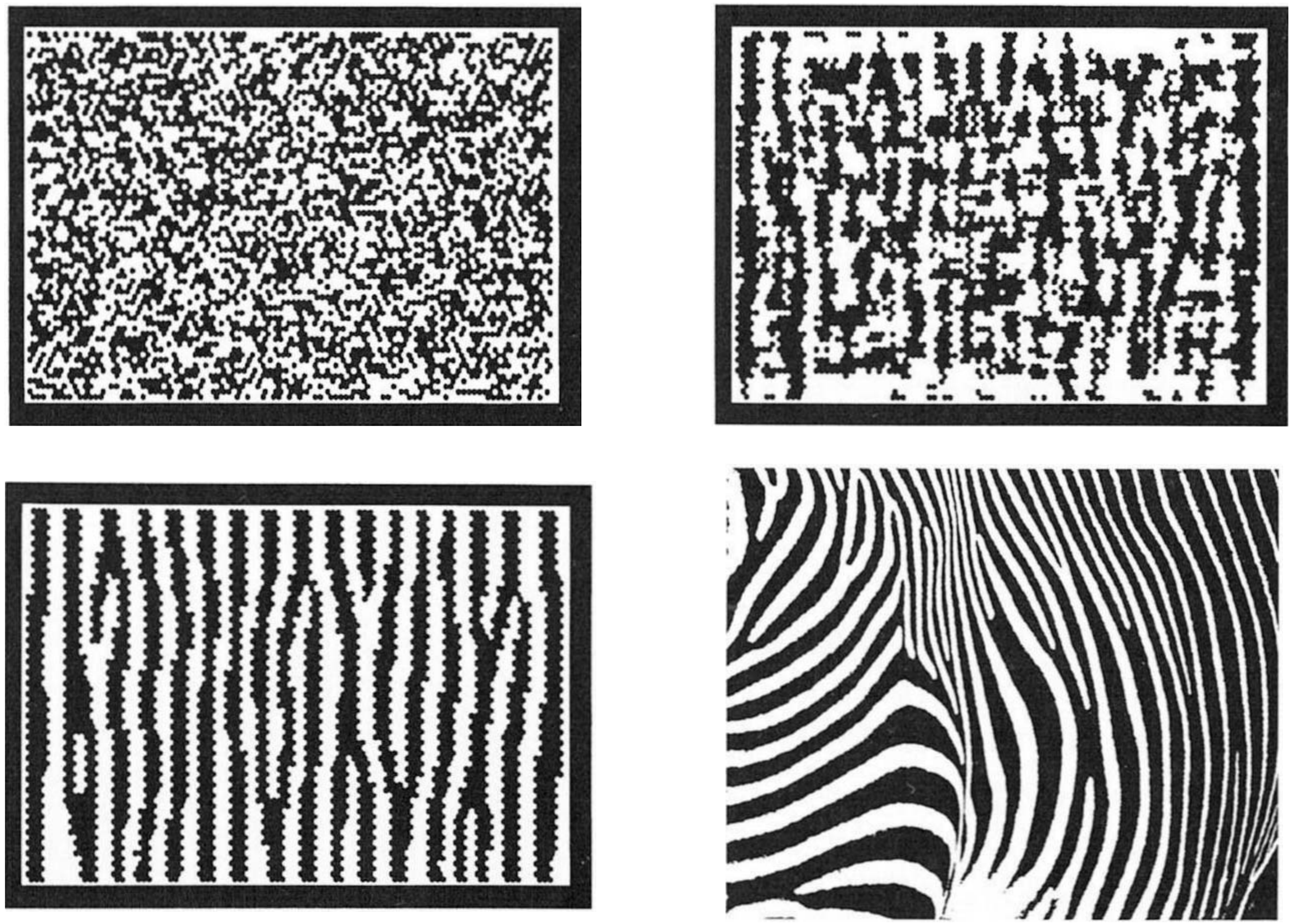
D.
Pattern Formation

Differentiation & Pattern Formation

- A central problem in development: How do cells differentiate to fulfill different purposes?
- How do complex systems generate spatial & temporal structure?
- CAs are natural models of intercellular communication

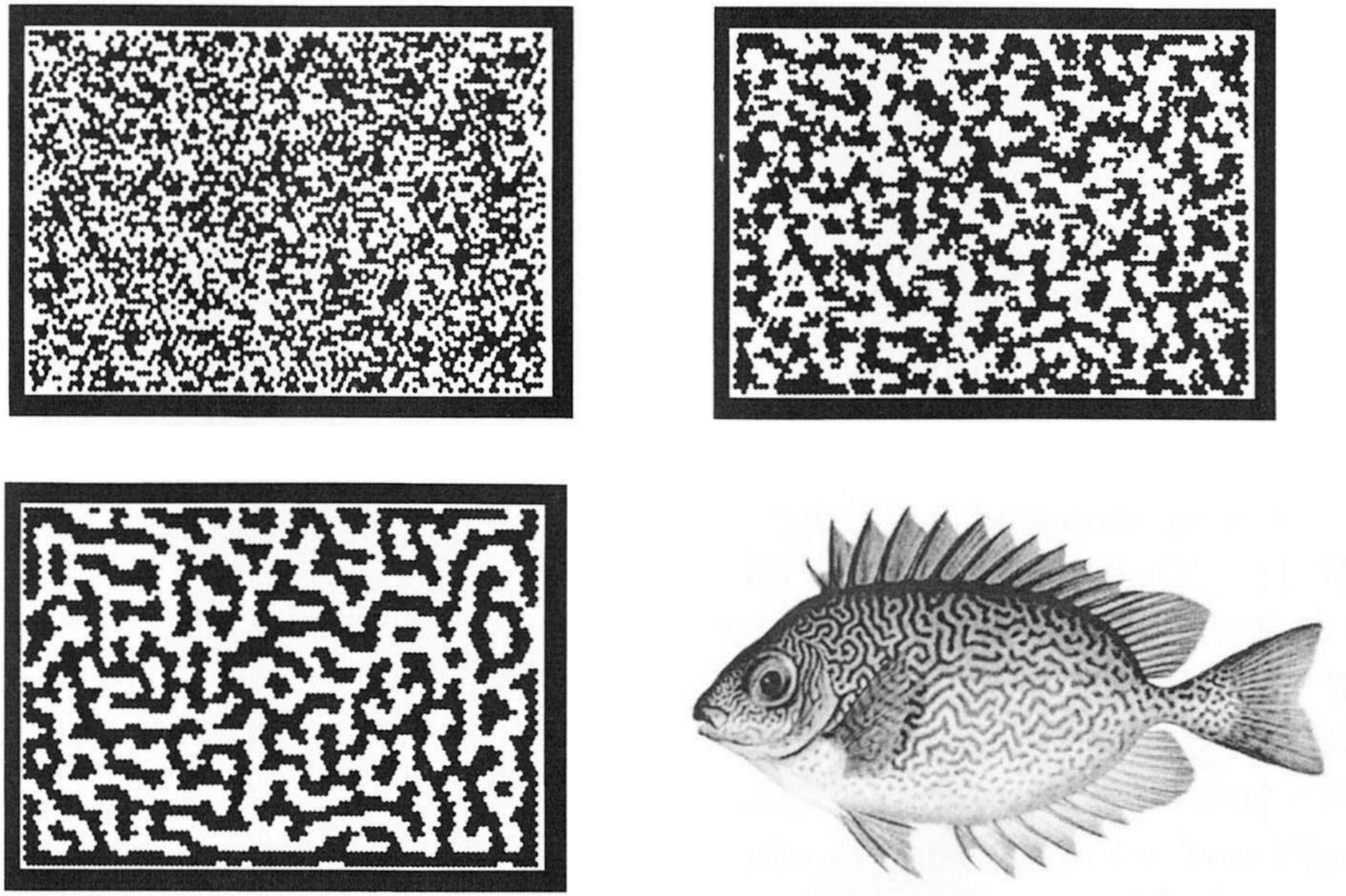
 photos ©2000, S. Cazamine

Zebra



figs. from Camazine & al.: *Self-Org. Biol. Sys.*

Vermiculated Rabbit Fish

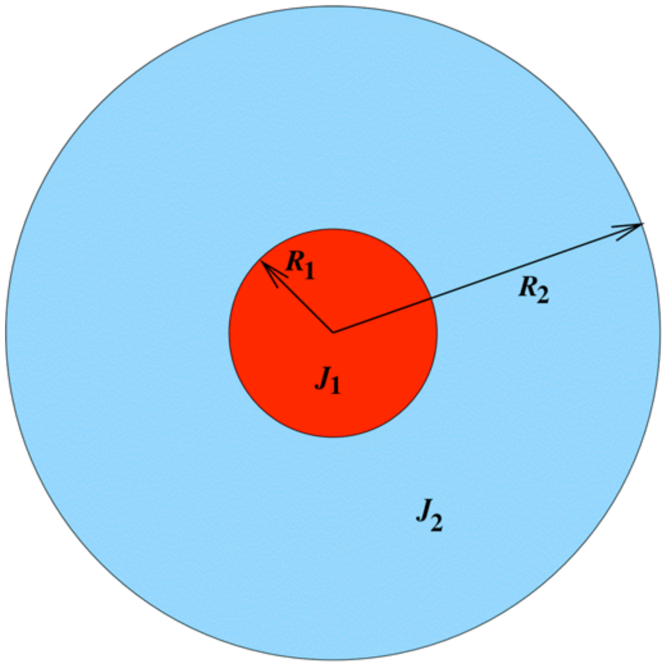


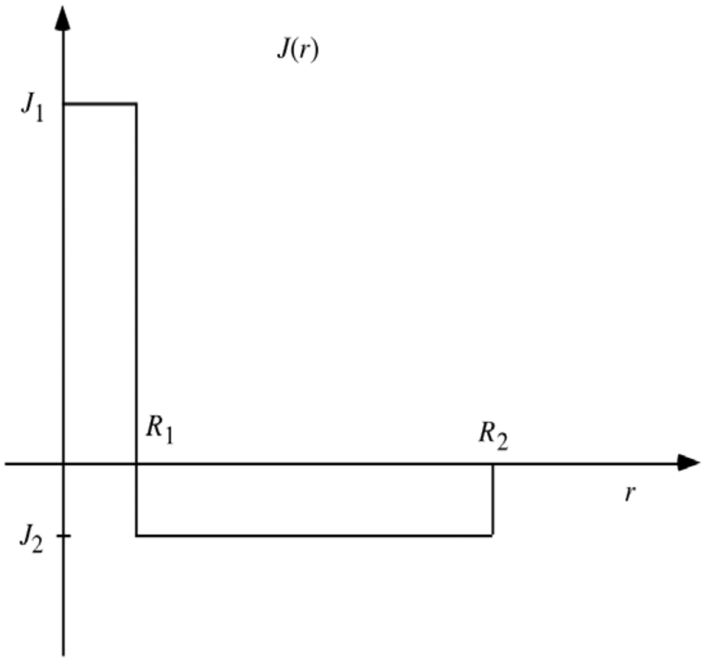
figs. from Camazine & al.: *Self-Org. Biol. Sys.*

Activation & Inhibition in Pattern Formation

- Color patterns typically have a characteristic length scale
- Independent of cell size and animal size
- Achieved by:
  - short-range activation ⇒ local uniformity
  - long-range inhibition ⇒ separation

Interaction Parameters





- R_1 and R_2 are the interaction ranges
- J_1 and J_2 are the interaction strengths

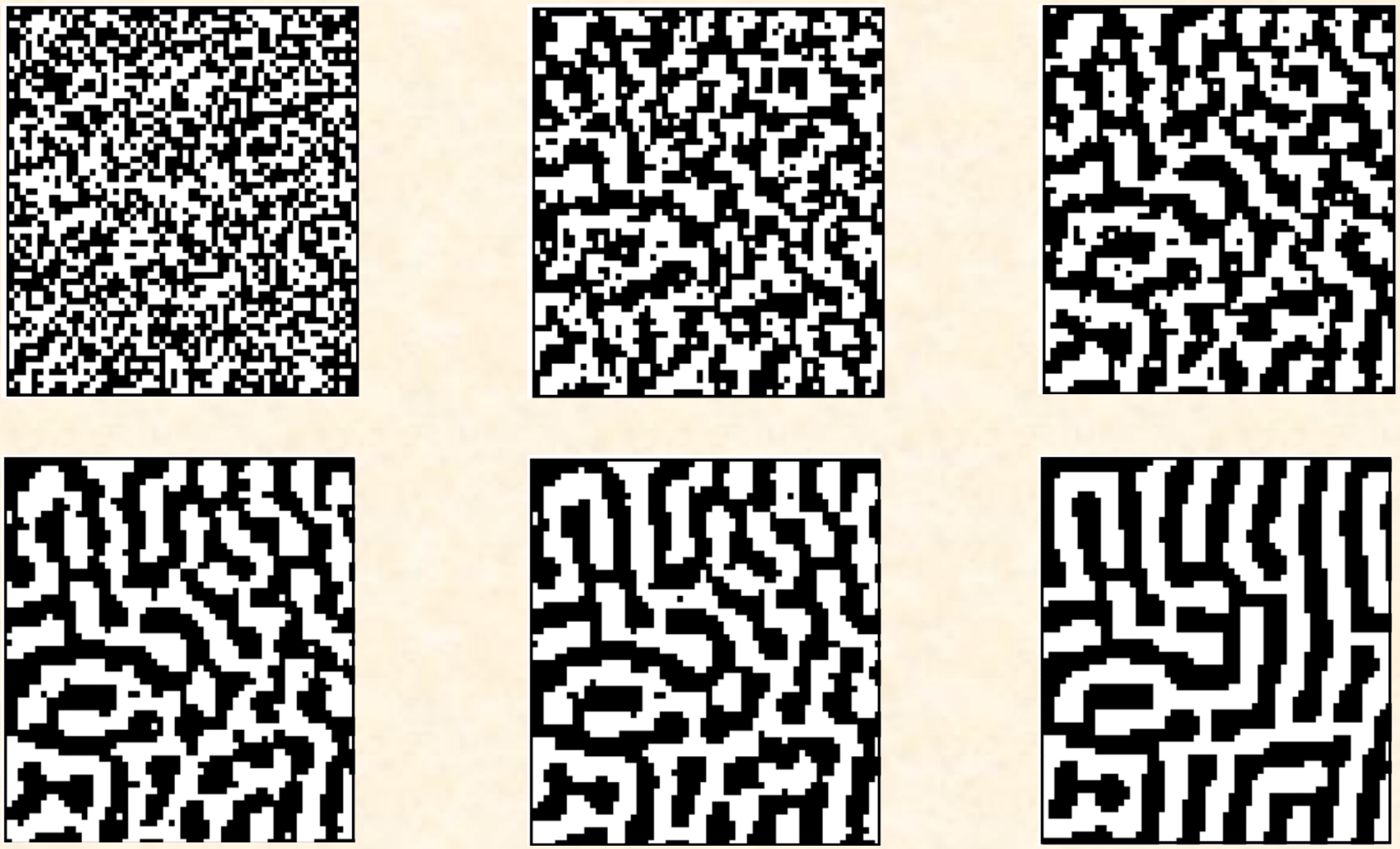
CA Activation/Inhibition Model

- Let states $s_i \in \{-1, +1\}$
- and h be a bias parameter
- and r_{ij} be the distance between cells i and j
- Then the state update rule is:

$$s_i(t+1) = \operatorname{sign}\left[h + J_1 \sum_{r_{ij} < R_1} s_j(t) + J_2 \sum_{R_1 \le r_{ij} < R_2} s_j(t) \right]$$

Example

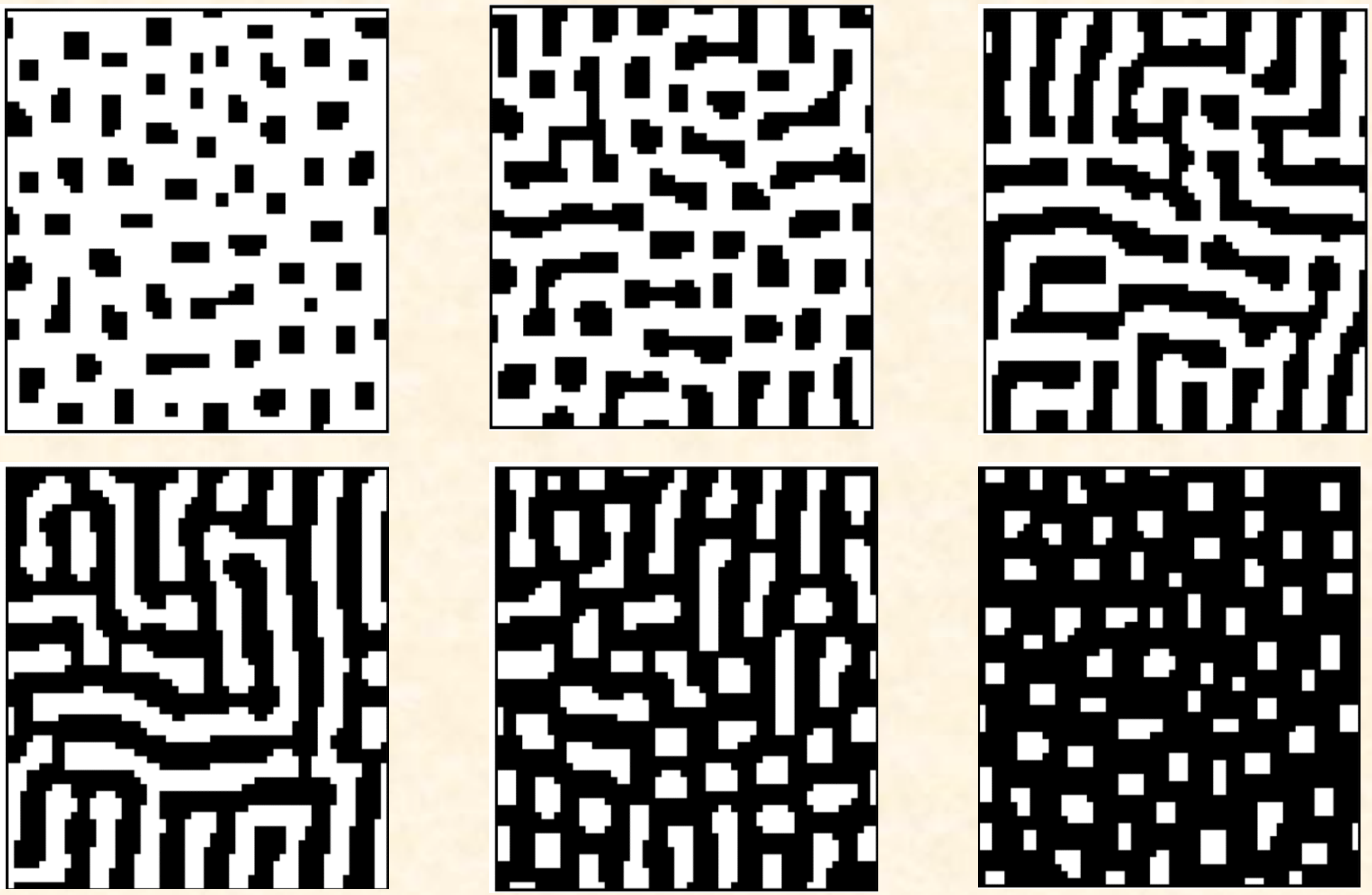
$(R_1=1,\ R_2=6,\ J_1=1,\ J_2=-0.1,\ h=0)$



figs. from Bar-Yam

Effect of Bias

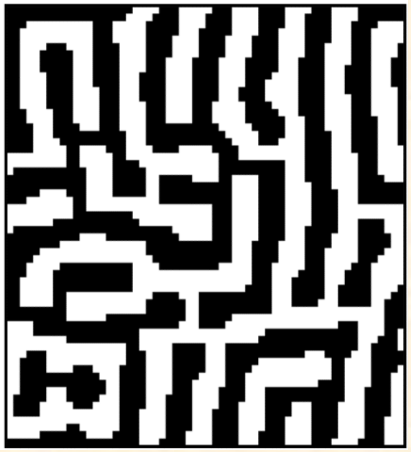
(h = –6, –3, –1; 1, 3, 6)



figs. from Bar-Yam

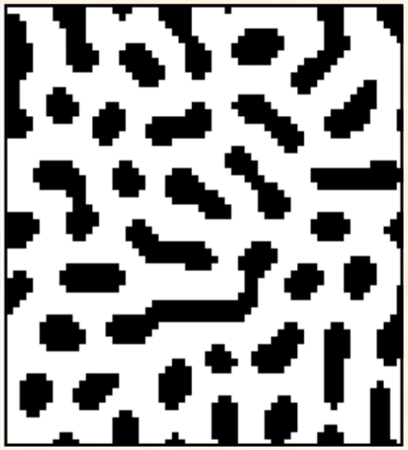
Effect of Interaction Ranges

$R_2 = 6$
$R_1 = 1$
$h = 0$



$R_2 = 8$
$R_1 = 1$
$h = 0$

$R_2 = 6$
$R_1 = 1.5$
$h = 0$



$R_2 = 6$
$R_1 = 1.5$
$h = -3$

figs. from Bar-Yam

Demonstration of NetLogo Program for Activation/Inhibition Pattern Formation: Fur

Run AICA.nlogo

Differential Interaction Ranges

- How can a system using strictly local interactions discriminate between states at long and short range?
- E.g. cells in developing organism
- Can use two different *morphogens* diffusing at two different rates
  - activator diffuses slowly (short range)
  - inhibitor diffuses rapidly (long range)

Digression on Diffusion

- Simple 2-D diffusion equation:

$$\dot{A}(x,y) = c\nabla^2 A(x,y)$$

- Recall the 2-D Laplacian:

$$\nabla^2 A(x,y) = \frac{\partial^2 A(x,y)}{\partial x^2} + \frac{\partial^2 A(x,y)}{\partial y^2}$$

- The Laplacian (like 2nd derivative) is:
  - positive in a local minimum
  - negative in a local maximum

Reaction-Diffusion System

diffusion

$$\frac{\partial A}{\partial t} = \boxed{d_\mathrm{A} \nabla^2 A} + \boxed{f_\mathrm{A}(A,I)}$$

$$\frac{\partial I}{\partial t} = \boxed{d_\mathrm{I} \nabla^2 I} + \boxed{f_\mathrm{I}(A,I)}$$

reaction

$$\frac{\partial}{\partial t}\begin{pmatrix} A \\ I \end{pmatrix} = \begin{pmatrix} d_\mathrm{A} & 0 \\ 0 & d_\mathrm{I} \end{pmatrix}\begin{pmatrix} \nabla^2 A \\ \nabla^2 I \end{pmatrix} + \begin{pmatrix} f_\mathrm{A}(A,I) \\ f_\mathrm{I}(A,I) \end{pmatrix}$$

$$\dot{\mathbf{c}} = \mathbf{D}\nabla^2\mathbf{c} + \mathbf{f}(\mathbf{c}), \quad \text{where } \mathbf{c} = \begin{pmatrix} A \\ I \end{pmatrix}$$

Example: Activation-Inhibition System

- Let σ be the logistic sigmoid function
- Activator *A* and inhibitor *I* may diffuse at different rates in *x* and *y* directions
- Cell is "on" if activator + bias exceeds inhibitor

$$\frac{\partial A}{\partial t} = d_{\mathrm{Ax}} \frac{\partial^2 A}{\partial x^2} + d_{\mathrm{Ay}} \frac{\partial^2 A}{\partial y^2} + k_{\mathrm{A}} \sigma\left[m_{\mathrm{A}}\left(A + B - I\right)\right]$$

$$\frac{\partial I}{\partial t} = d_{\mathrm{Ix}} \frac{\partial^2 I}{\partial x^2} + d_{\mathrm{Iy}} \frac{\partial^2 I}{\partial y^2} + k_{\mathrm{I}} \sigma\left[m_{\mathrm{I}}\left(A + B - I\right)\right]$$

NetLogo Simulation of Reaction-Diffusion System

1. Diffuse activator in X and Y directions
2. Diffuse inhibitor in X and Y directions
3. Each patch performs:

    stimulation = bias + activator – inhibitor + noise

    if stimulation > 0 then

        set activator and inhibitor to 100

    else

        set activator and inhibitor to 0

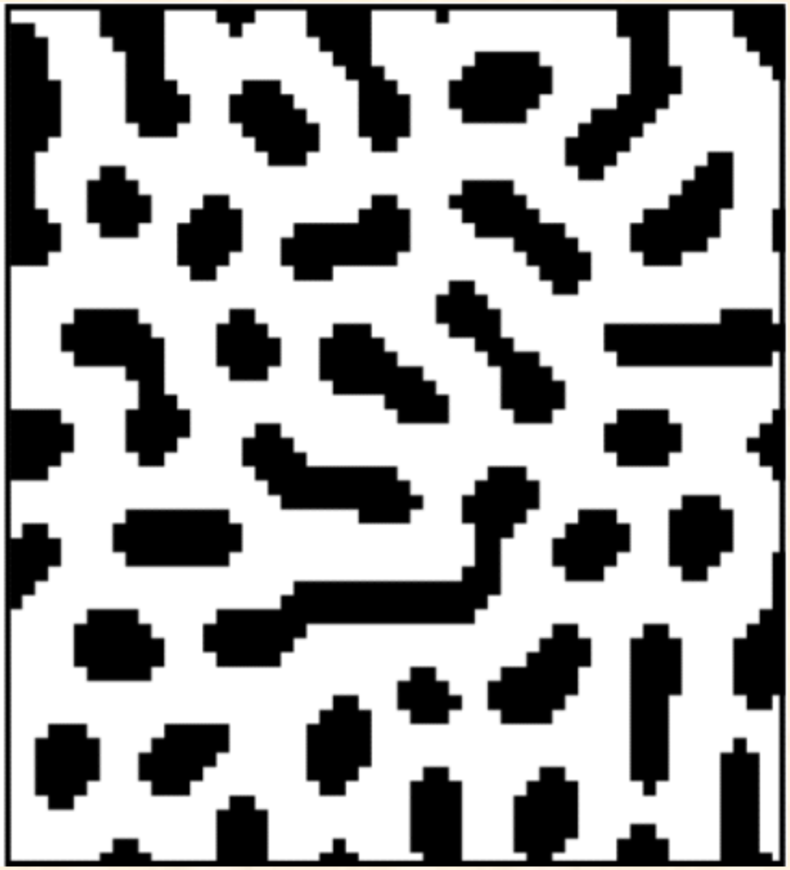
Demonstration of NetLogo Program for Activation/Inhibition Pattern Formation

Run Pattern.nlogo

Abstract Activation/Inhibition Spaces

- Consider two axes of cultural preference
  - E.g. hair length & interpersonal distance
  - Fictitious example!
- Suppose there are no objective reasons for preferences
- Suppose people approve/encourage those with similar preferences
- Suppose people disapprove/discourage those with different preferences
- What is the result?

Emergent Regions of Acceptable Variation



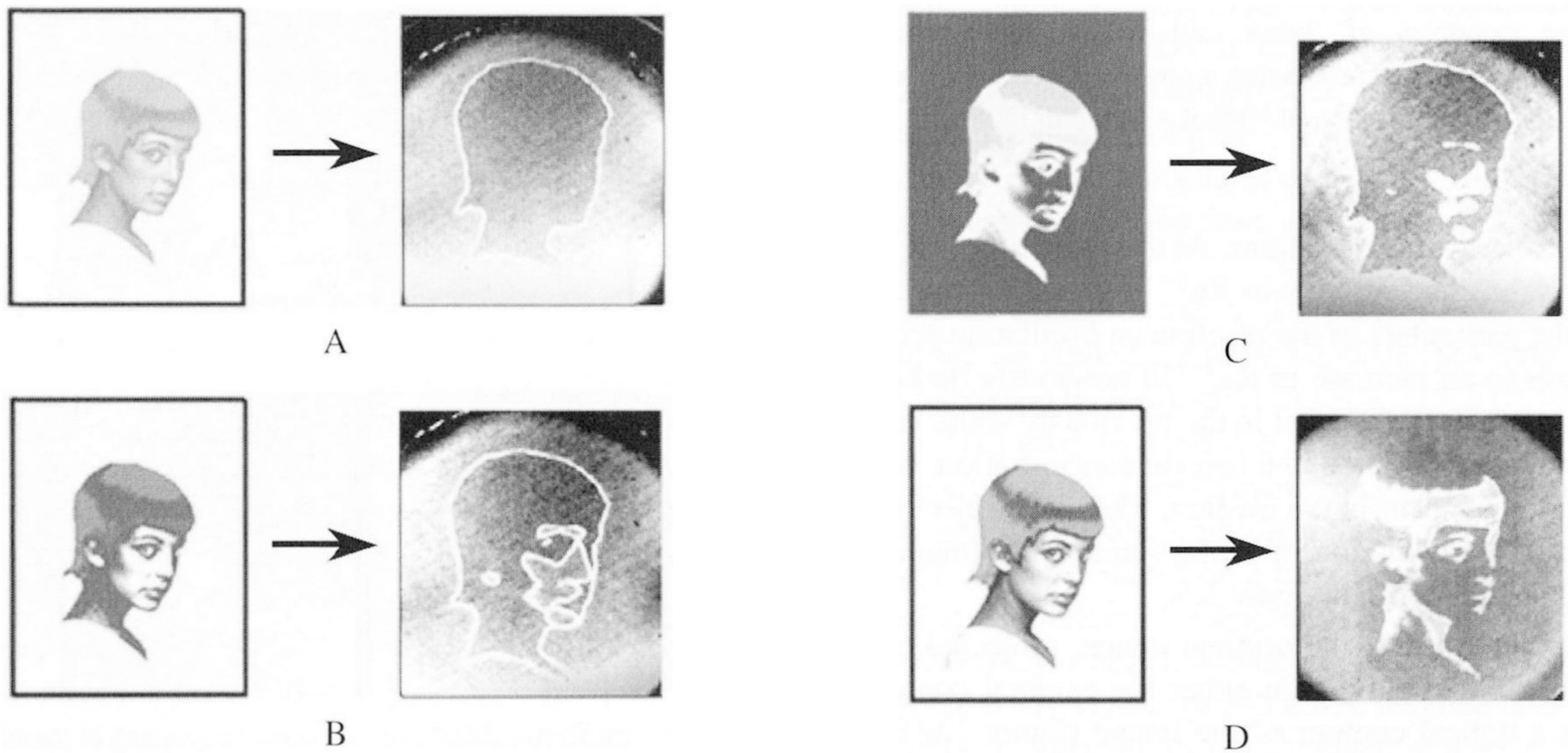
A Key Element of Self-Organization

- Activation vs. Inhibition
- Cooperation vs. Competition
- Amplification vs. Stabilization
- Growth vs. Limit
- Positive Feedback vs. Negative Feedback
  – Positive feedback creates
  – Negative feedback shapes

Reaction-Diffusion Computing

- Has been used for image processing
  - diffusion ⇒ noise filtering
  - reaction ⇒ contrast enhancement
- Depending on parameters, RD computing can:
  - restore broken contours
  - detect edges
  - improve contrast

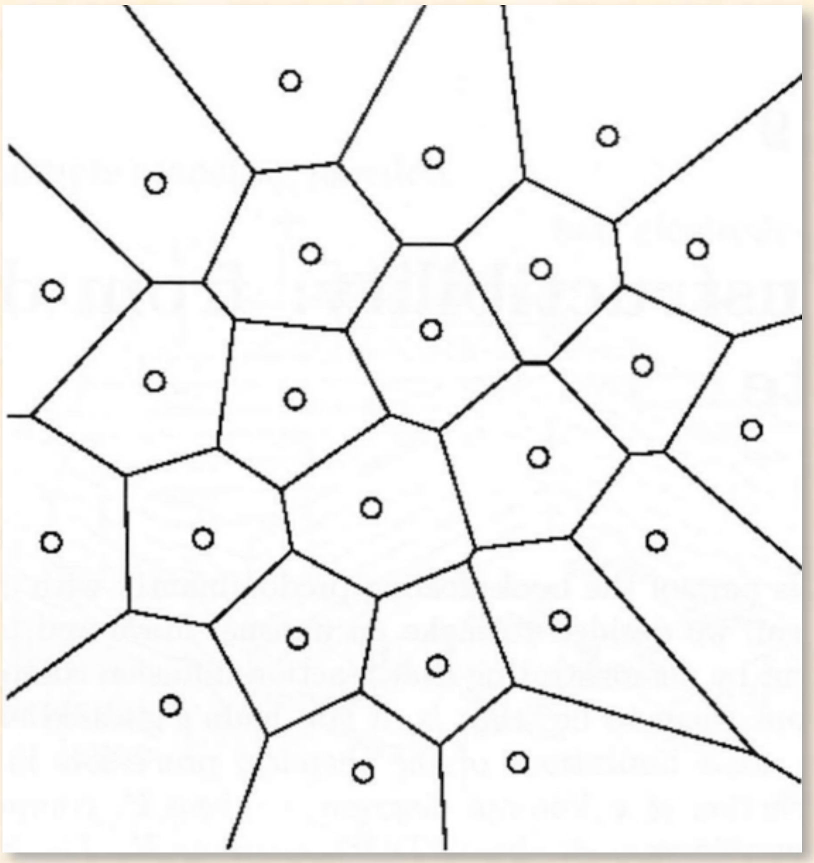
Image Processing in BZ Medium



- (A) boundary detection, (B) contour enhancement, (C) shape enhancement, (D) feature enhancement

Image < Adamatzky, *Comp. in Nonlinear Media & Autom. Coll.*

Voronoi Diagrams



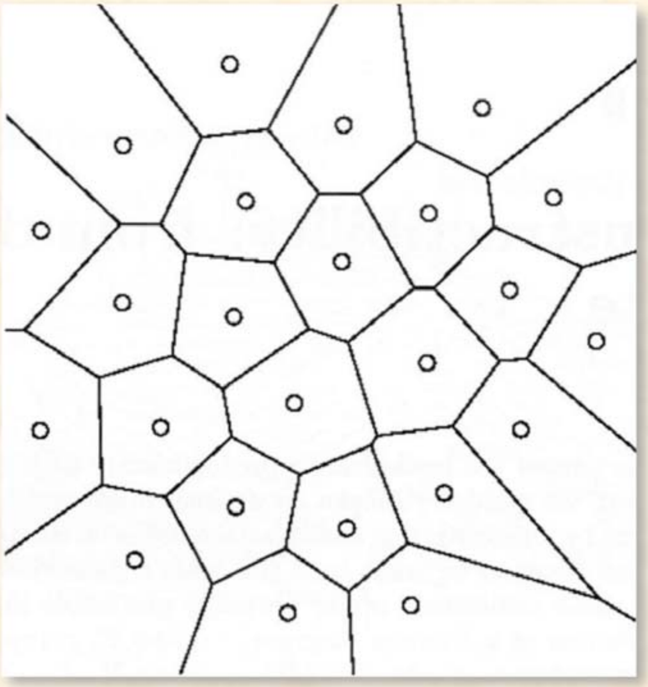
- Given a set of generating points:
- Construct polygon around each gen. point of set, so all points in poly. are closer to its generating point than to any other generating points.

Image < Adamatzky & al., *Reaction-Diffusion Computers*

Some Uses of Voronoi Diagrams

- Collision-free path planning
- Determination of service areas for power substations
- Nearest-neighbor pattern classification
- Determination of largest empty figure

Computation of Voronoi Diagram by Reaction-Diffusion Processor



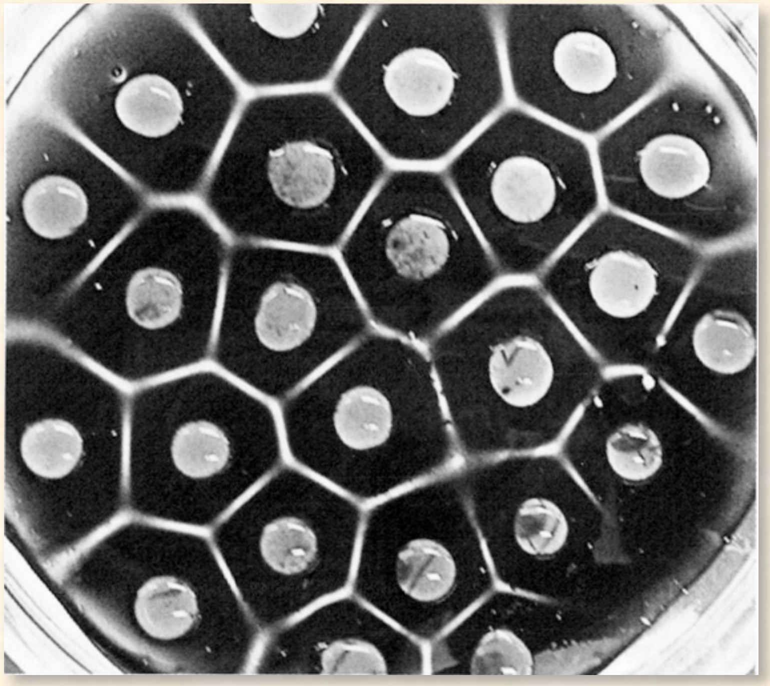


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Mixed Cell Voronoi Diagram

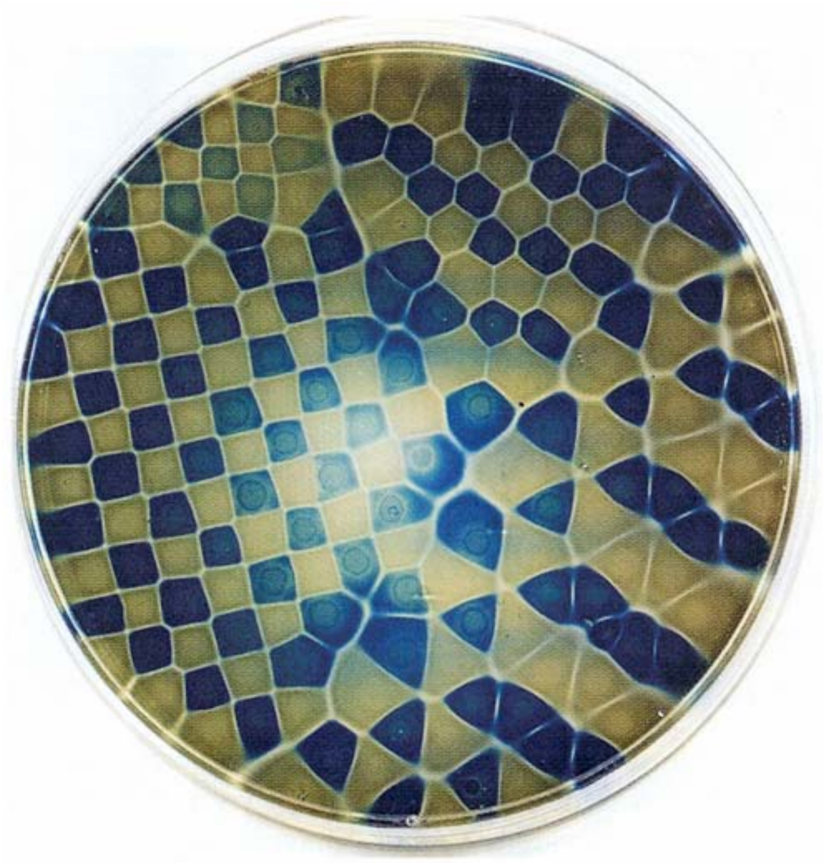


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Path Planning via BZ medium: No Obstacles

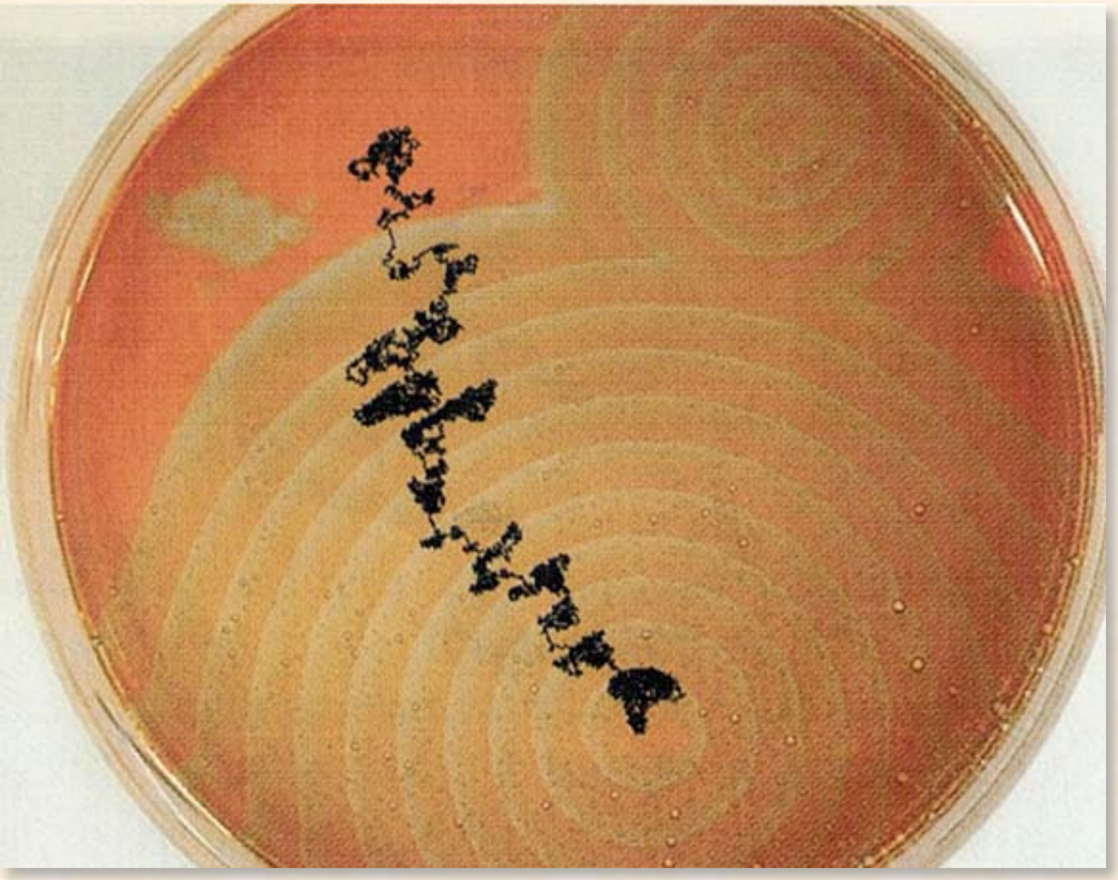


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Path Planning via BZ medium: Circular Obstacles

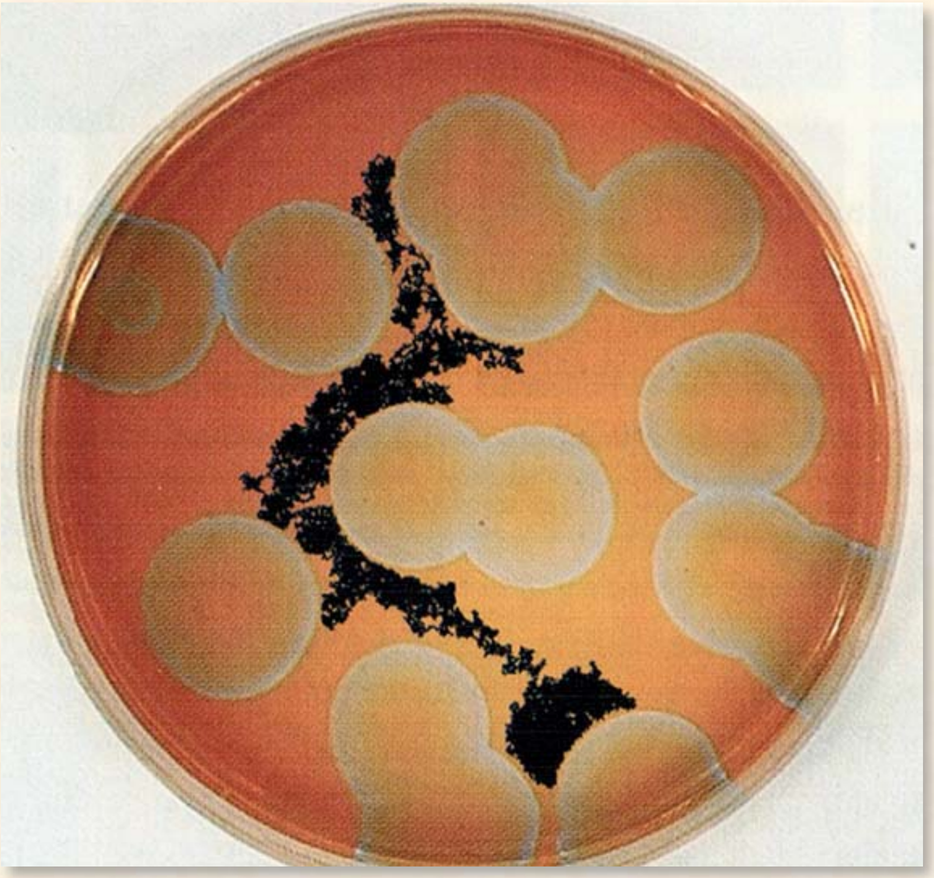


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Mobile Robot with Onboard Chemical Reactor

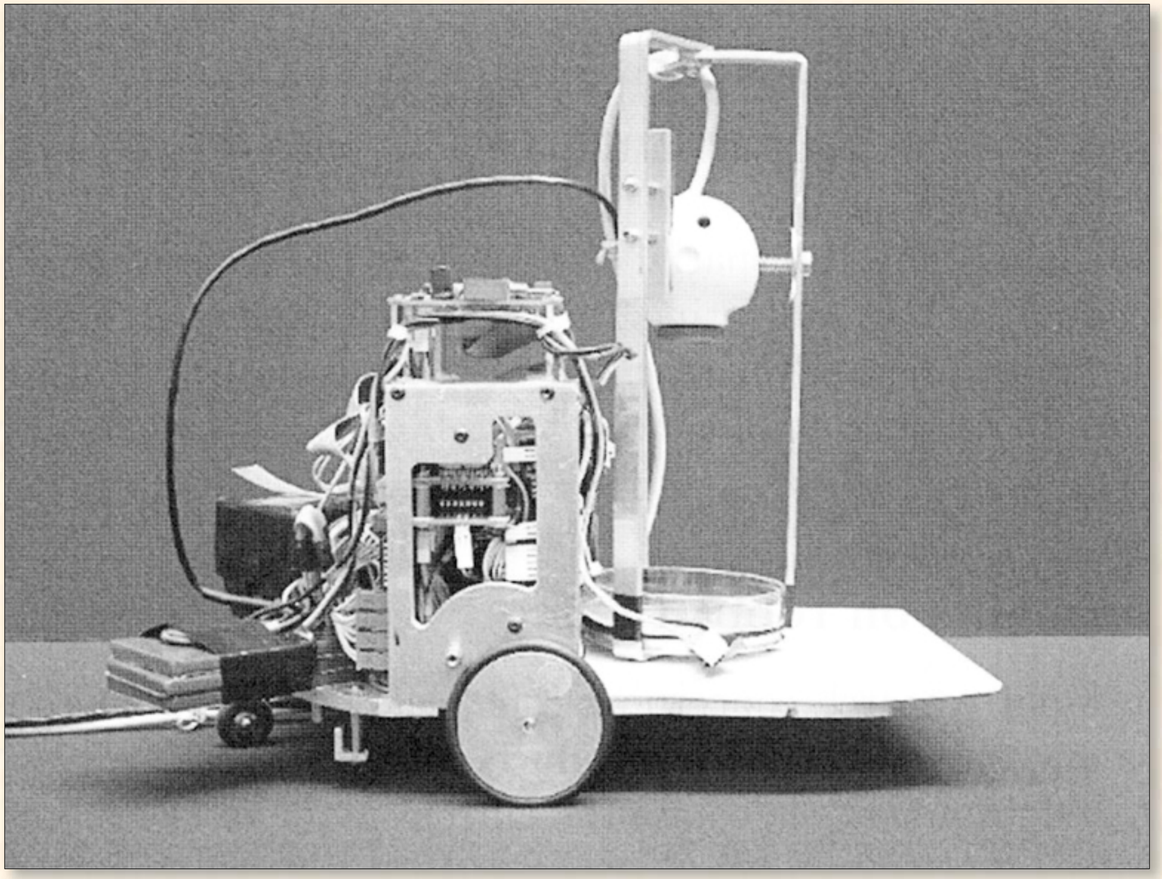


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Actual Path: Pd Processor

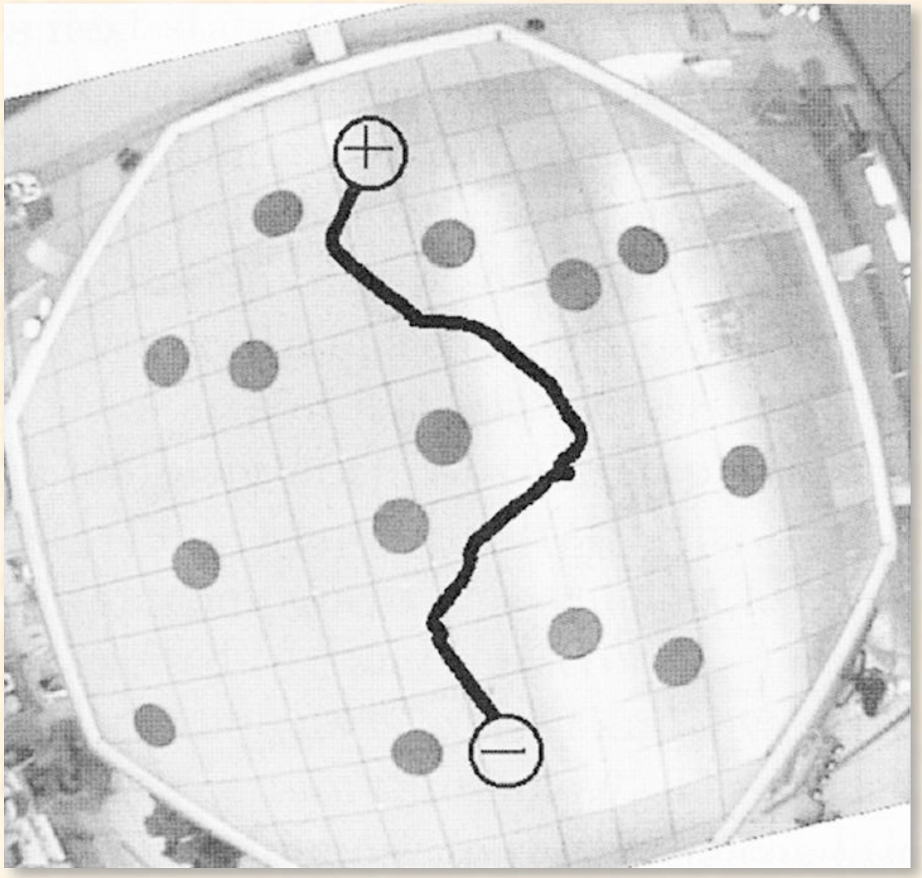


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Actual Path: Pd Processor

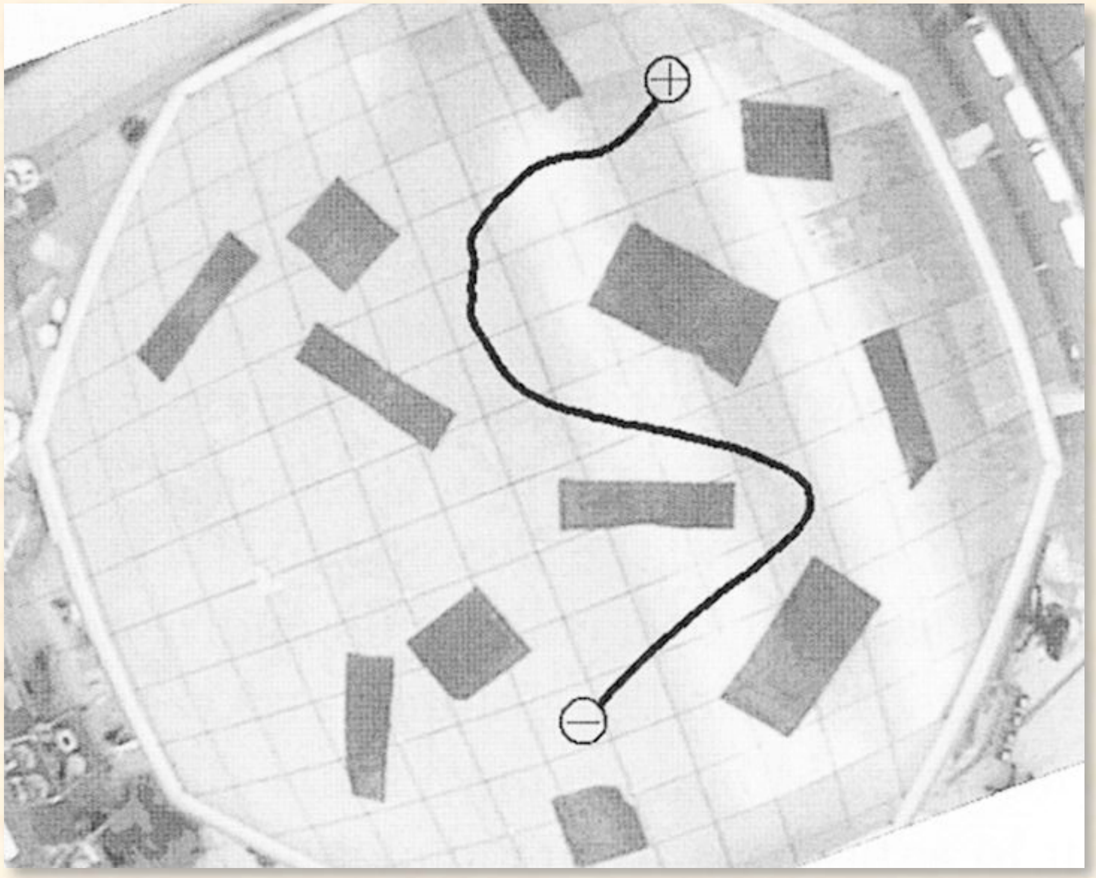


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Actual Path: BZ Processor

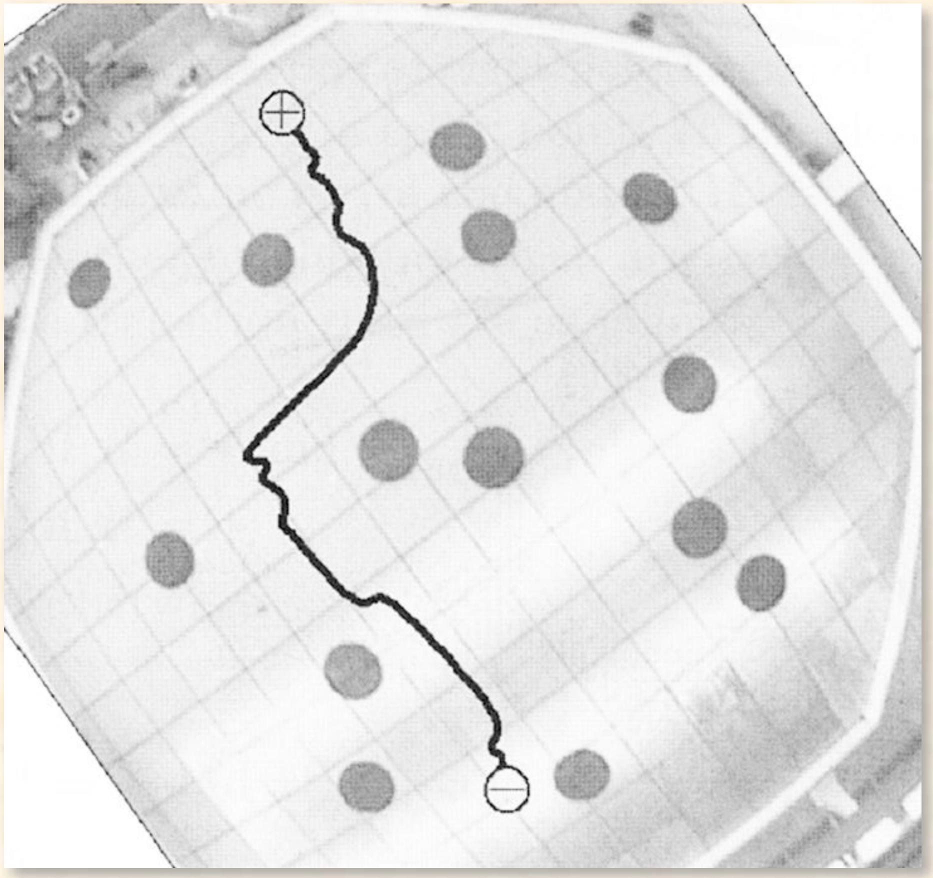


Image < Adamatzky & al., *Reaction-Diffusion Computers*

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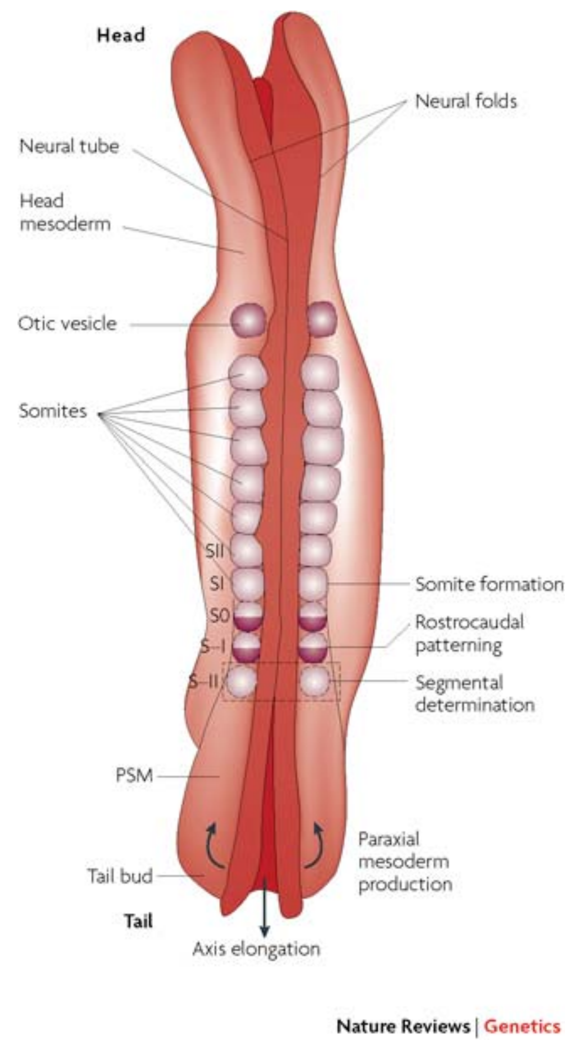
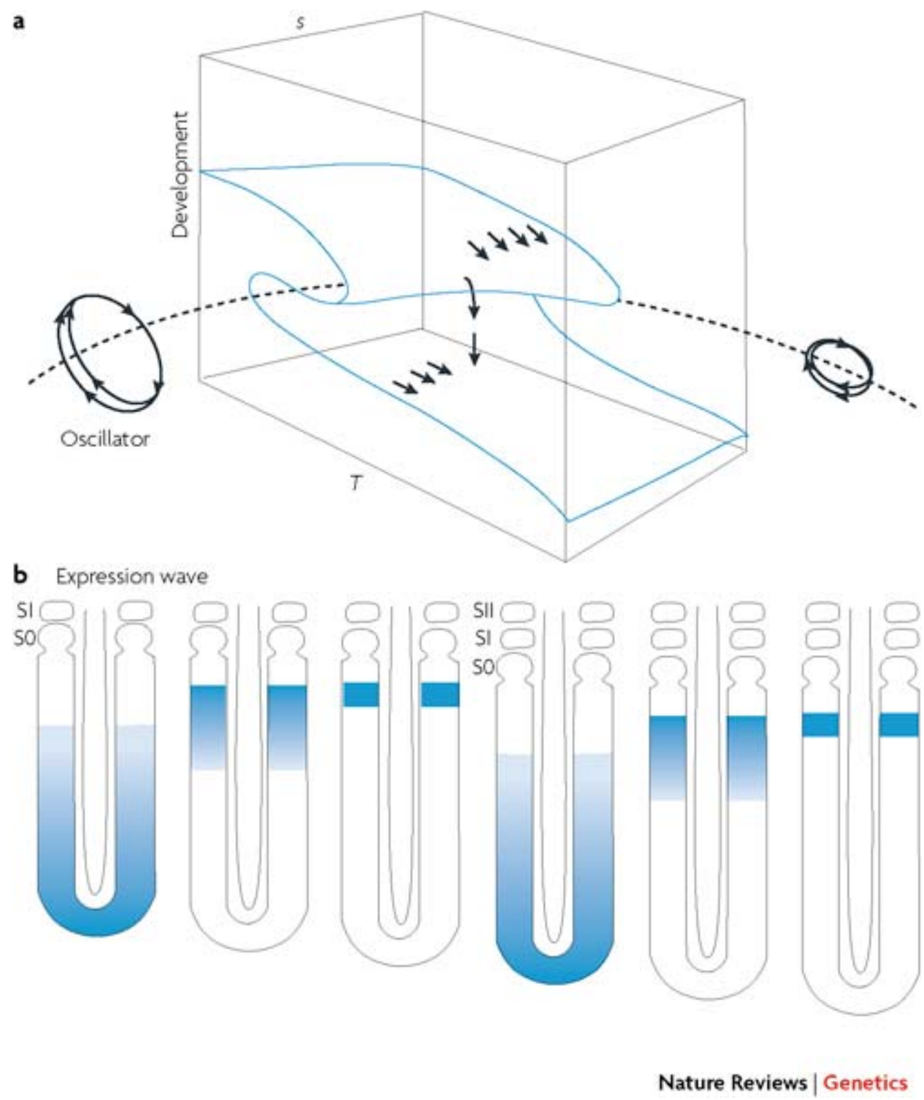
Segmentation

(in embryological development)

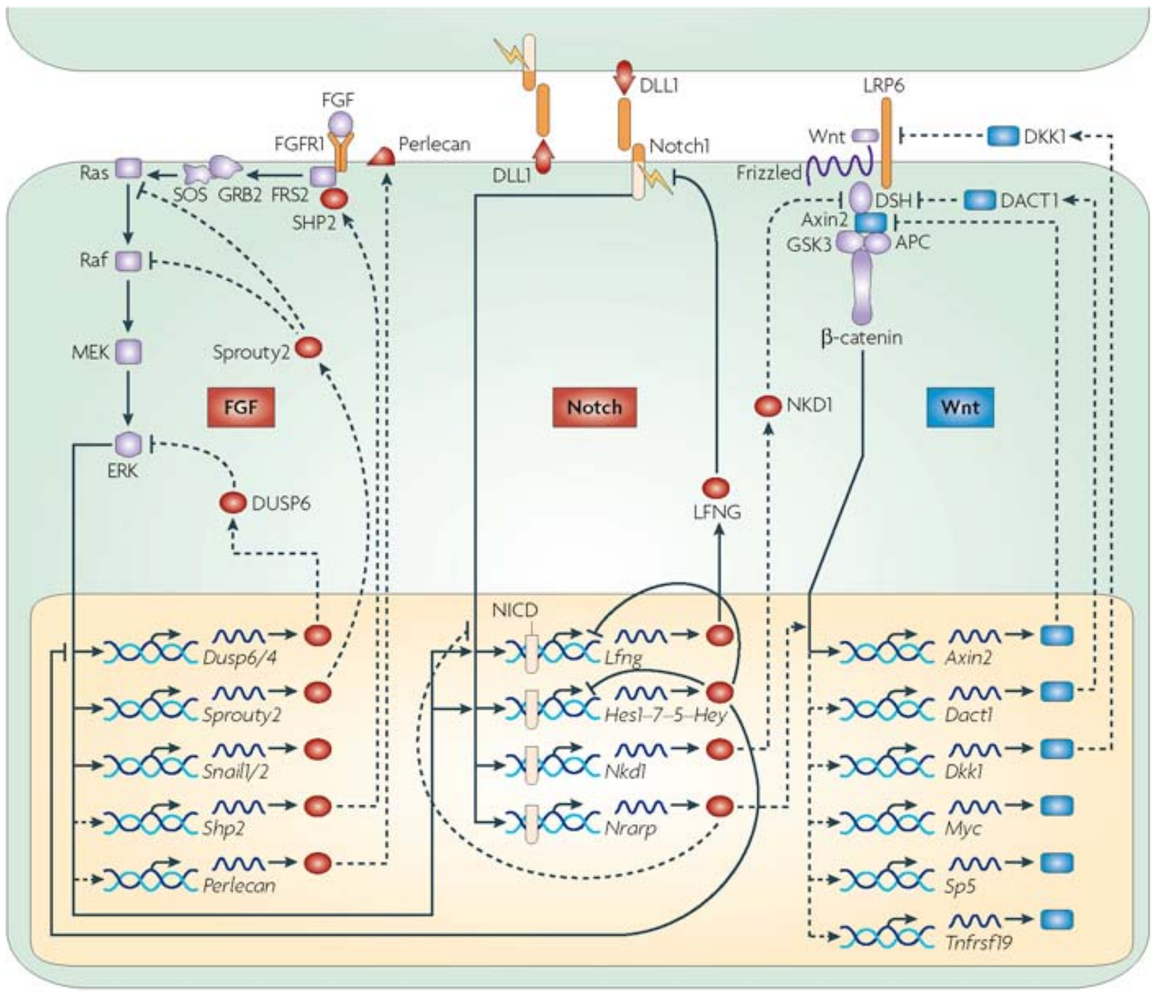
Vertebrae

- Humans: 33, chickens: 55, mice: 65, corn snake: 315
- Characteristic of species
- How does an embryo “count” them?
- “Clock and wavefront model” of Cooke & Zeeman (1976).

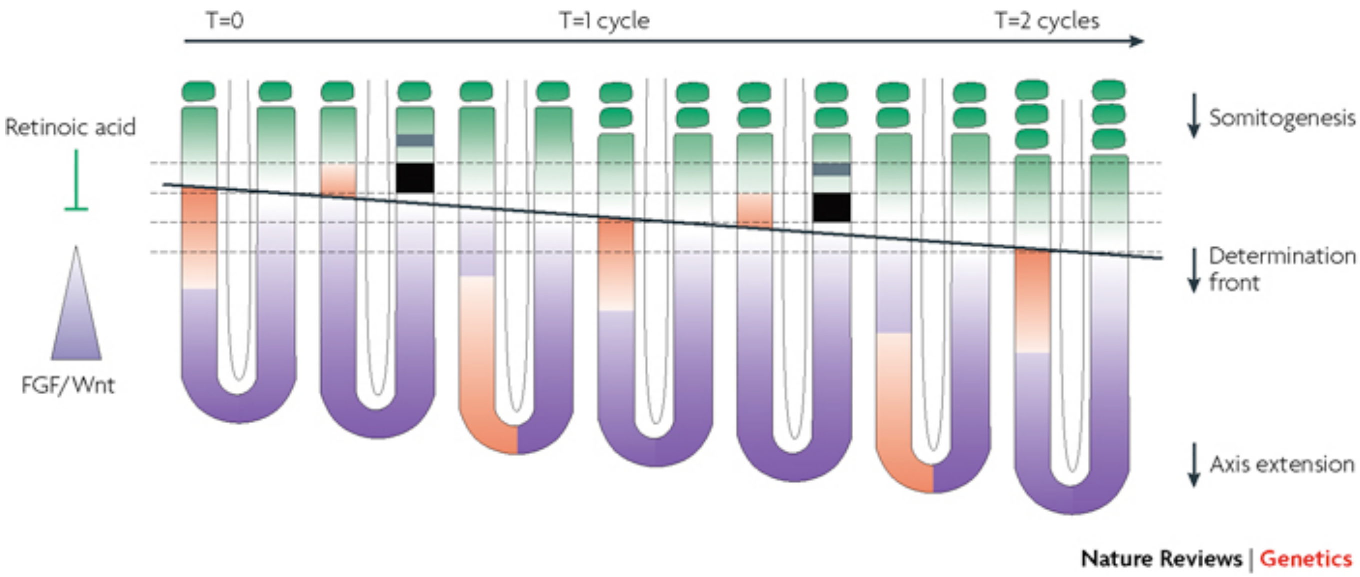

Head
Neural folds
Neural tube
Head
mesoderm
Otic vesicle
Somites
SII
SI
S0
S–I
S–II
Somite formation
Rostrocaudal
patterning
Segmental
determination
PSM
Paraxial
mesoderm
production
Tail bud
Tail
Axis elongation
Nature Reviews | Genetics



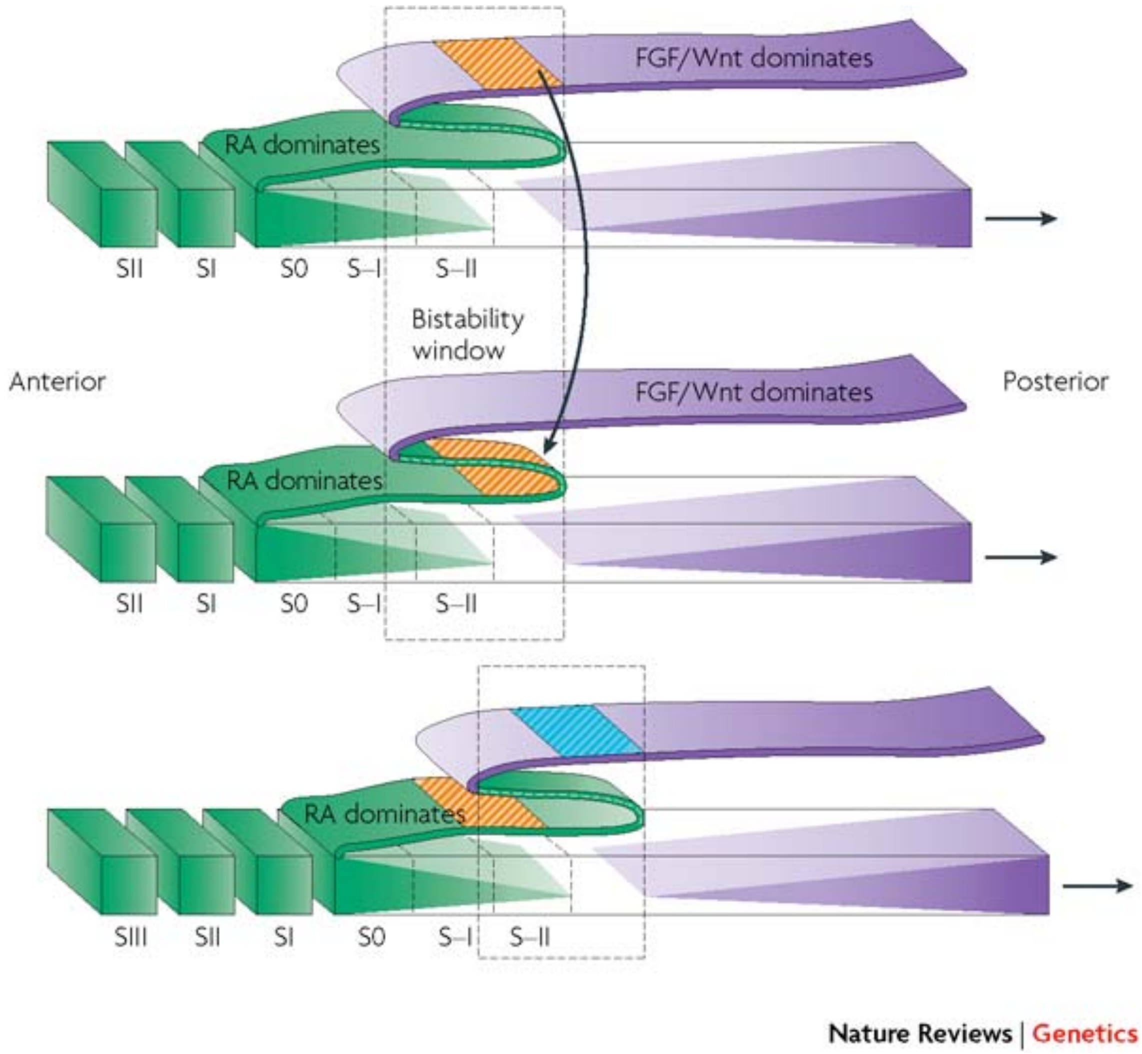
a
s
Development
Oscillator
T
b
Expression wave
SI
S0
SII
SI
S0
Nature Reviews | Genetics



Nature Reviews | Genetics



T=0
T=1 cycle
T=2 cycles
Retinoic acid
FGF/Wnt
Somitogenesis
Determination front
Axis extension
Nature Reviews | Genetics


FGF/Wnt dominates
RA dominates
SII
SI
S0
S–I
S–II
Bistability window
Anterior
FGF/Wnt dominates
Posterior
RA dominates
SII
SI
S0
S–I
S–II
RA dominates
SIII
SII
SI
S0
S–I
S–II
Nature Reviews | Genetics

NetLogo Simulation of Segmentation

Run Segmentation.nlogo

Segmentation References

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2. Dequéant, M.-L., & Pourquié, O. (2008). Segmental patterning of the vertebrate embryonic axis. *Nature Reviews Genetics* **9**: 370–82.
3. Gomez, C., Özbudak, E.M., Wunderlich, J., Baumann, D., Lewis, J., & Pourquié, O. (2008). Control of segment number in vertebrate embryos. *Nature* **454**: 335–9.

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5. Pálsson, E., & Cox, E. C. "Origin and Evolution of Circular Waves and Spiral in *Dictyostelium discoideum* Territories," *Proc. Natl. Acad. Sci. USA*: **93** (1996): 1151-5.
6. Solé, R., & Goodwin, B. *Signs of Life: How Complexity Pervades Biology*. Basic Books, 2000.

continue to "Part 3A"