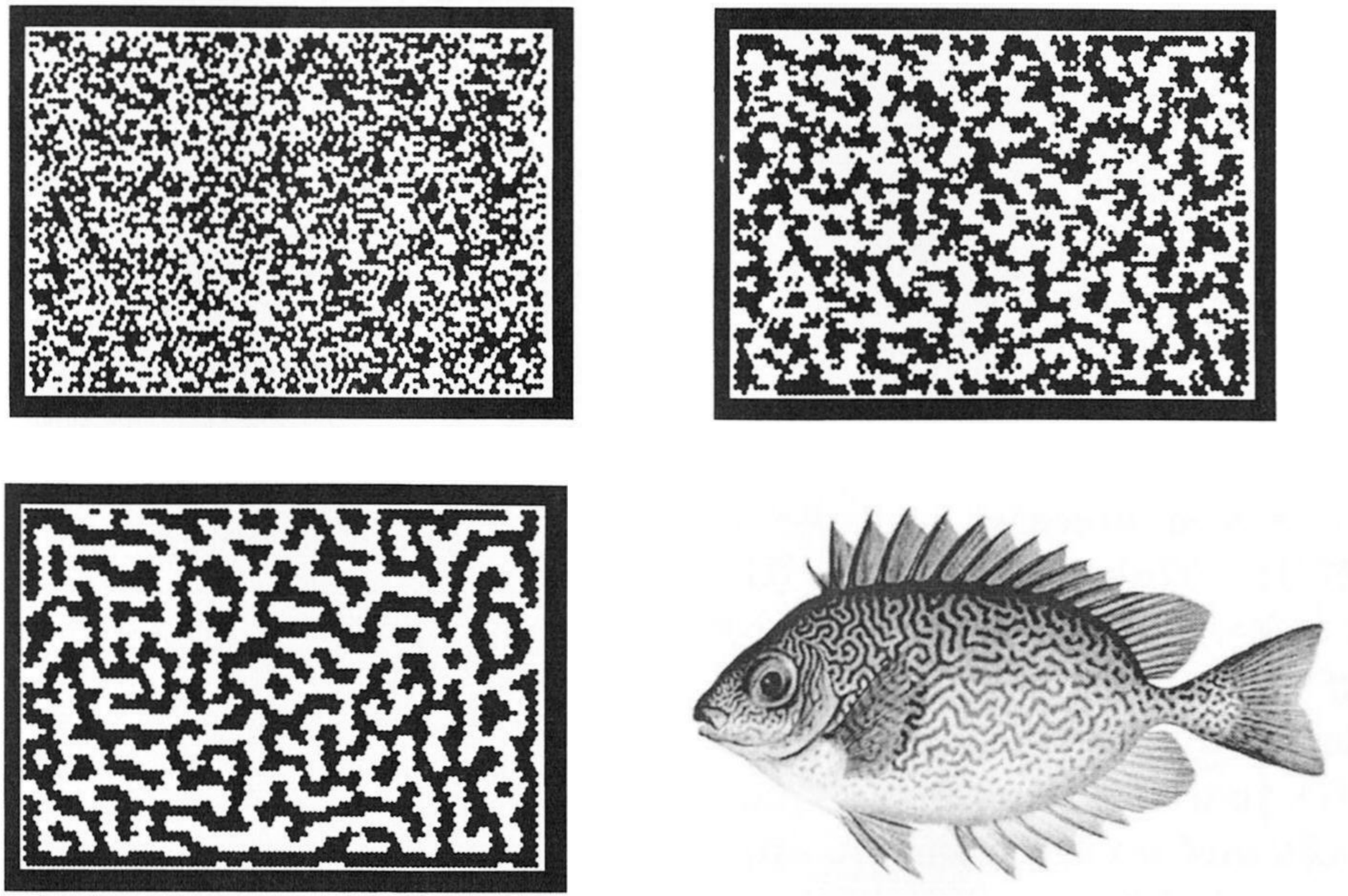
B.
Pattern Formation

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

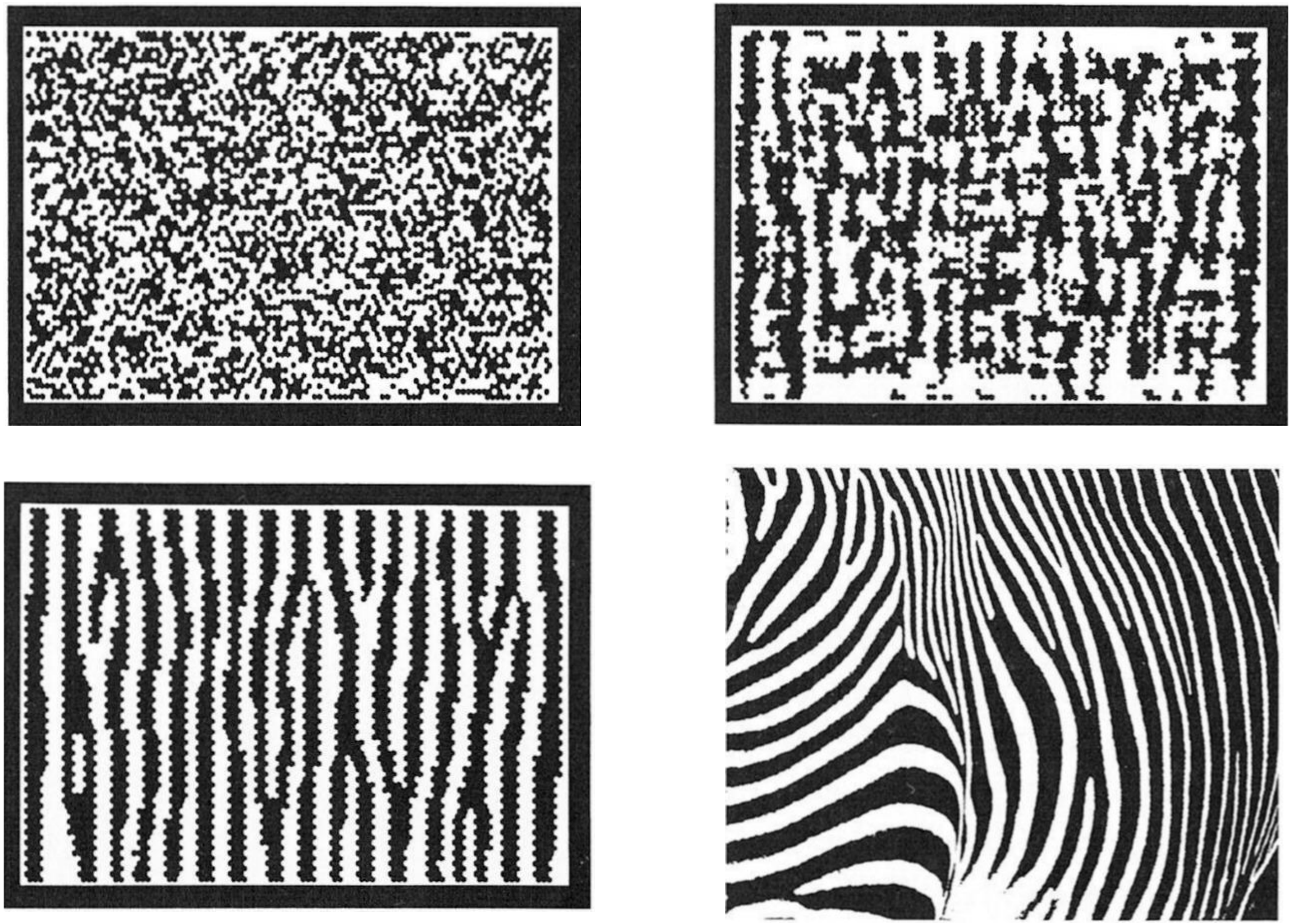
Plecostomus

Vermiculated Rabbit Fish



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

Zebra

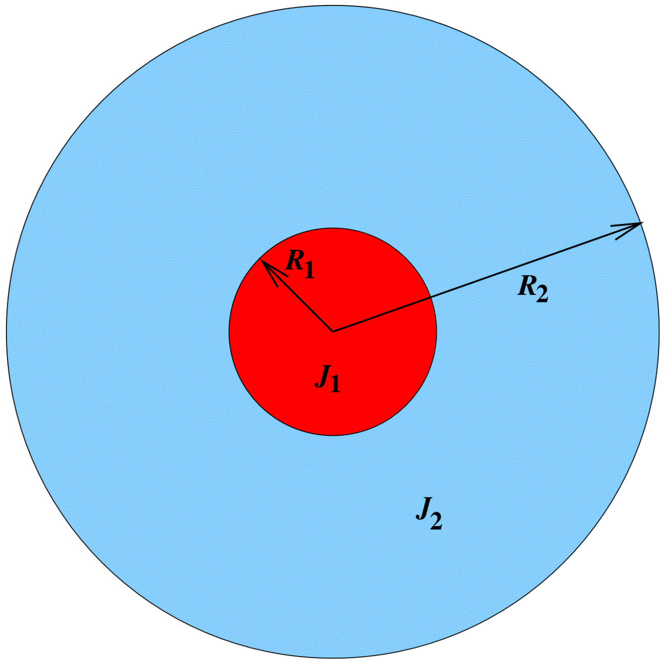


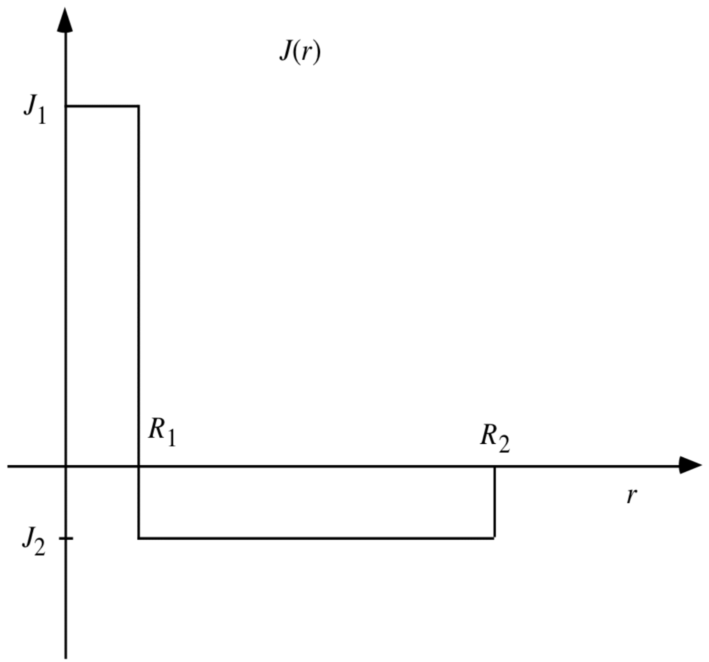
figs. from Camazine & al.: *Self-Org. Biol. Sys.*

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:

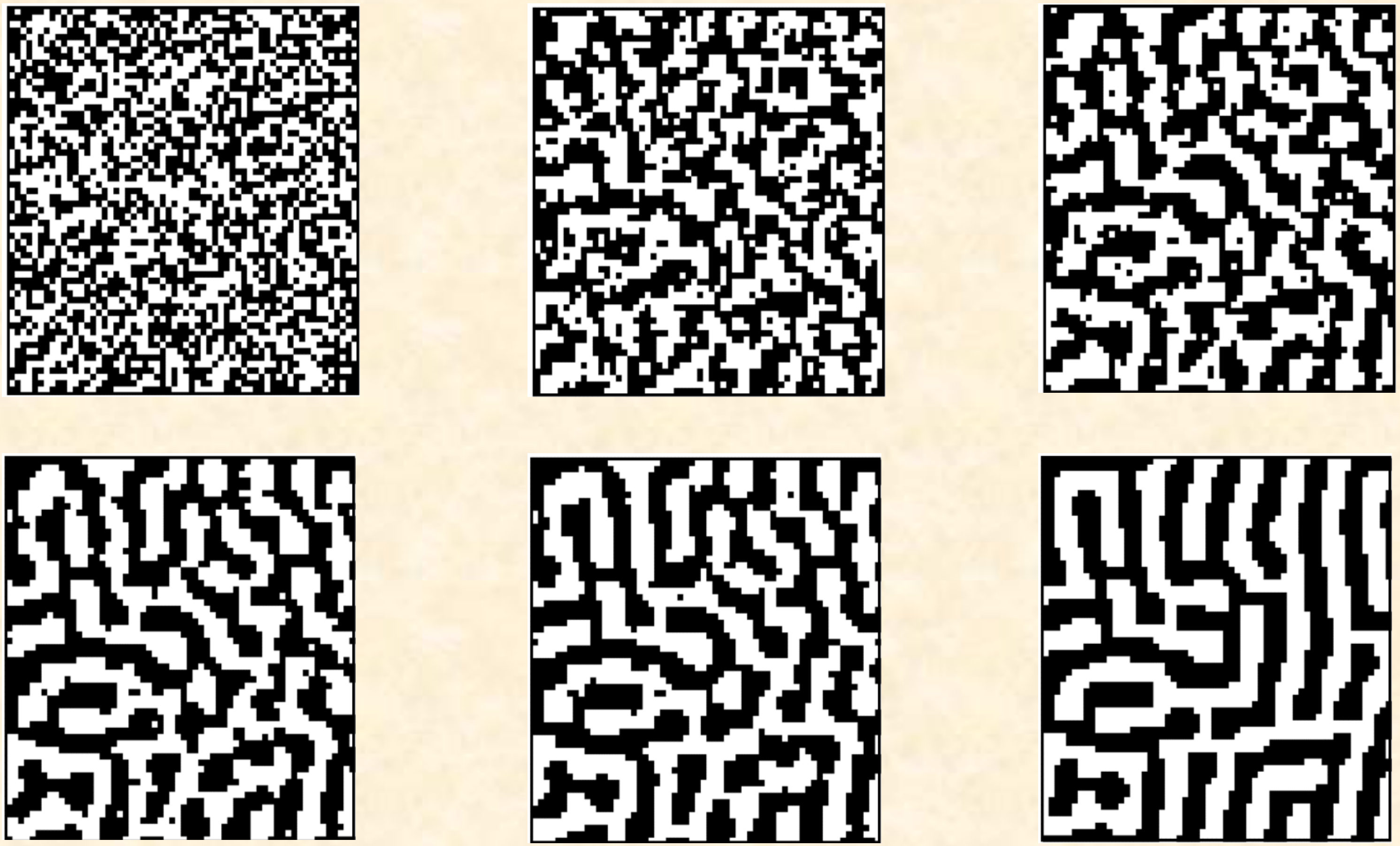
$$s_i(t+1) = \operatorname{sign}\left[h + J_1 \sum_{r_{ij} < R_1} s_j(t) + J_2 \sum_{R_1 \le r_{ij} < R_2} s_j(t)\right]$$

Demonstration of NetLogo Program for Activation/Inhibition Pattern Formation

Run AICA.nlogo

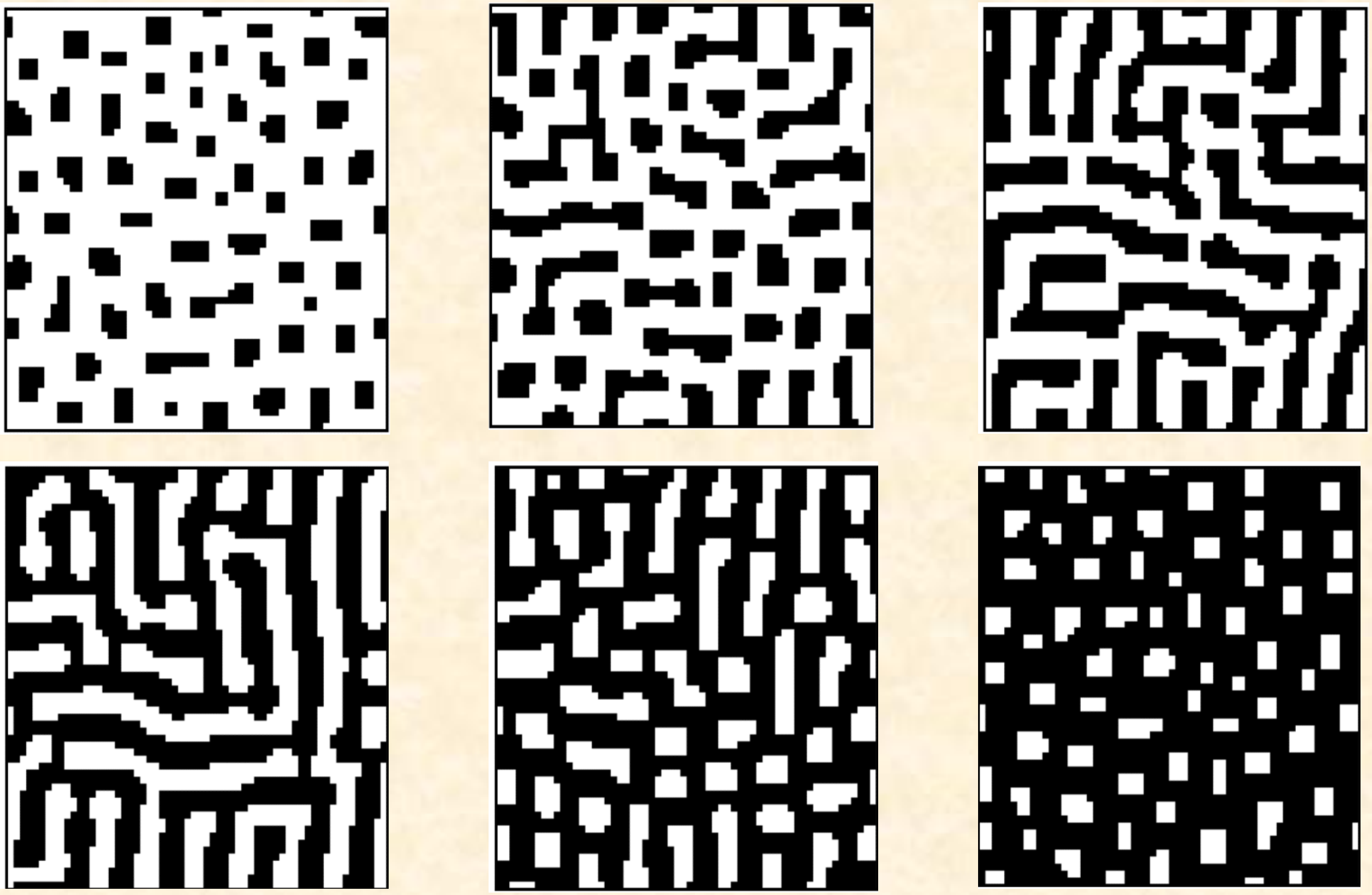
Example

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



figs. from Bar-Yam

Effect of Bias
(h = –6, –3, –1; 1, 3, 6)



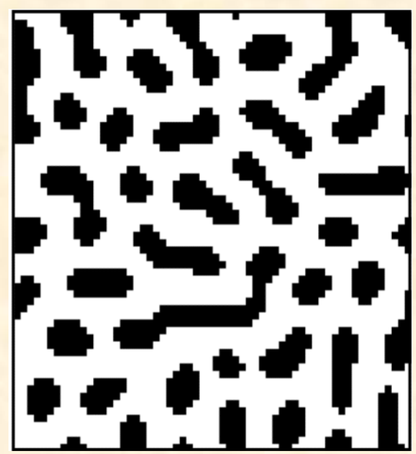
figs. from Bar-Yam

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

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:

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

- 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

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

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

General Reaction-Diffusion System

$$\frac{\partial c_i}{\partial t} = \sum_\alpha k_\alpha \nu_{i\alpha} \left(\prod_{k=1}^{n} c_k^{m_{k\alpha}} \right) - \nabla \cdot \mathbf{j}_i$$

where $\mathbf{j}_i = \vec{\mu}_i c_i - \cancel{\mathbf{div}}\ \mathbf{D}_i c_i$ (flux) **grad**

where k_α = rate constant for reaction α

and $\nu_{i\alpha}$ = stoichiometric coefficient

and $m_{k\alpha}$ = a non-negative integer

and $\vec{\mu}_i$ = drift vector

and $\mathbf{D}_i$ = diffusivity matrix

where $\mathbf{div}\ \mathbf{D}c = \sum_j \mathbf{e}_j \sum_k D_{jk} \partial c / \partial x_k$

Framework for Complexity

- change = source terms + transport terms
- source terms = local coupling
  = interactions local to a small region
- transport terms = spatial coupling
  = interactions with contiguous regions
  = advection + diffusion
  - advection: non-dissipative, time-reversible
  - diffusion: dissipative, irreversible

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

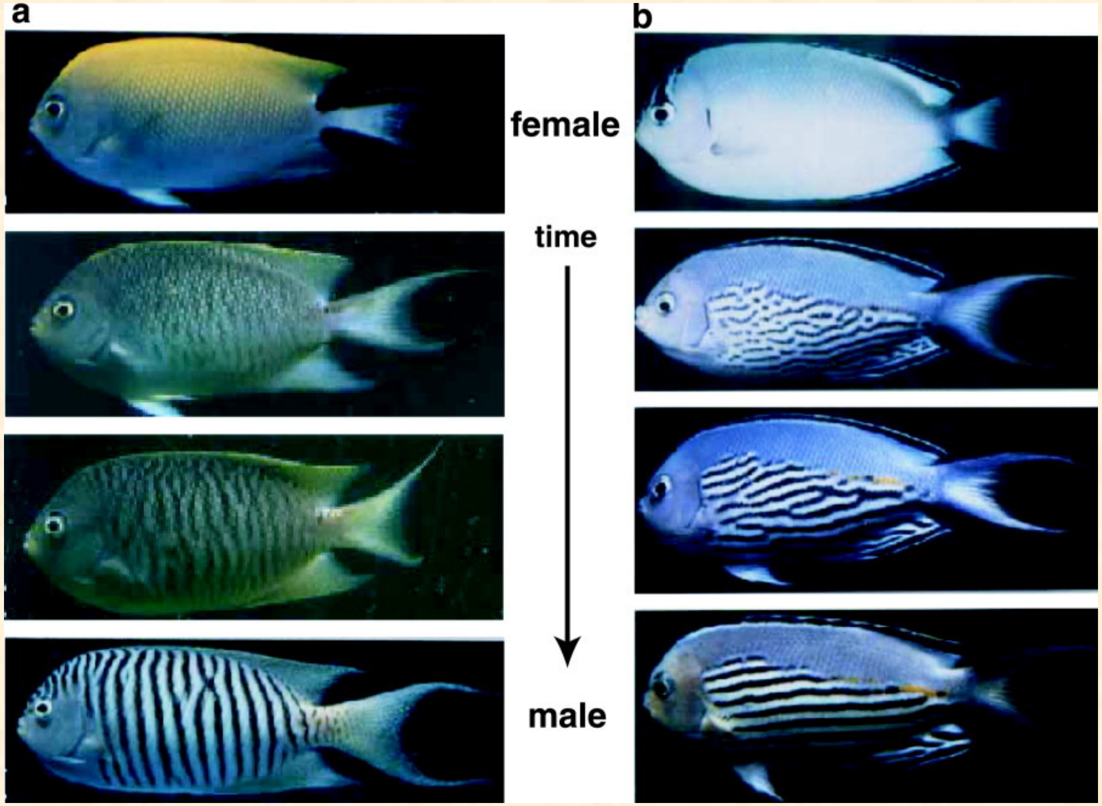
    set activator and inhibitor to 0

Demonstration of NetLogo Program for Activator/Inhibitor Pattern Formation

Run Pattern.nlogo

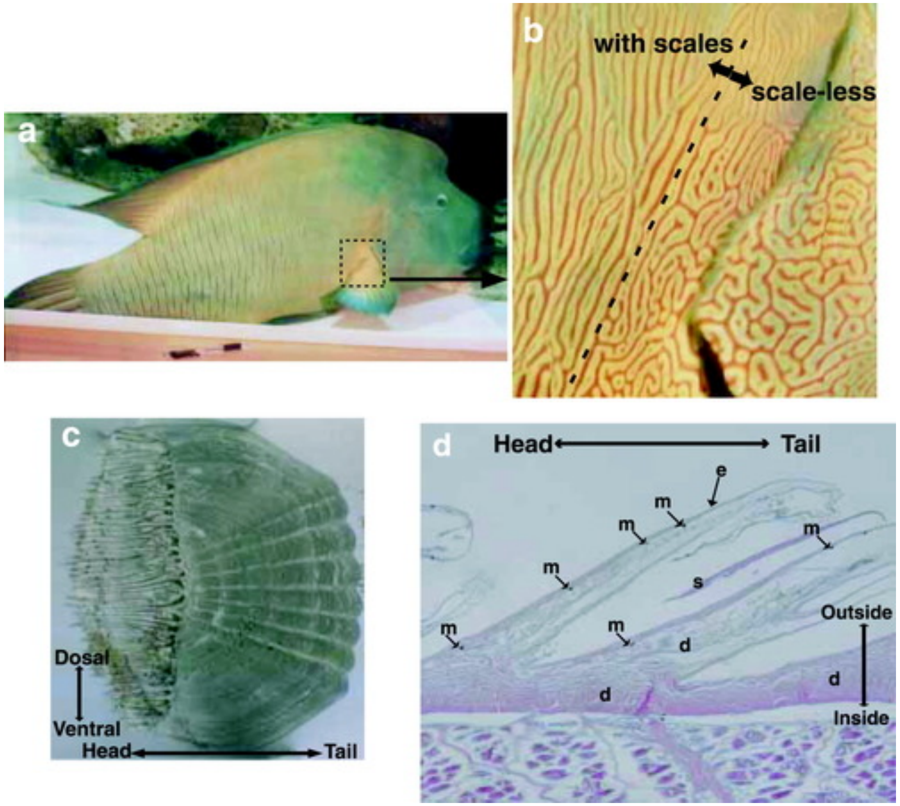
Stripes in two closely related species

Genicanthus melanospilos Genicanthus watanabei



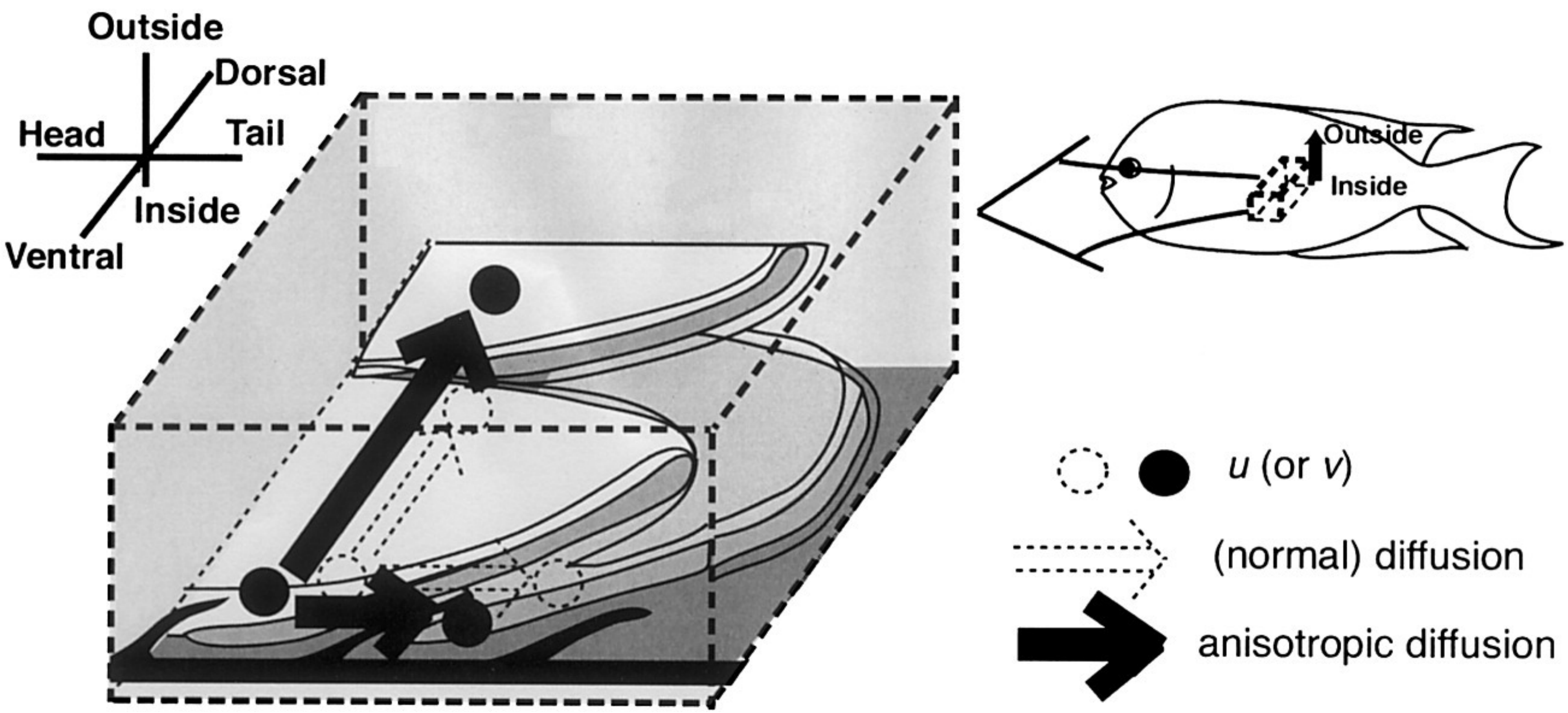
Hiroto Shoji, Atsushi Mochizuki, Yoh Iwasa, Masashi Hirata, Tsuyoshi Watanabe, Syozo Hioki, and Shigeru Kondo. "Origin of Directionality in the Fish Stripe Pattern." *Developmental Dynamics*, Volume: 226, Issue: 4, Pages: 627–633, First published: 28 February 2003, DOI: (10.1002/dvdy.10277)

Scales and directionality in fish stripe pattern



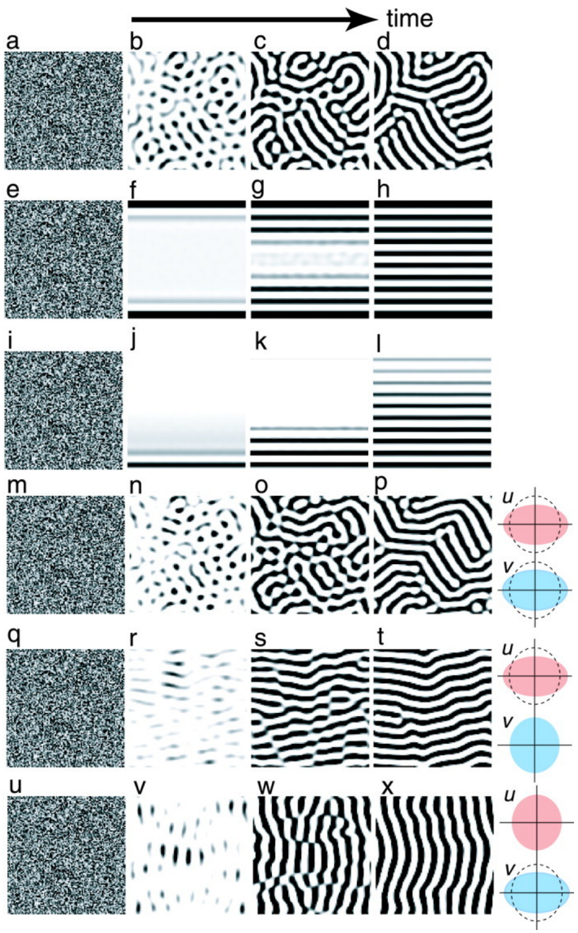
Developmental Dynamics, Volume: 226, Issue: 4, Pages: 627-633, First published: 28 February 2003, DOI: (10.1002/dvdy.10277)

Schematic structure of fish skin



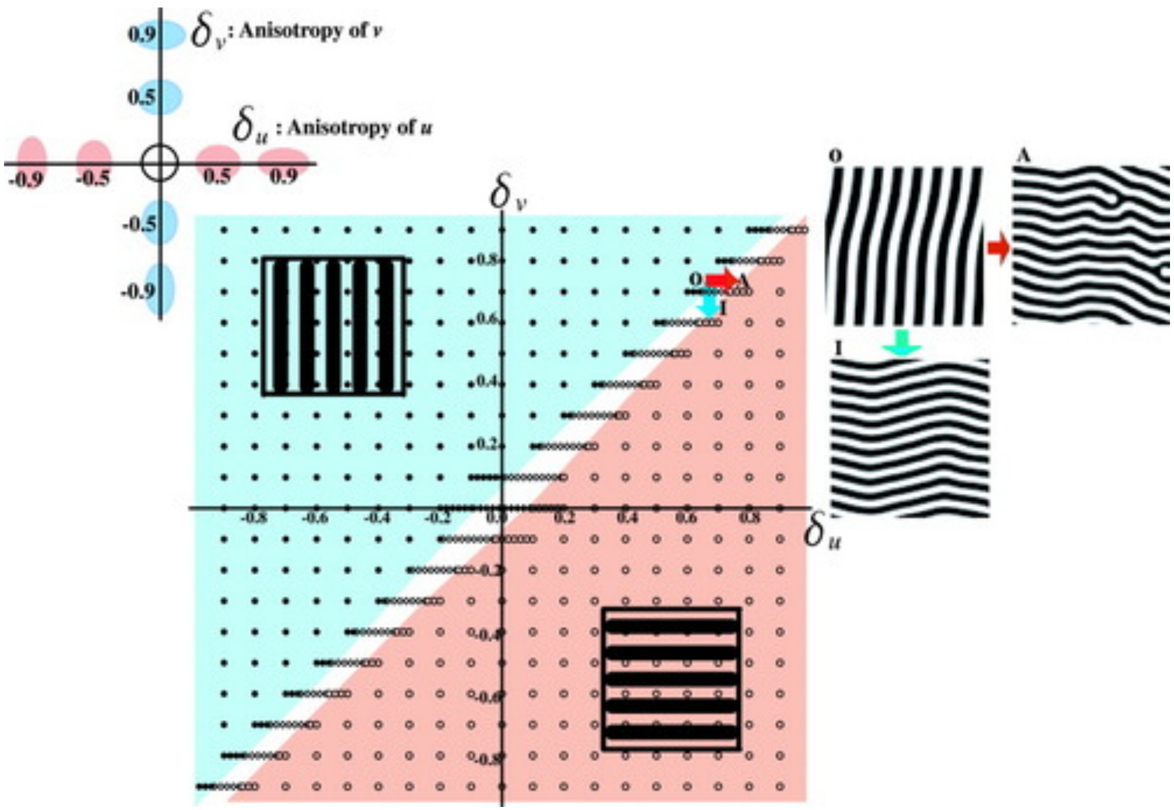
Developmental Dynamics, Volume: 226, Issue: 4, Pages: 627-633, First published: 28 February 2003, DOI: (10.1002/dvdy.10277)

Patterns obtained by computer simulations



- a–d: Pattern formation under a periodic boundary condition.
- e–h: Pattern formation under a boundary condition fixed at zero at the top and bottom and periodic along the sides.
- i–l: Pattern formation from a model that assumes a spatial gradient of parameter B. The value of B changes linearly, taking a maximum value of 1.8 at the top and a minimum value of 1.5 at the bottom of the space.
- m–x: Pattern formation from a model of anisotropic diffusion (model 2).
  The magnitude of anisotropy of these two substances are (m–p) $\delta u = \delta v = 0.5$; (q–t) $\delta u = 0.5$, $\delta v = 0$; (u–x) $\delta u = 0$, $\delta v = 0.5$.

Summary of the direction of stripe patterns obtained by the anisotropic diffusion



Developmental Dynamics, Volume: 226, Issue: 4, Pages: 627-633, First published: 28 February 2003, DOI: (10.1002/dvdy.10277)

Some Conclusions

- Results do not depend on form of reaction or form of anisotropy
- Resulting stripes tend to run parallel to most-diffusive direction of activator, and perpendicular to that of inhibitor
- The substance with greater anisotropy decides the direction of resulting stripes
- A pattern with no directional stripes only occurs when the values of anisotropy are almost identical

Continuous-time Activator-Inhibitor System

- Activator *A* and inhibitor *I* may diffuse at different rates in *x* and *y* directions
- Cell becomes more active if activator + bias exceeds inhibitor
- Otherwise, less active
- *A* and *I* are limited to [0, 100] (depletion/saturation)

$$\frac{\partial A}{\partial t} = d_{\mathrm{Ax}} \frac{\partial^2 A}{\partial x^2} + d_{\mathrm{Ay}} \frac{\partial^2 A}{\partial y^2} + k_A f(A + B, I)$$

$$\frac{\partial I}{\partial t} = d_{\mathrm{Ix}} \frac{\partial^2 I}{\partial x^2} + d_{\mathrm{Iy}} \frac{\partial^2 I}{\partial y^2} + k_I f(A + B, I)$$

Demonstration of NetLogo Program for Activator/Inhibitor Pattern Formation with Continuous State Change

Run Activator-Inhibitor.nlogo

Turing Patterns

- Alan Turing studied the mathematics of reaction-diffusion systems
- Turing, A. (1952). The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society* **B 237**: 37–72.
- The resulting patterns are known as *Turing patterns*

Some of Turing's Results

- Homogeneous steady state defined by $f_A(A_0, I_0) = 0 = f_I(A_0, I_0)$
- Steady state is stable with respect to very long wavelength fluctuations
- Steady state is unstable with respect to shorter wavelength fluctuations
- These conditions place constraints on reaction parameters, defining "Turing space"
- Relative position of steady state to limits is important

Observations

- With local activation and lateral inhibition
- And with a random initial state
- You can expect to get Turing patterns
- These are stationary states (dynamic equilibria)
- Macroscopically, Class I behavior
  - Microscopically, may be class III

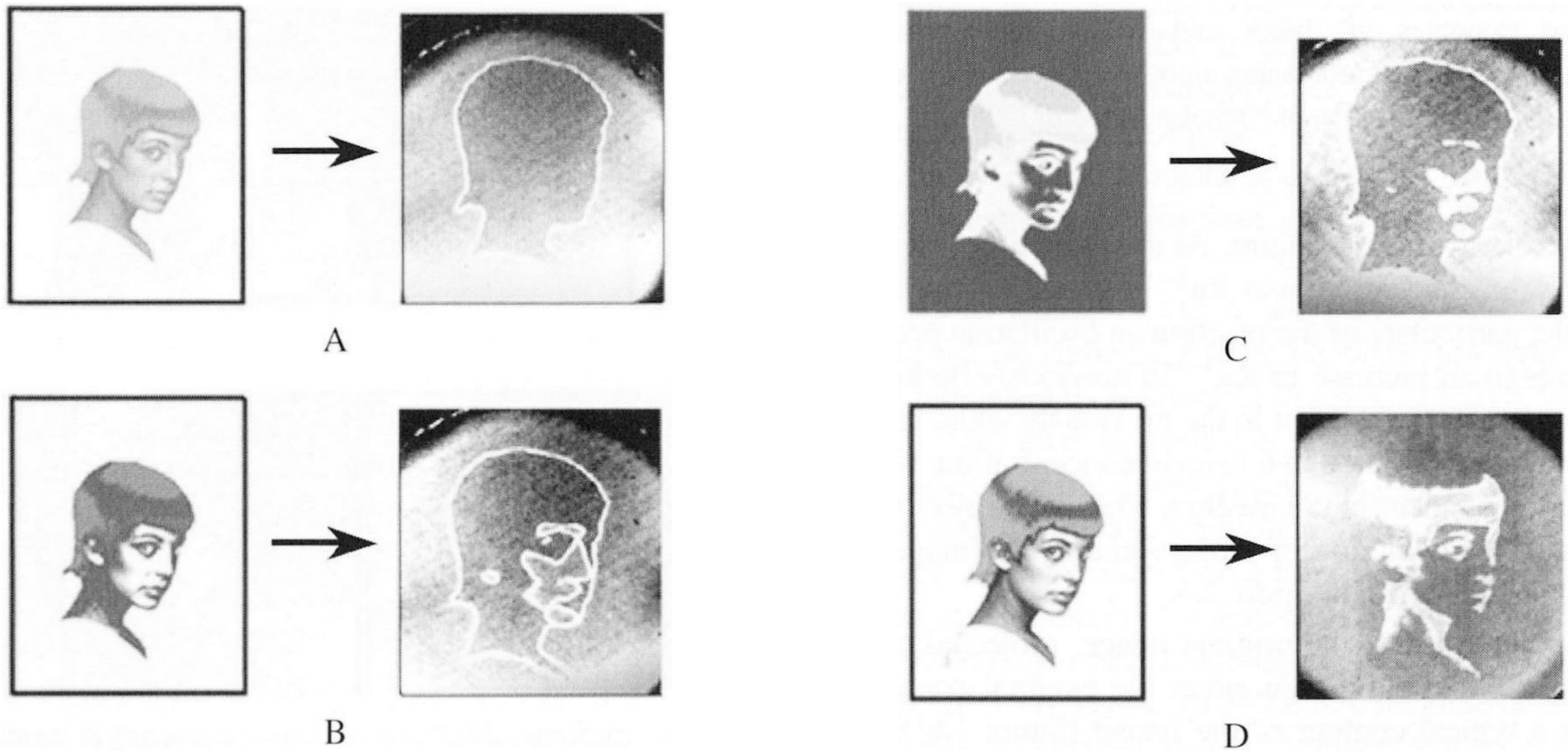
A Key Element of Self-Organization

- 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

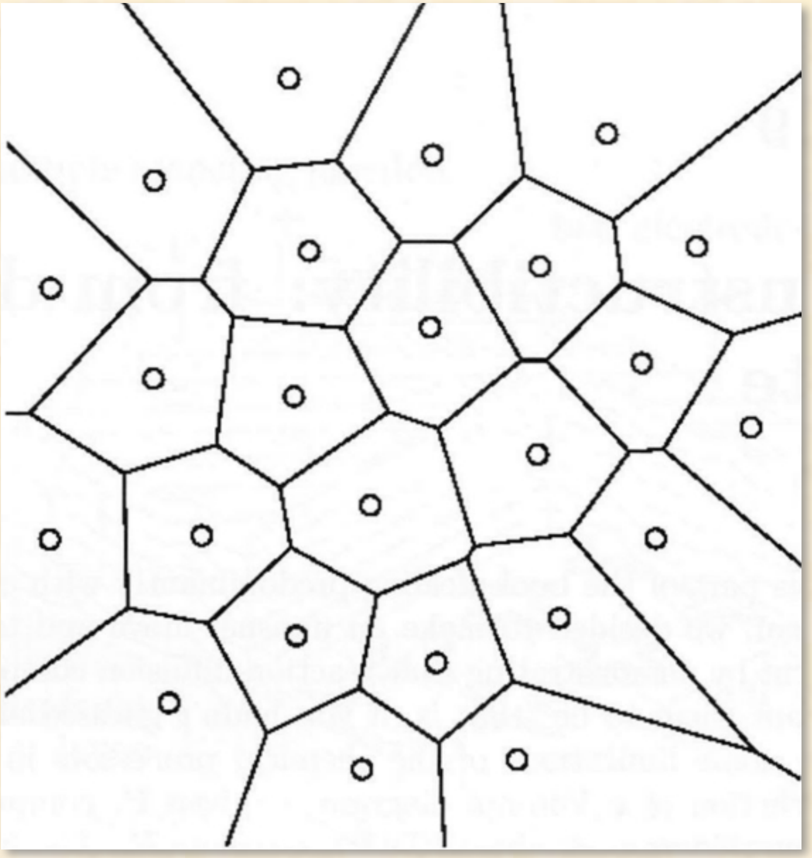
- Has been used for image processing
  - diffusion ⇒ noise filtering
  - reaction ⇒ contrast enhancement
- Depending on parameters, RD computing can:
  - restore broken contours
  - detect edges
  - improve contrast

Image Processing in BZ Medium



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

Voronoi Diagrams



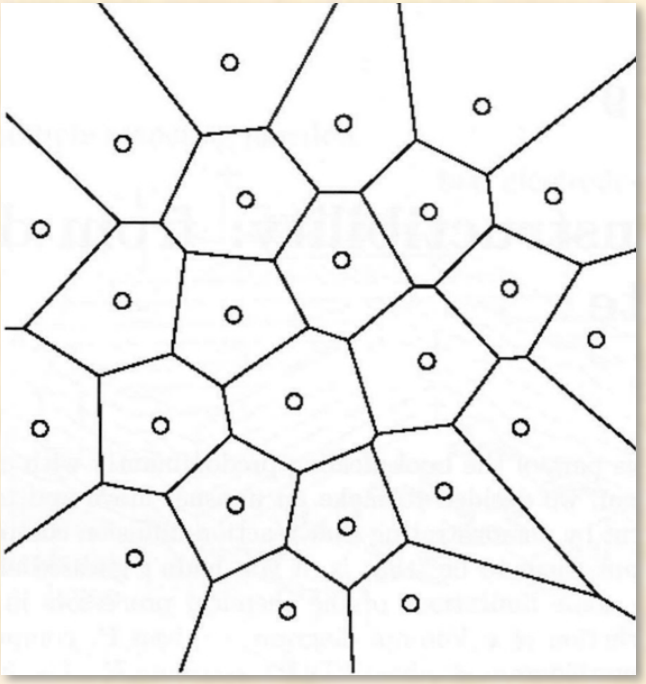
- Given a set of generating points:
- Construct a polygon around each generating point of set, so all points in a polygon are closer to its generating point than to any other generating points.

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



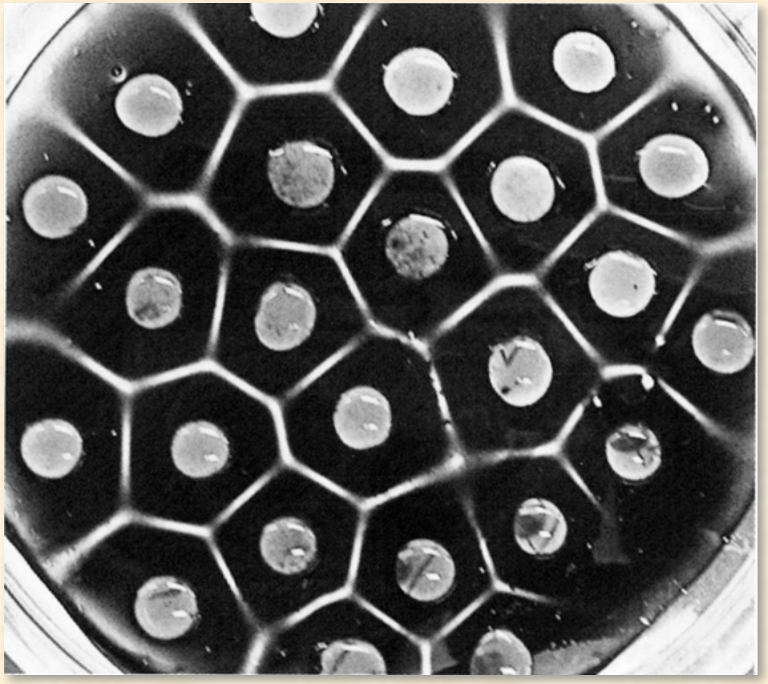


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Mixed Cell Voronoi Diagram

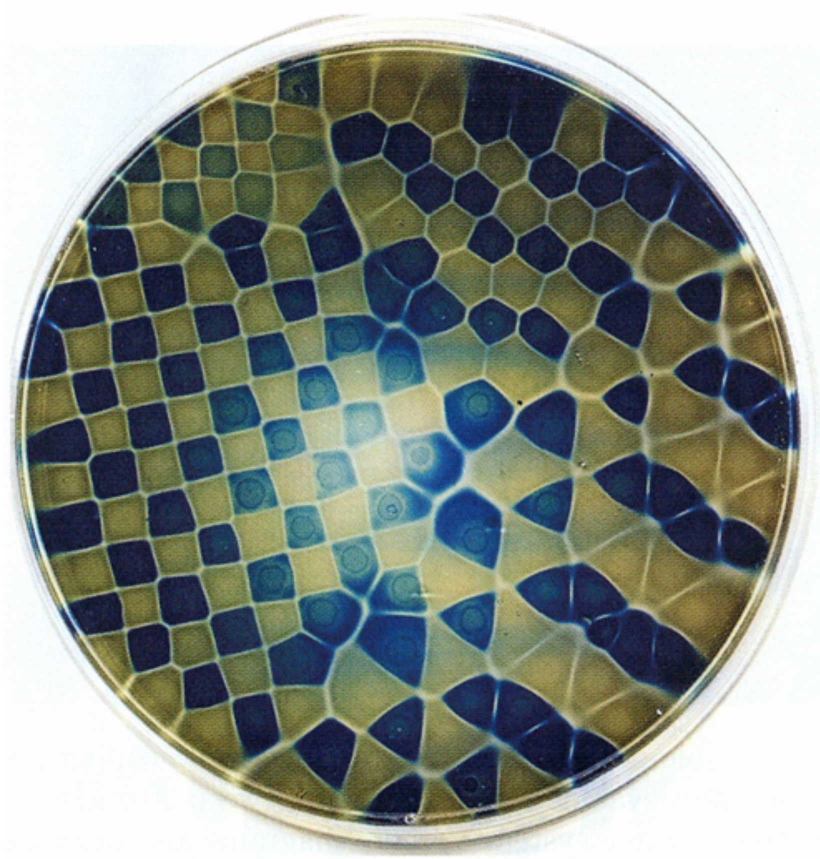


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Path Planning via BZ medium: No Obstacles

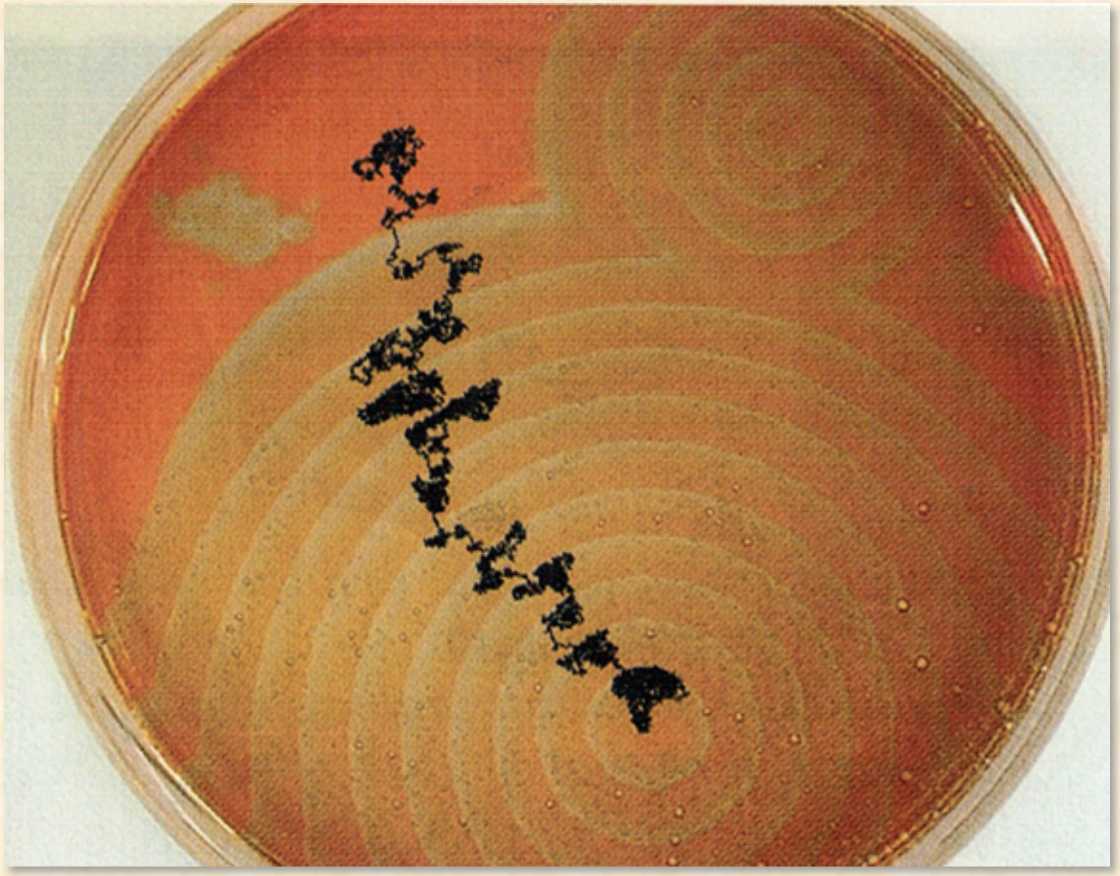


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Path Planning via BZ medium: Circular Obstacles

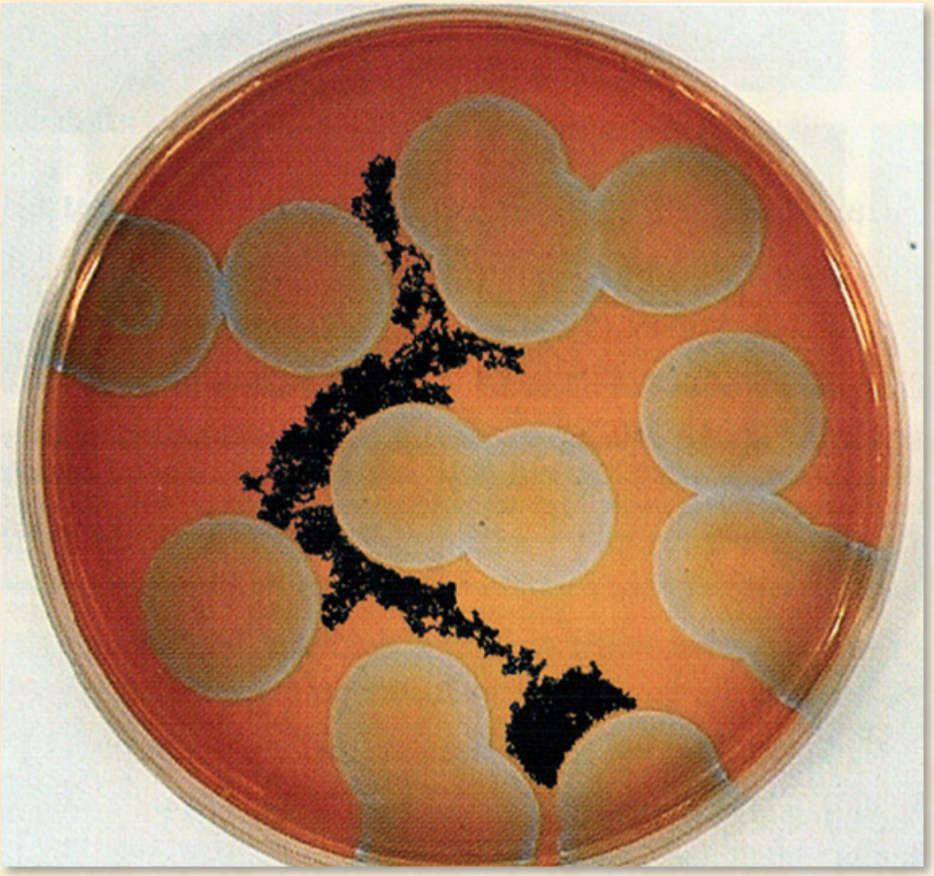


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Mobile Robot with Onboard Chemical Reactor

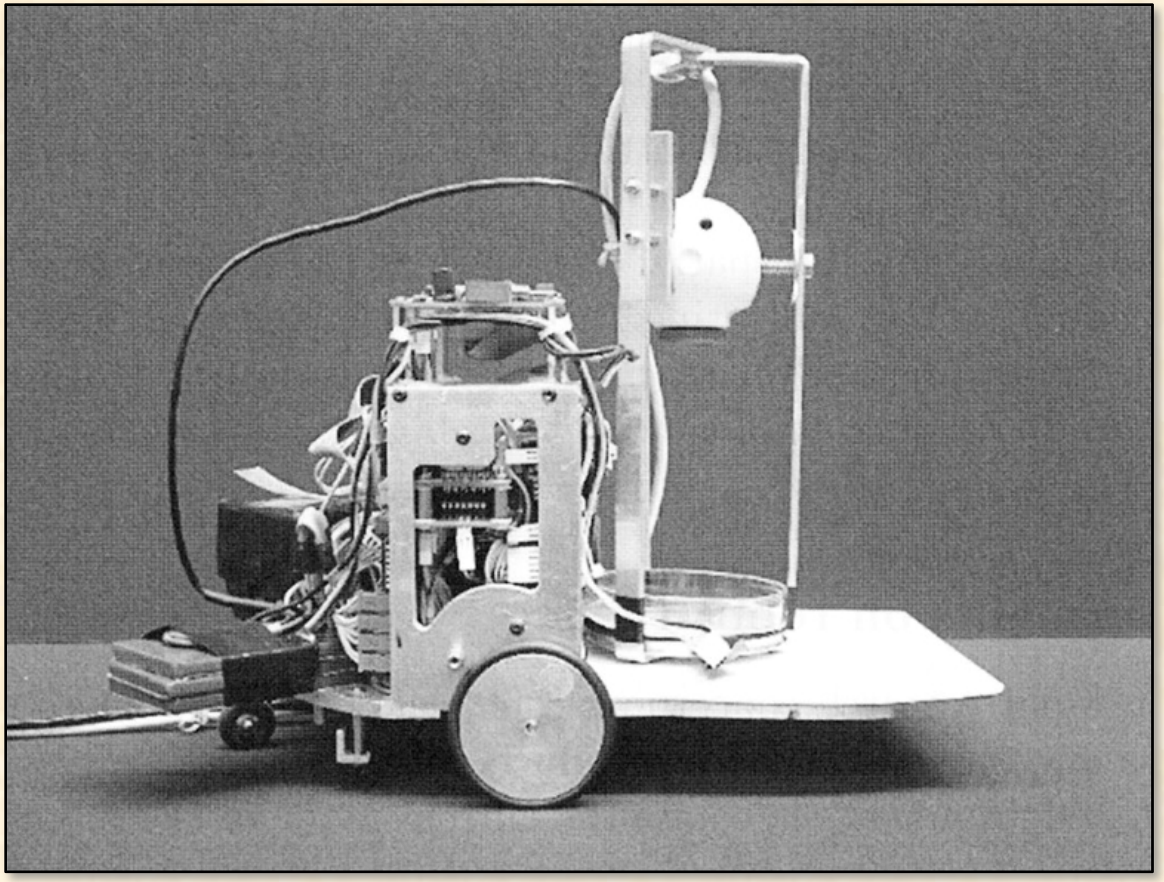


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Actual Path: Pd Processor

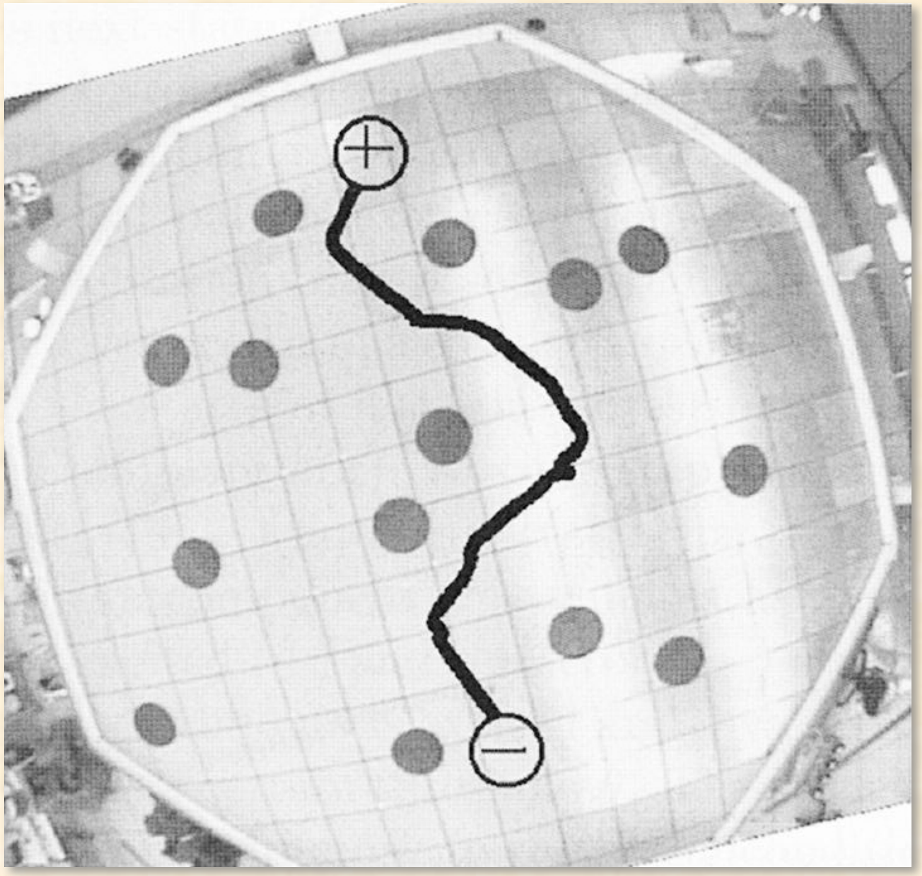


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Actual Path: Pd Processor

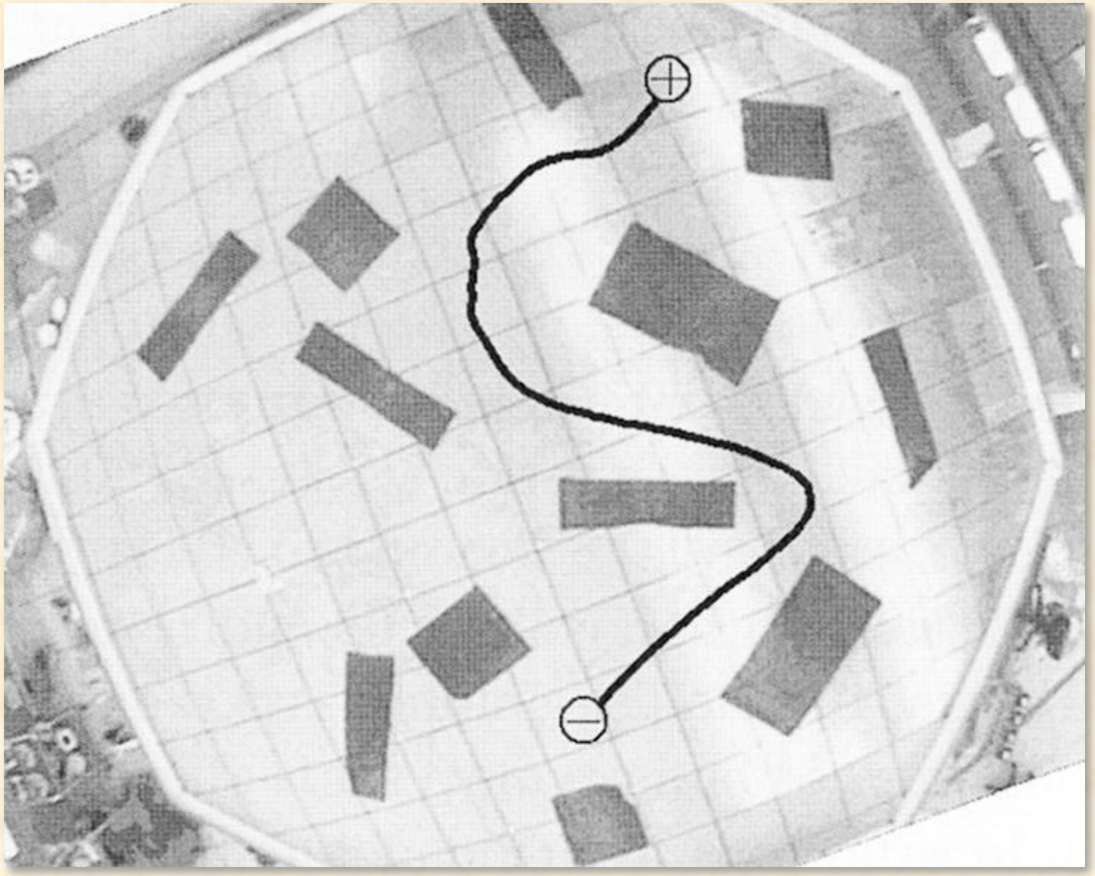


Image < Adamatzky & al., *Reaction-Diffusion Computers*

Actual Path: BZ Processor

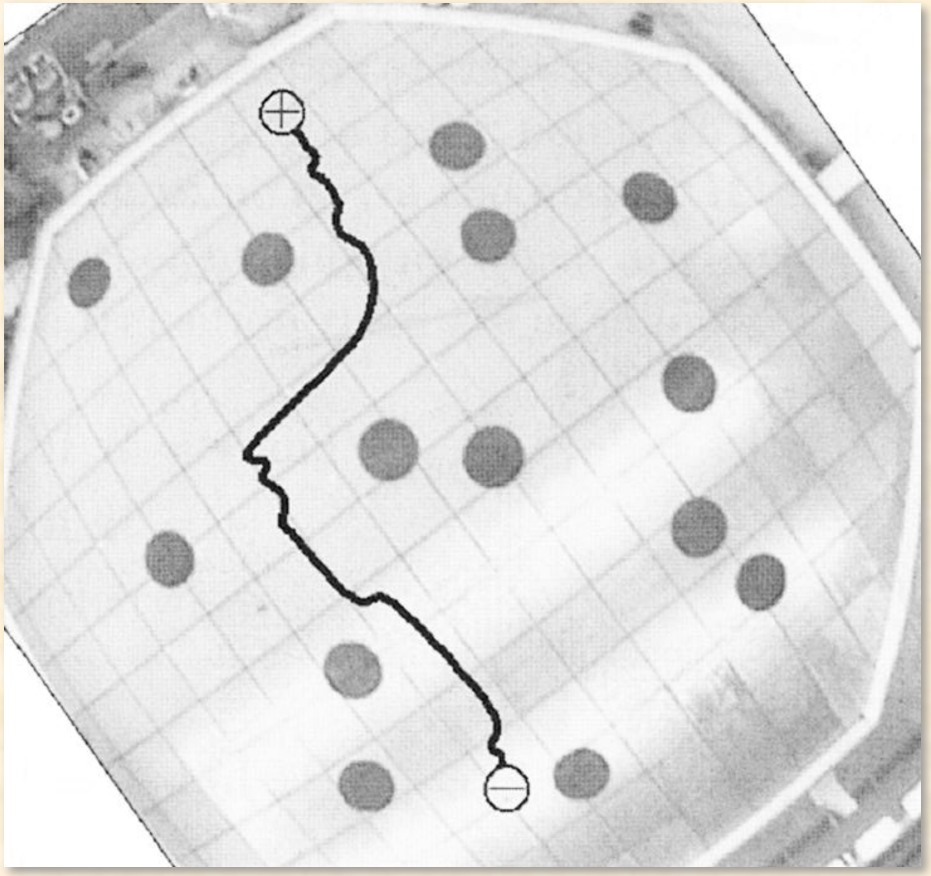


Image < Adamatzky & al., *Reaction-Diffusion Computers*

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1. Adamatzky, Adam. *Computing in Nonlinear Media and Automata Collectives*. Bristol: Inst. of Physics Publ., 2001.
2. Adamatzky, Adam, De Lacy Costello, Ben, & Asai, Tetsuya. *Reaction Diffusion Computers*. Amsterdam: Elsevier, 2005.

Project 2 is assigned!

Due Feb. 21