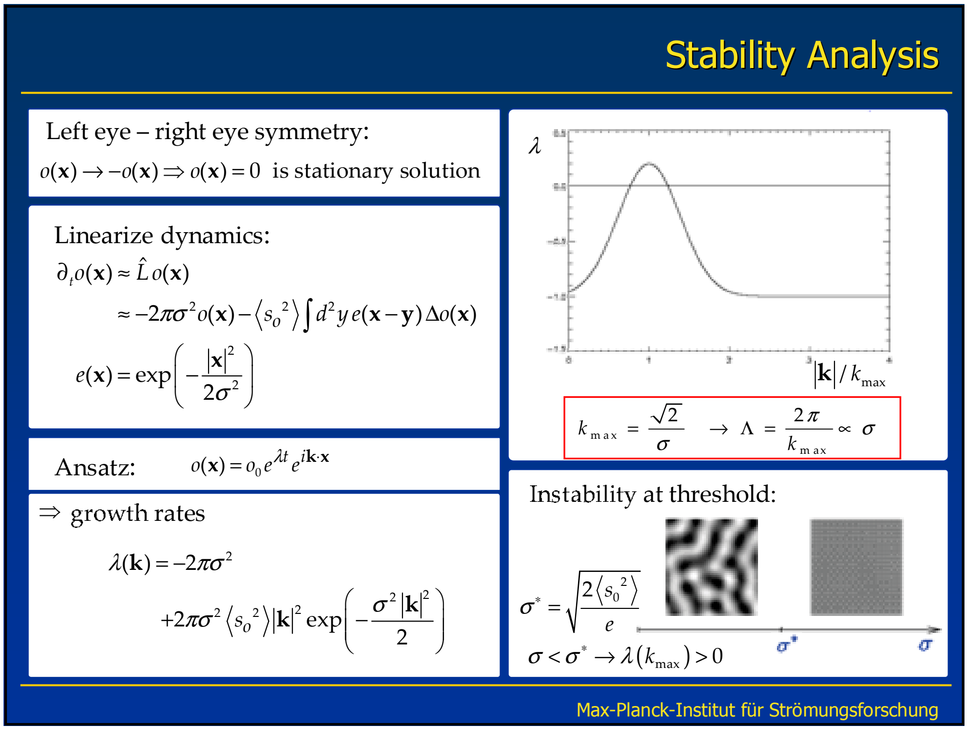
Stability Analysis
Left eye – right eye symmetry:
$o(\mathbf{x}) \to -o(\mathbf{x}) \Rightarrow o(\mathbf{x}) = 0$ is stationary solution
Linearize dynamics:
$\partial_t o(\mathbf{x}) \approx \hat{L}\, o(\mathbf{x})$
$\approx -2\pi\sigma^2 o(\mathbf{x}) - \langle s_o{}^2 \rangle \int d^2y\, e(\mathbf{x}-\mathbf{y}) \Delta o(\mathbf{x})$
$e(\mathbf{x}) = \exp\left(-\frac{|\mathbf{x}|^2}{2\sigma^2}\right)$
Ansatz: $o(\mathbf{x}) = o_0 e^{\lambda t} e^{i\mathbf{k}\cdot\mathbf{x}}$
$\Rightarrow$ growth rates
$\lambda(\mathbf{k}) = -2\pi\sigma^2$
$+2\pi\sigma^2 \langle s_o{}^2 \rangle |\mathbf{k}|^2 \exp\left(-\frac{\sigma^2 |\mathbf{k}|^2}{2}\right)$
λ
$|\mathbf{k}|/k_{\max}$
$k_{\max} = \frac{\sqrt{2}}{\sigma} \to \Lambda = \frac{2\pi}{k_{\max}} \propto \sigma$
Instability at threshold:
$\sigma^* = \sqrt{\frac{2\langle s_0{}^2 \rangle}{e}}$
$\sigma < \sigma^* \to \lambda(k_{\max}) > 0$
σ^*
σ
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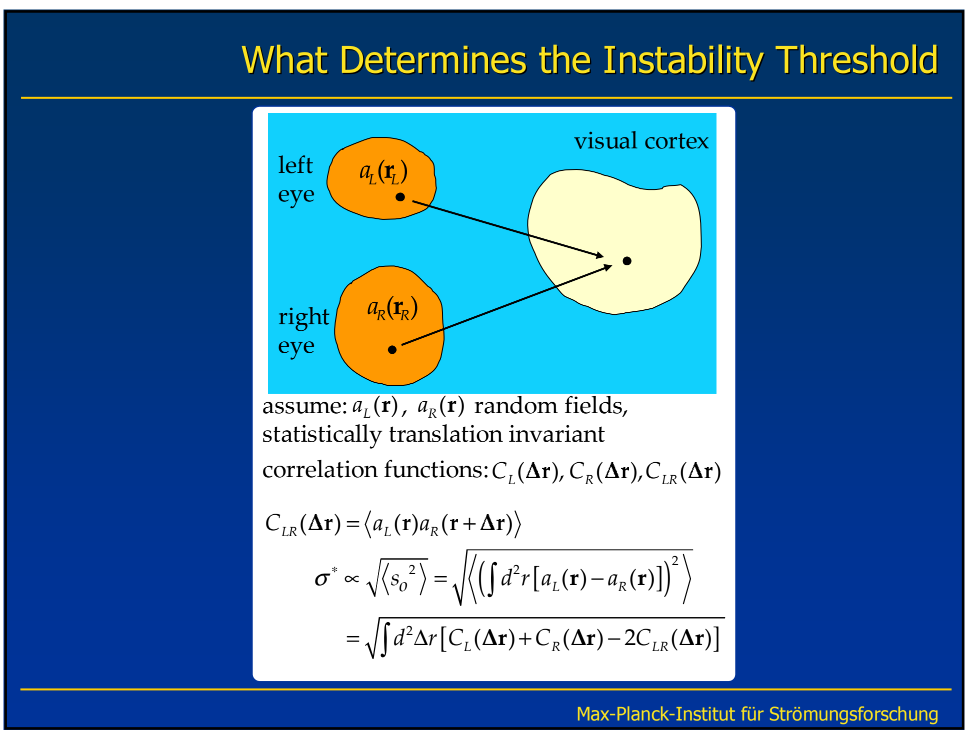
What Determines the Instability Threshold
left eye
$a_L(\mathbf{r}_L)$
right eye
$a_R(\mathbf{r}_R)$
visual cortex
assume: $a_L(\mathbf{r})$, $a_R(\mathbf{r})$ random fields,
statistically translation invariant
correlation functions: $C_L(\Delta\mathbf{r})$, $C_R(\Delta\mathbf{r})$, $C_{LR}(\Delta\mathbf{r})$
$C_{LR}(\Delta\mathbf{r}) = \langle a_L(\mathbf{r}) a_R(\mathbf{r}+\Delta\mathbf{r}) \rangle$
$\sigma^* \propto \sqrt{\langle s_o{}^2 \rangle} = \sqrt{\left\langle \left(\int d^2r\, [a_L(\mathbf{r}) - a_R(\mathbf{r})] \right)^2 \right\rangle}$
$= \sqrt{\int d^2\Delta r\, [C_L(\Delta\mathbf{r}) + C_R(\Delta\mathbf{r}) - 2C_{LR}(\Delta\mathbf{r})]}$
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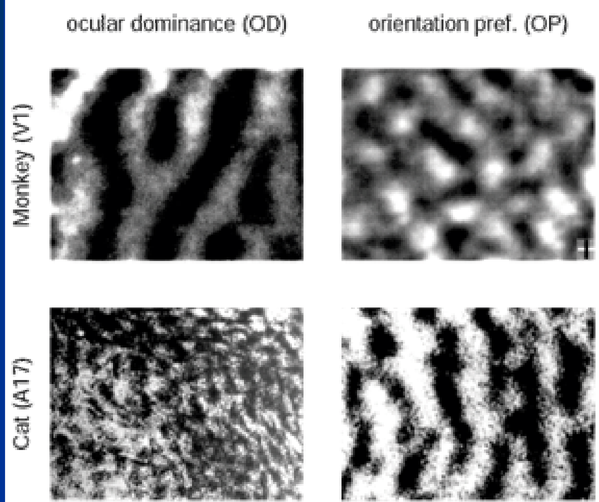
Wavelength from Timing – A General Principle

Test: interspecies differences in pattern layout



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Generalization: Dynamics of Interacting Maps

ocular dominance dynamics

$$\partial_t o(\mathbf{x}) = \left\langle (s_O - o(\mathbf{x})) \exp\left(-\frac{|\mathbf{x}-\mathbf{x}^*|^2}{2\sigma^2} \right) \right\rangle_{\mathbf{s}_\mathbf{R}, s_O}$$

$$\mathbf{x}^* : \quad \left(|\mathbf{s}_\mathbf{R} - \mathbf{R}(\mathbf{x}^*)|^2 + |s_O - o(\mathbf{x}^*)|^2 \right) = \min$$

New:

- orientation of stimuli $s_z \in$ □
- coupling by $\mathbf{x}^* = \mathbf{x}^*(o(\mathbf{x}), z(\mathbf{x}), \ldots)$

coupled dynamics for $z(\mathbf{x}), o(\mathbf{x})$:

$$\partial_t o(\mathbf{x}) = \left\langle (s_O - o(\mathbf{x})) \exp\left(-\frac{|\mathbf{x}-\mathbf{x}^*|^2}{2\sigma^2} \right) \right\rangle_{\mathbf{s}_\mathbf{R}, s_O, s_z}$$

$$\partial_t z(\mathbf{x}) = \left\langle (s_z - z(\mathbf{x})) \exp\left(-\frac{|\mathbf{x}-\mathbf{x}^*|^2}{2\sigma^2} \right) \right\rangle_{\mathbf{s}_\mathbf{R}, s_O, s_z}$$

$$\mathbf{x}^* : \quad |s_O - o(\mathbf{x}^*)|^2 + |s_z - z(\mathbf{x}^*)|^2 + |\mathbf{s}_\mathbf{R} - \mathbf{R}(\mathbf{x}^*)|^2 = \min$$

properties: two critical values

$$\sigma_O^* \propto \sqrt{\langle s_O{}^2 \rangle}$$

$$\sigma_z^* \propto \sqrt{\langle |s_z|^2 \rangle}$$

in general: $\sigma_O^* \neq \sigma_z^*$

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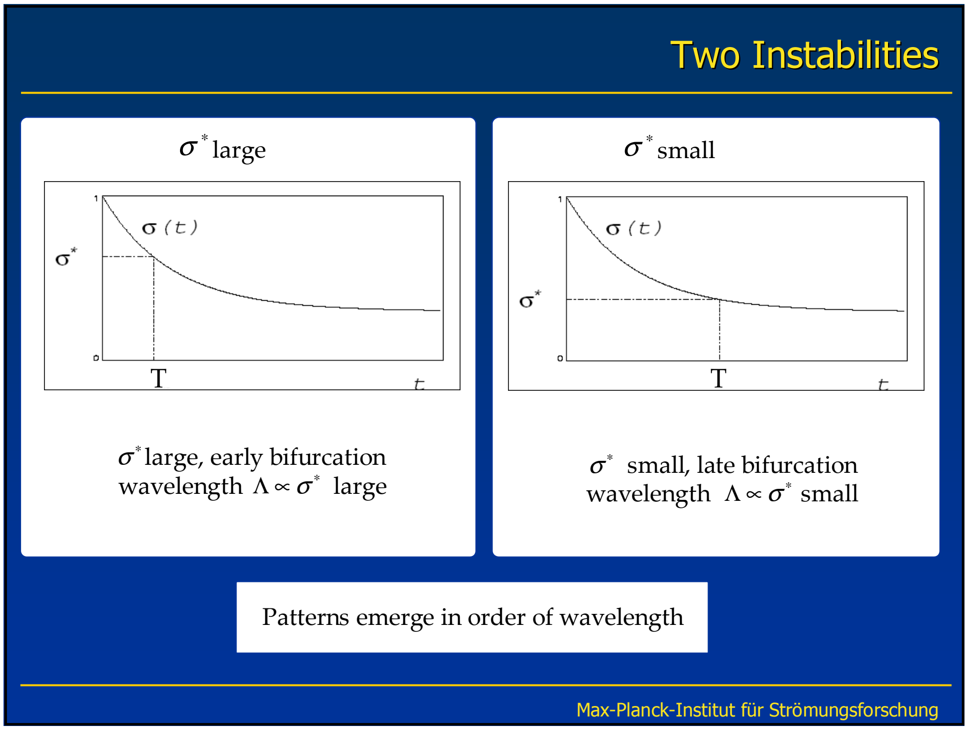
Two Instabilities
σ^* large
$\sigma(t)$
σ^*
T
t
σ^* large, early bifurcation
wavelength $\Lambda \propto \sigma^*$ large
σ^* small
$\sigma(t)$
σ^*
T
t
σ^* small, late bifurcation
wavelength $\Lambda \propto \sigma^*$ small
Patterns emerge in order of wavelength
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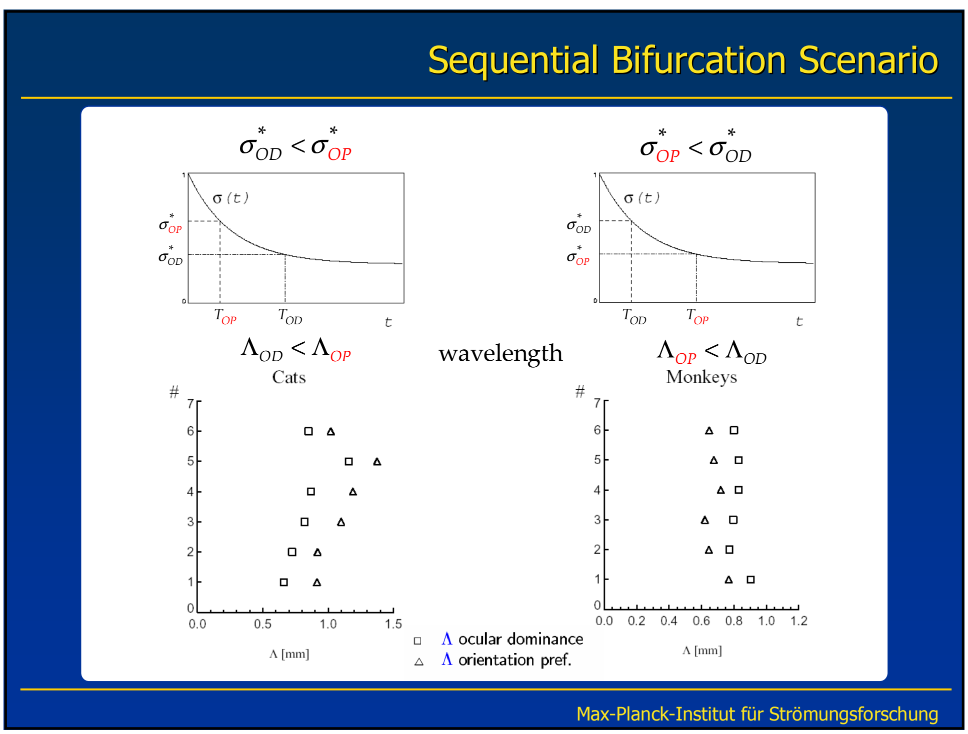
Sequential Bifurcation Scenario
$\sigma^*_{OD} < \sigma^*_{OP}$
$\sigma(t)$
σ^*_{OP}
σ^*_{OD}
T_{OP} T_{OD} t
$\Lambda_{OD} < \Lambda_{OP}$
Cats
$\sigma^*_{OP} < \sigma^*_{OD}$
$\sigma(t)$
σ^*_{OD}
σ^*_{OP}
T_{OD} T_{OP} t
$\Lambda_{OP} < \Lambda_{OD}$
Monkeys
wavelength
Λ [mm]
Λ ocular dominance
Λ orientation pref.
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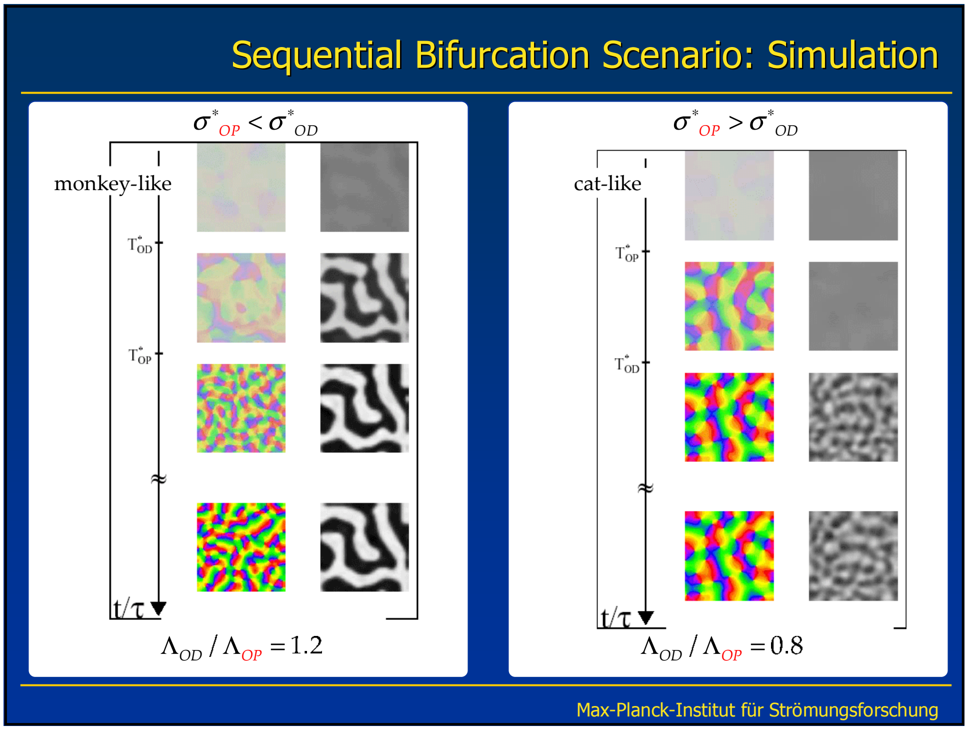
Sequential Bifurcation Scenario: Simulation
σ*OP < σ*OD
monkey-like
T*OD
T*OP
t/τ
ΛOD / ΛOP = 1.2
σ*OP > σ*OD
cat-like
T*OP
T*OD
t/τ
ΛOD / ΛOP = 0.8
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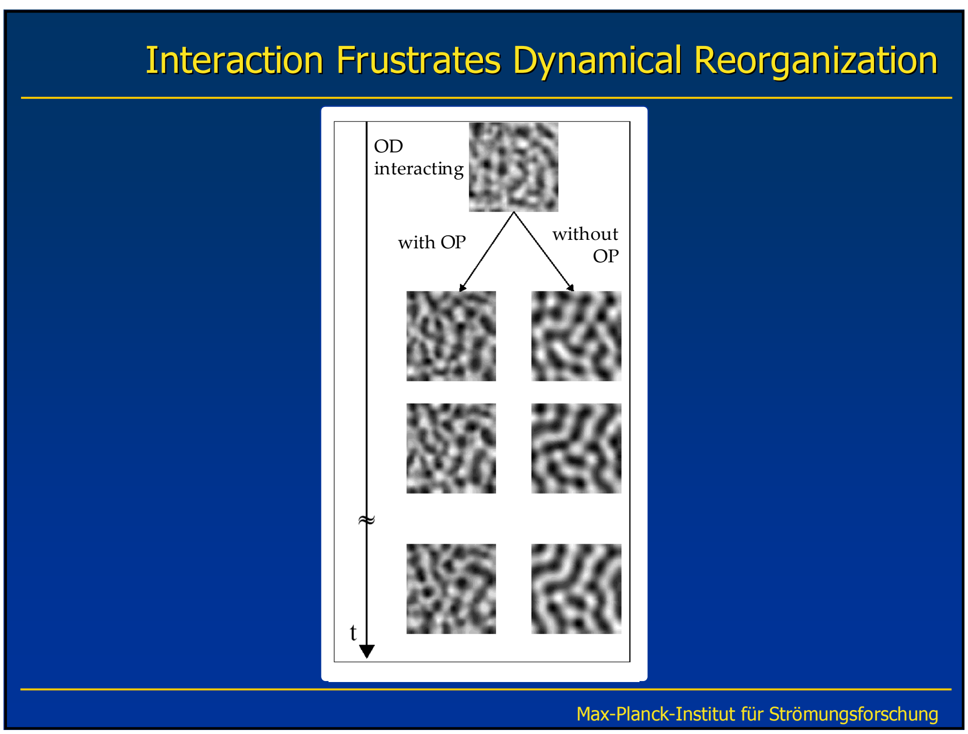
Interaction Frustrates Dynamical Reorganization
OD
interacting
with OP
without
OP
t
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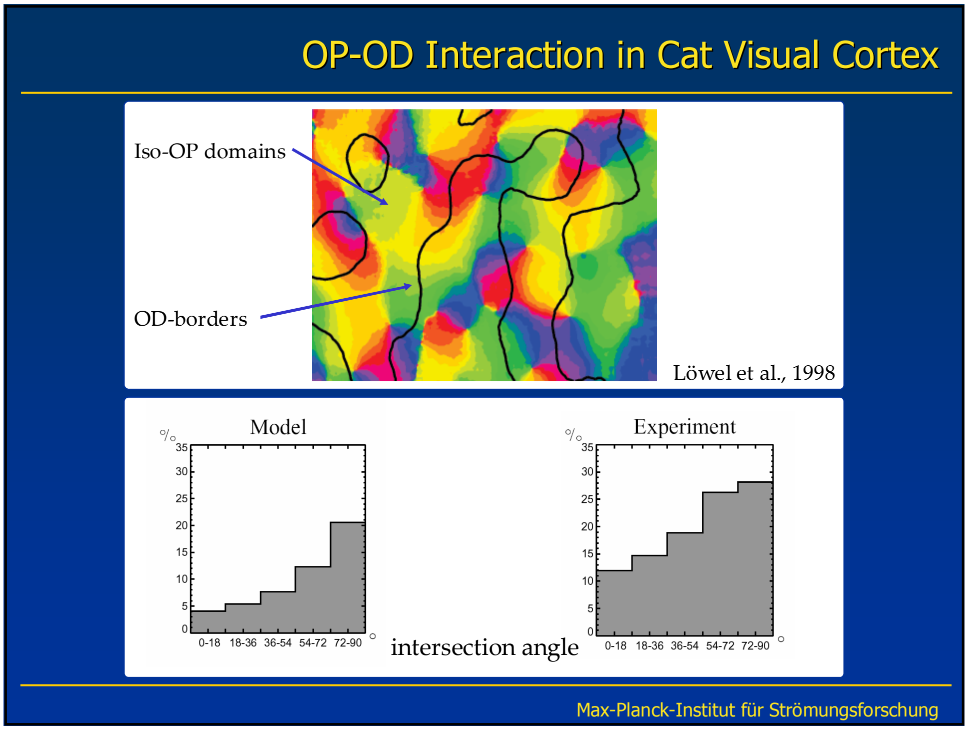
OP-OD Interaction in Cat Visual Cortex
Iso-OP domains
OD-borders
Löwel et al., 1998
Model
Experiment
%
35
30
25
20
15
10
5
0
0-18
18-36
36-54
54-72
72-90
°
intersection angle
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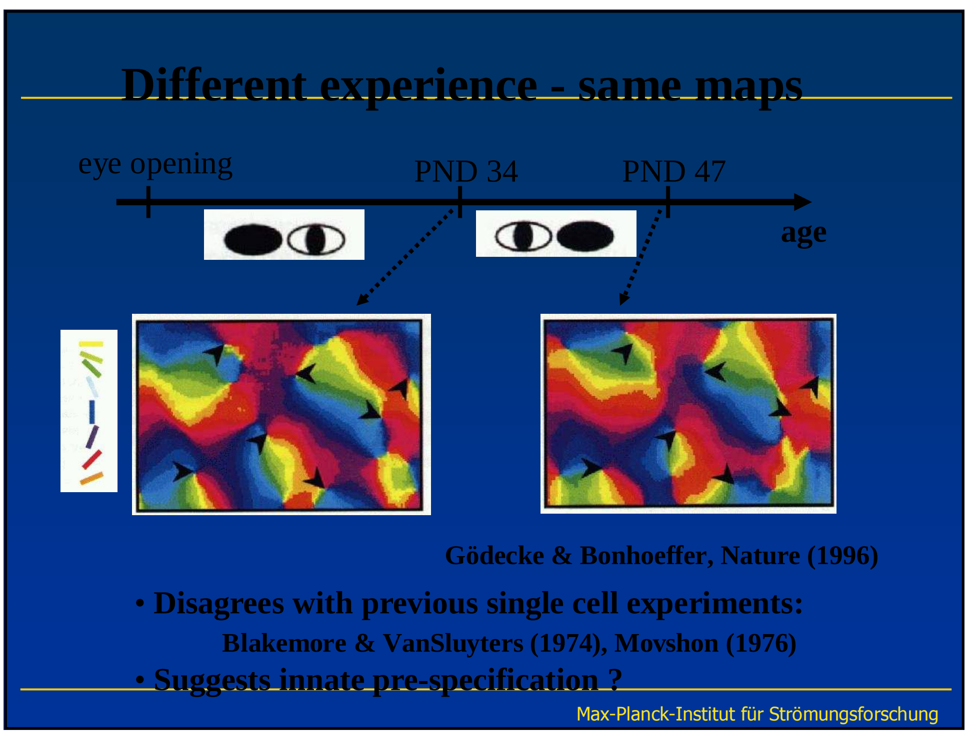
Different experience - same maps
eye opening
PND 34
PND 47
age
Gödecke & Bonhoeffer, Nature (1996)
• Disagrees with previous single cell experiments:
Blakemore & VanSluyters (1974), Movshon (1976)
• Suggests innate pre-specification ?
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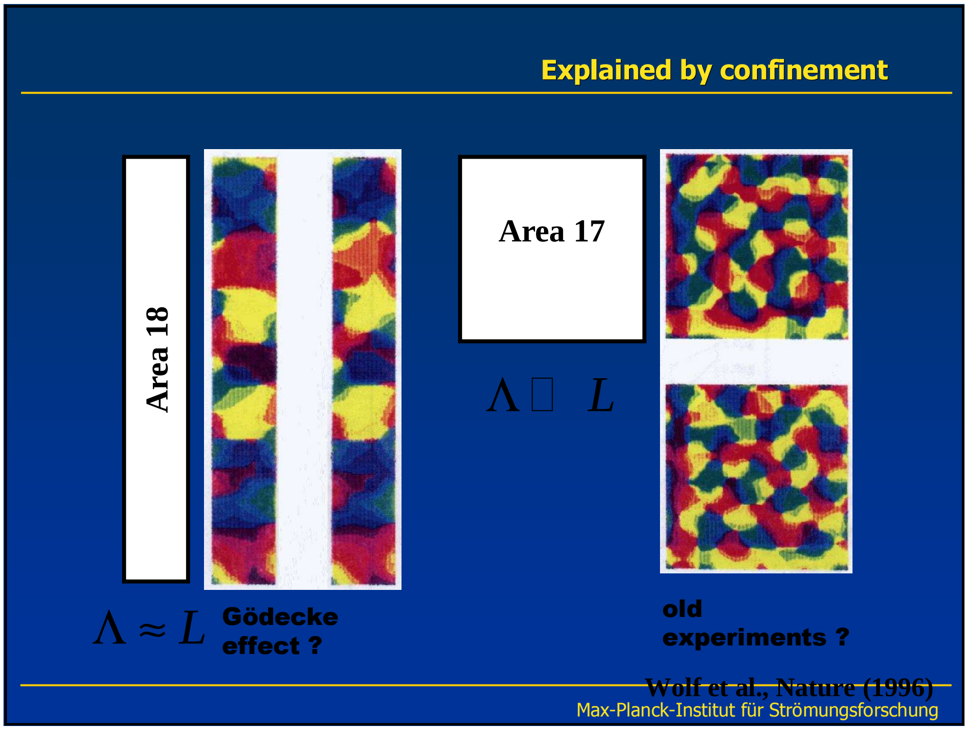

Conclusion

- discrete, instability-like events in visual development
- instabilities controlled by intrinsic size σ <u>and</u> experienced stimuli $\langle s^2 \rangle$
- observed wavelengths and patterns explained by sequential bifurcation and pattern interaction
- patterns must emerge in order of wavelength

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