Excitable Media

Kara DeSouza

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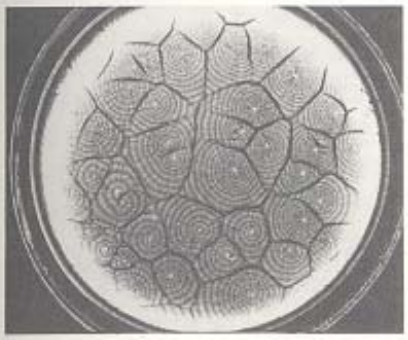
University of Nevada, Reno

Slime Mold et al

- Slime mold (D. discoideum)
- E. coli and Salmonella
  - Form concentric rings or wave patterns as part of development/reproduction
- Myxobacteria
  - Form clusters as part of feeding behavior

- All these systems are only acting/reacting according to their chemical surround, and this leads to self-organization
  - No need for higher order or top-down processes

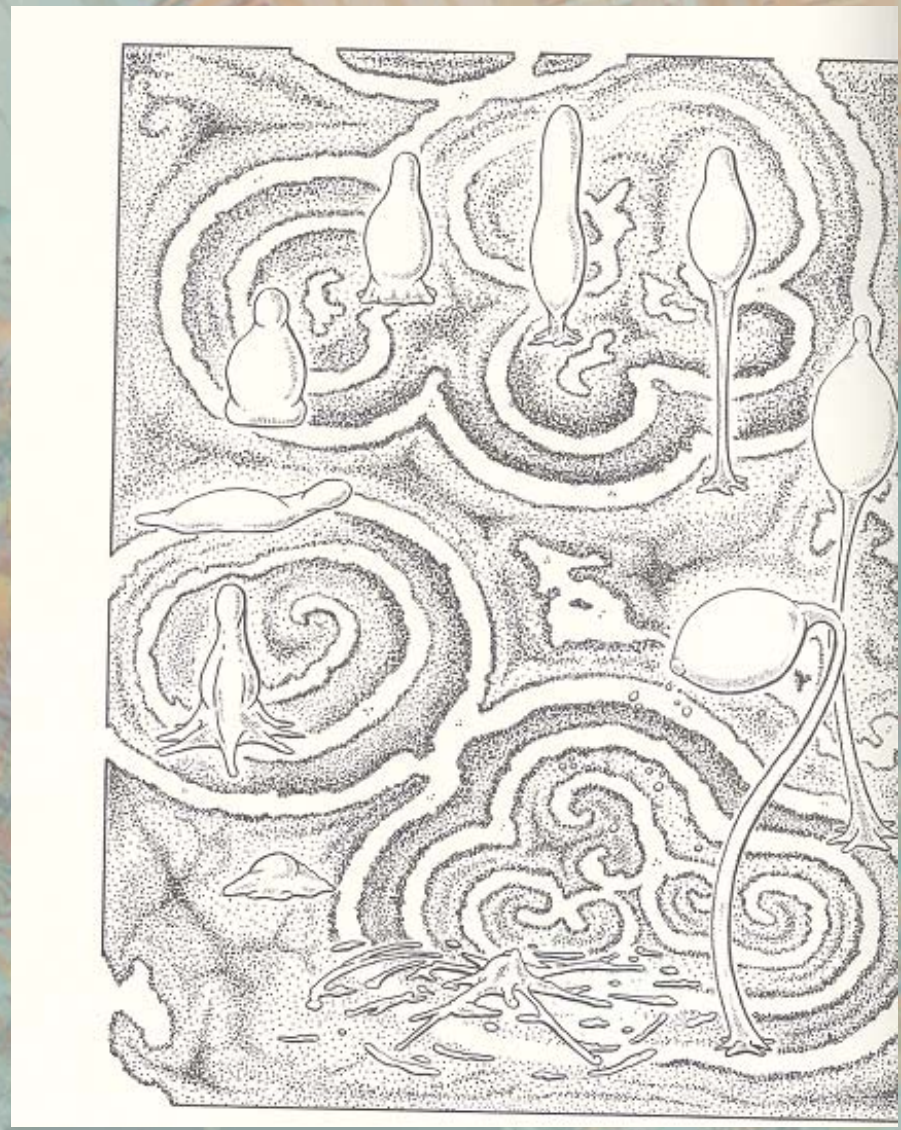
a



b

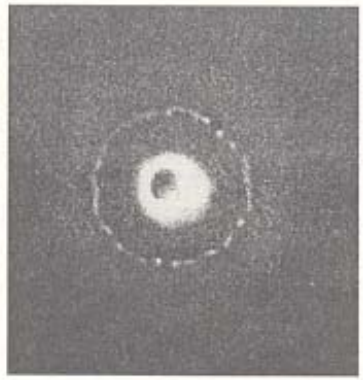
c

Figure 8.2 Aggregation of *Dictyostelium discoideum* on an agar plate (5 cm in diameter) reveals the formation of spiral waves of cAMP that induce (a) cell movement, (b) the onset of cell streaming, and (c) well-developed stream morphology. The photos were taken approximately 30 min apart. Using dark-field photography, the position of the cAMP waves in (a) and (b) can be inferred from the differential light scattering responses of elongated (moving) and rounded (stationary) cells. In (b), each spiral wave defines an approximate domain from which it has begun recruiting cells. After another 30 min (c) each domain is clearly separated from its neighbors. Inside each domain the cells have begun to form streams as they move toward the center. (Photographs courtesy of P.C. Newell)



- Lifecycles of Slime Amoeba
  - When food is present they eat
  - When food is gone they enter developmental/reproductive stage
  - Amoeba follow the cAMP gradient around the dish, forming patterns as they go.
  - Amoeba can undergo morphogenesis and differentiate into the types of cells needed to form slug and then stalk
  - Some cells which undergo development first may be responsible for setting off the cAMP reaction across the entire group

a



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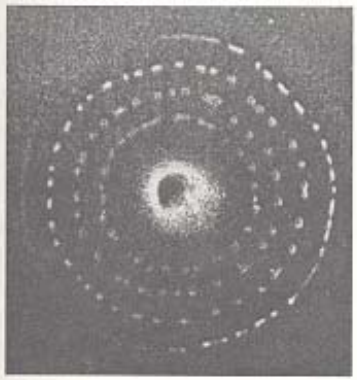

c

Figure 8.4 Evolution of an aggregation pattern of *Salmonella typhimurium* grown on agar: time after inoculation is (a) 38 h, (b) 40 h, and (c) 46 h. (Reproduced from Woodward et al. 1995, figure 2; used with permission)

Salmonella and Ecoli form complex patterns that are static rather than dynamic

How do they do this?

- During development period, amoeba secrete cAMP
- The more cAMP released, the more cAMP that the amoeba will produce thanks to a positive feedback function
- The “brakes” for this reaction is the fact that cAMP also desensitizes the cell to the presence of cAMP

- Myxobacteria, likened to hunting in a wolf pack, travel in clusters, and attack food sources enmasse

- Slime molds (swirling pattern) may form the fruiting bodies, to make the dispersal of offspring go farther, particularly away from area where food source has already been depleted.

- Spiral waves, as opposed to concentric rings, etc, have a higher frequency of rotation than other periodic waves, and predominate the immediate area, pushing any other waves out of the way. This leads to higher concentration of amoeba in one area, and therefore more amoeba to form a larger fruiting body….

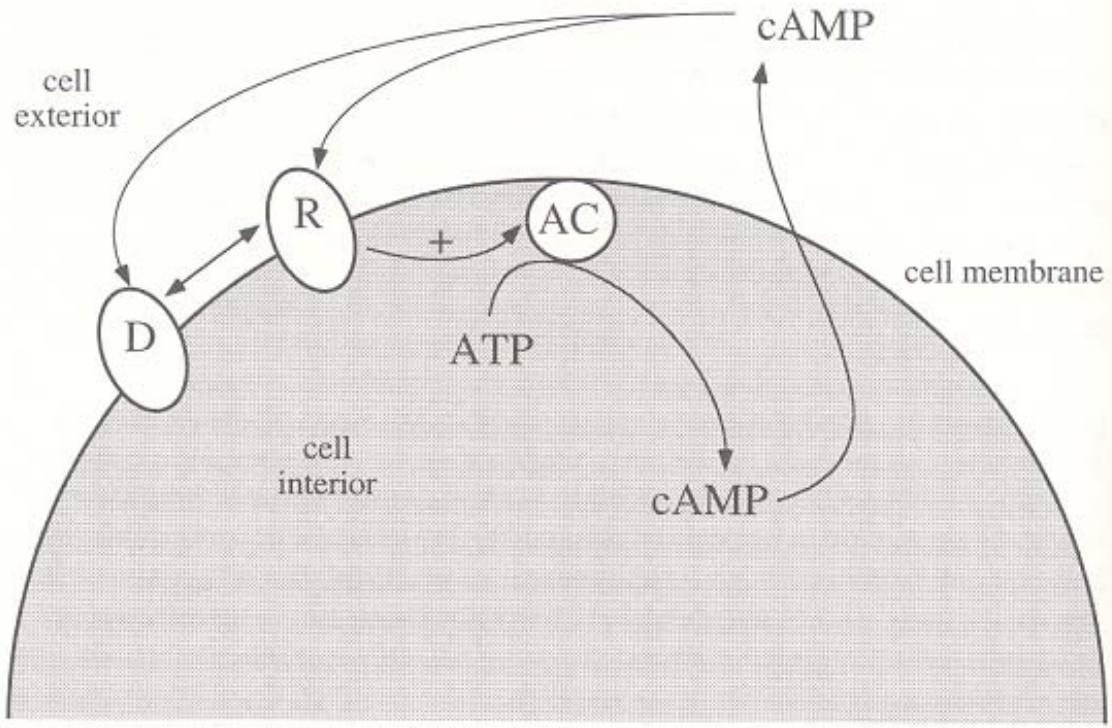

Figure 8.5 Schematic diagram of the mechanisms underlying control of cAMP secretion in *Dictyostelium* indicating that binding of cAMP to its receptor (R) leads to the activation of adenylate cyclase (AC) and subsequent production of further cAMP that is transported out of the cell. This positive feedback loop is indicated by a "+". In the negative feedback loop extracellular cAMP inactivates the cAMP receptor, converting it to the inactive form (D), thus leading to a decrease in further cAMP production.

How do circles/waves form?

- Amoeba move in the direction of increased cAMP, thus “following” the cAMP gradient around the dish.
  - Leads to clumping at core of swirl or circle
- Amoeba gradient (?) remains virtually stable, because…
  - However, amoeba move at 1/10th the speed of the cAMP waves,

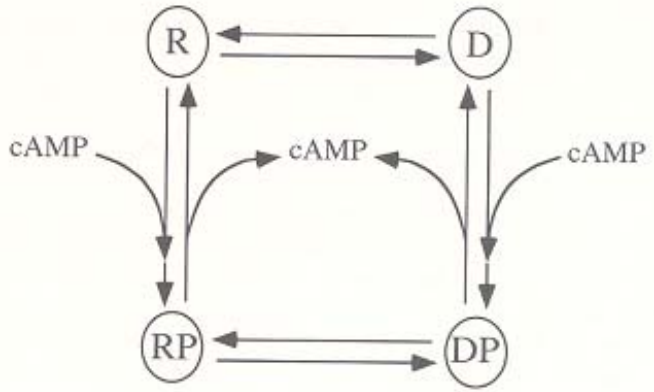

Figure 8.6 The cAMP receptor assumed to exist in four states: R, the active state with no cAMP bound; D, the inactive state with no cAMP bound; RP and DP, the active and inactive states, respectively, with cAMP bound. State RP combines with and activates AC.

ρ = total fraction of receptors in active form,
β = nondimensional intracellular concentration of cAMP,
γ = nondimensional extracellular concentration of cAMP.

It is assumed that extracellular cAMP is degraded by a phosphodiesterase at a rate equal to $k_e\gamma$ and secreted by the cell at a rate $(k_t/h)\beta$, and diffuses with diffusion coefficient d. The constant parameter h is the ratio of the extracellular to the intracellular volume. Thus, the equation for the conservation of extracellular cAMP is, in English and in mathematical notation,

rate of change of extracellular cAMP = secretion by cells – degradation,

$$\frac{\partial \gamma}{\partial t} = \frac{k_t}{h}\beta - k_e\gamma.$$

Similarly, the equation for the rate of change of intracellular cAMP is

rate of change of intracellular cAMP = synthesis by cells – secretion – degradation,

$$\frac{\partial \beta}{\partial t} = \Phi(\rho, \gamma) - k_t\beta - k_i\beta.$$

This is the negative feedback step.

The final equation in this model describes the rate at which receptors are converted to the active form:

rate of change of active form of receptor = resensitization of receptor – desensitization of receptor,

$$\frac{\partial \rho}{\partial t} = f_2(\gamma)(1-\rho) - f_1(\gamma)\rho.$$

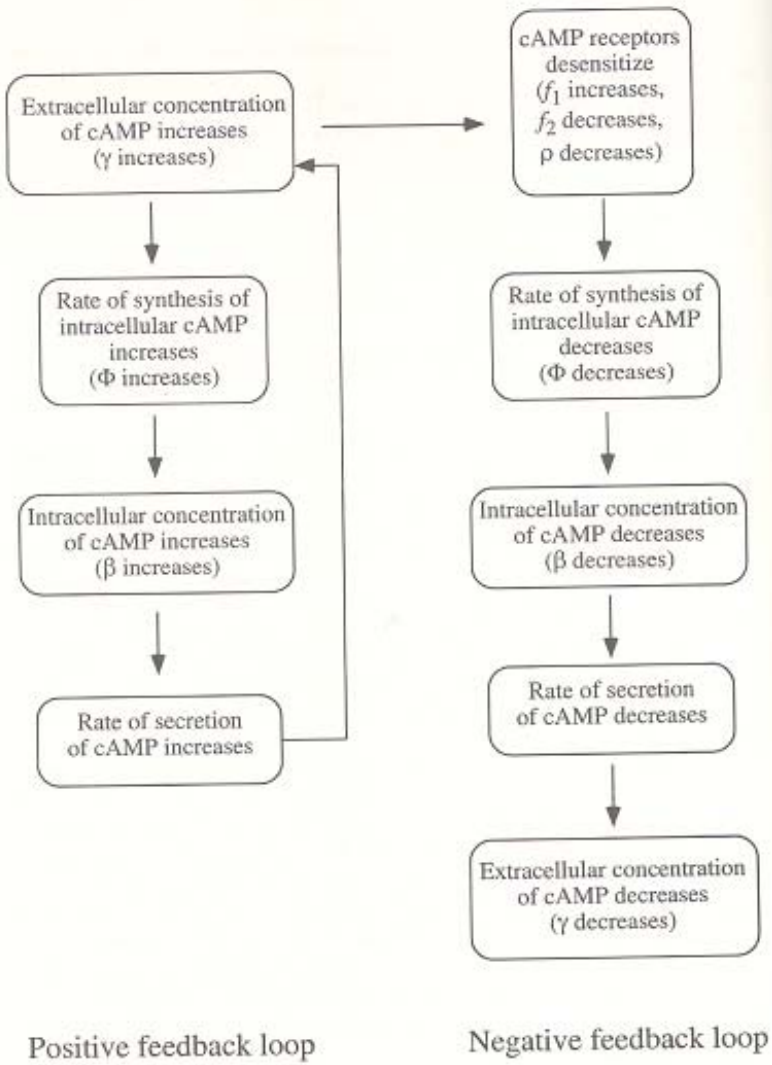

Figure 8.7 Positive and negative feedback loops are involved in the control of cAMP secretion.

Cellular Automaton Describing the Formation of Spatially Ordered Structures in Chemical Systems

Gerhardt & Schuster, 1989

Why Cellular Automaton as Model?

- CA are discrete dynamical systems
  - Difficult to describe with traditional mathematics, but easier to model with digital (computing) technology
  - G&S investigate a chemical oscillator that produces ordered structures from local interactions among the catalytic units
  - Sound Familiar?
    - More or less what CA are known for…

Palladium Oxidation for the Non-Metallurgist

- Palladium crystallites are on a zeolite matrix
- They're absorbing CO and O
- They produce CO_2 under these conditions, but at varying rates depending on the quantity of CO on the crystallites
- A cyclical oxidation-reduction mechanism is proposed and supported by finding both palladium and palladiumoxide in the mixture at the same time.

What this means to the model

- Palladium + a few neighbors = Palladiumoxidization Party!
- Process of palladium transitioning to a palladiumoxide phase is known as “infection”
- Pure Palladium phase is “healthy”
- A complete palladiumoxide crystallite is “ill”

- Each cell in the CA representation has either four neighbors (n) and eight neighbors (m) (depending on CA model) from which it gains its health status
  - A cell's likelihood to get ill depends on it's sick and infected neighbors and can be manipulated by the parameters k1 and k2
  - Becomes increasingly infected due to g (the constant of infection) plus the average of infected neighbors of the cell
  - A fully infected (ill) cell reverts to a fully healthy cell in one step
- AKA The Hodge Podge Machine

Conclusion

- So, what are excitable media?
  - Media which undergo a state change when a stimulus reaches a certain threshold, and which undergo a refractory period that disallows an autocatalytic response from growing out of control
  - Two or more compounds that can dissociate and recombine under the influence of a catalyst

- And oscillatory reactions?
  - Are composed of simultaneous positive and negative feedback reactions that set up the oscillation