Abstract

We present examples of quantitative (or potentially so) models of a variety of natural and social phenomena, loosely aiming to form analogies (where useful) between the cells of an organism and the individuals of a society. We argue for the philosophical importance of understanding pattern-forming systems, ranging from how the bodyplan of multicellular organisms might be encoded to a few instances of how organized groups of individuals might arise.

Tags: sociobiology, mathematical biology, computer modelling

1 Motivation

1.1 Why pattern recognition?

As humans, one of (if not the) first task(s) in controlling the world around us is to categorize the things and processes that comprise it. To do this, we define certain patterns - how many legs does each animal have? Which people are dangerous? - that are followed by most members of a category. (How we manage to reason based on criteria such as 'most but not all' is another topic.)

In being able to recognize (and somewhat articulate) what counts as a threat, a potential dinner, or whatever other category of object we may be interested in, we presumably derive a boost to our reproductive success that outweighs the cost of maintaining such mental facilities. Further, with the existence of such sophisticated knowledge bases and tools for analysis nowadays, we can derive societal benefit (or at least, some form of fulfilment) by analyzing how a given pattern arises.

The tools for analysis are not even strictly necessary, if all we are really trying to do is to gain memetic success - where a meme is the unit of cultural heredity, analogous to a gene, spread by teaching and story-telling. In theory, having just enough insight (or sensory exploitation) to make our packet of information go viral suffices. (Or this form of success might be negligable as a source of cultural evolution compared to raising children in our own image. Without quantification, it is hard to tell.)

In practice, we gain insight from observation. Preferably, reproducible observation - hence the utility of analysis and other culturally-inherited tools. Nature in particular, being the ecological context(s) in which humans inextricably exist, is (subjectively) a very rich and observable source of sharable ideas.

1.2 Why pattern formation?

Life, however, is chaotic. It fits the (a) mathematical definition - that slight variations in the input parameters of a given scenario change how it unfolds in an ever-escalating way, as one thing leads to another. Consider (as a physics problem) the opening of a round of pool, where minute variations in the angle and force with which the cue ball strikes the bracket produce highly variable arrangements of balls on the table.

Life is not deterministic, either. Since it is chaotic, any slight error in measurement is amplified over time, which is why it is surprising that our weather models make predictions good for more-or-less the coming week. Of course, due to issues of instrumentation (and in even the best case, the uncertainty principle), error in measurement is inevitable.

So how is it that any given neuron wlll fire in the same way every time? How is it that organisms reliably produce such accurate copies of themselves? Why are there islets of order and reproducibility amidst a guranteed global increase in entropy?

Suppose we perform a quantitative analysis. Systems of differential equations capture deterministic, chaotic systems in a mathematically rigorous way. When a differential equation is too messy to integrate, we can use a computer to approximate the outcome, and preferably also the error bounds. In general, where necessary, techniques from probability and statistics can be used to obtain theoretical guarantees (or, via computer, empirical ones at least) regarding the behavior of nondeterministic systems.

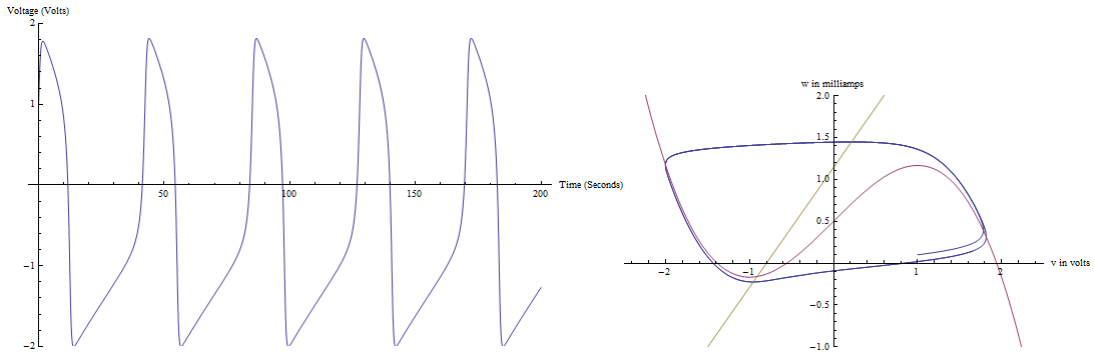

Figure 1: FitzHugh-Nagumo model (left: action potential, right: phase space) with parameters extern_input$(t) = .5$, $a = .7$, $b = .8$, $\tau = 12.5$. (From Wikipedia page, attribution given in references.)

2 Signals to Other Cells

2.1 Axonal transmission

How is information flow achieved within a biologically-occurring neural network? Simply getting a boolean value (encoded as a depolarization of a certain shape) from the cell body of a neuron to the end of its axon is nontrivial.

To describe the firing of a single biological neuron, kinetic models such as that of Hodgkin-Huxley have been developed based on empirical data. To introduce these, it will be better to use a simplification thereof, in this case the FitzHugh-Nagomo model (developed in the '60s rather than the '50s). In either case, the model is expressed as a system of ordinary differential equations (ODEs). These can be solved numerically on the computer using a pre-existing solver or a simple iterative technique such as the 4th degree Runge-Kutta method.

Note that other models of the same system have their own uses. If we were considering algorithms on a neural network, we should use a simpler, non-kinetic model for each neuron. At each time t, we would sum the weighted dendritic inputs, and if they exceed the activation threshold (fixed or otherwise), send an impulse (to other neurons' dendrites) arriving at time $t + 1$.

Algorithm 1 FitzHugh-Nagumo model of an excitable neuron

$$\begin{aligned} \frac{dv}{dt} &= v - \frac{v^3}{3} - w + \text{extern\_input} \\ \tau\frac{dw}{dt} &= v + a - bw \end{aligned}$$

v, w vary with time. $\frac{dv}{dt}, \frac{dw}{dt}$ are the rates of change (over time) of v, w.

v represents membrane voltage, and w represents 'recovery'.

a, b, τ are real-valued parameters, which do not vary over time. a, b describe the rate of recovery, which is scaled by τ.

In this system of ODEs, note in particular that $\frac{dv}{dt}$ is cubic in v. When v is negative, v tends to increase. When v is large and positive, v tends to decrease. Otherwise, v tends to increase. There is a stable state at $v = 0$ that v is attracted towards - but it takes a roundabout path (in the phase space) if pushed past threshold potential, producing the action potential. If given continuous input, the system produces periodic spiking at a certain frequency, due to the requirement for recovery time.

Note that v is not in volts, to simplify the equations, but that we can recover voltage from a linear

function in v such as $(-v-70)mV$. In modelling in general, finding input parameters and output variables that correspond to a given set of empirical data is nontrivial, especially if the model is to be kept simple.

Note that the ODEs only describe the dynamics at a fixed point along the neuronal axon. By addding a single spatial dimension (discretized into 'segments' along the axon for computational tractability) and a diffusion term, the depolarization of each 'segment' triggers its neighbor (the one(s) who are not recovering) to depolarize.

So, given appropriate parameter values, a depolarization induced at one end will arrive at the other end of the axon as desired. Here, we see the robustness of the pattern generated. Given a noisy input signal - which can only propagate down the axon when conditions are right, - we receive a cleaned-up output signal (containing spikes of consistent amplitude & not too close together).

References: (2015). "FitzHugh–Nagumo model", Wikipedia. Images by Xelo747, released under Creative Commons Attribution-Share Alike 3.0.
http://en.wikipedia.org/w/index.php?title=FitzHugh%E2%80%93Nagumo_model&oldid=654266830

own unpublished (rough) implementation of FitzHugh-Nagomo over one spatial dimension
https://dl.dropboxusercontent.com/u/32135991/processing-js/neuron_web/neuron.html

2.2 Stripe formation & leaf arrangements

How do the coat patterns of animals form? As a mathematical topic, this drew the interest of Alan Turing towards the end of his life [?]. Here, we will concern ourselves with the models of Meinhardt and Gierer, which said authors have documented fairly extensively online.

The diffusion of two species of chemical (e.g. pigments) over space can be described by the following system of partial differential equations.

$$\begin{aligned} \frac{\partial a}{\partial t} &= D_a \Delta_a \\ \frac{\partial b}{\partial t} &= D_b \Delta_b \end{aligned}$$

D_a, D_b are constant diffusion coefficients, and Δ_a, Δ_b are Laplacians, which we will define in a moment.

By adding *reaction terms* to the right hand side of these equations, we can describe a wide variety of two-species dynamics. For instance, suppose we require large activated patches, but also that every activated cell have inactivated neighbors. Meinhardt and Gierer have documented a system of partial differential equations (PDEs) which displays such behavior.

Algorithm 2 a Gierer-Meinhardt model of stripe formation

$$\begin{aligned} \frac{\partial a}{\partial t} &= s\frac{a^2 + b_a}{b\,(1 + s_a a^2)} - r_a a + D_a \Delta_a \\ \frac{\partial b}{\partial t} &= s a^2 - r_b b + D_b \Delta_b \end{aligned}$$

a, b vary with time. $\frac{\partial a}{\partial t}, \frac{\partial b}{\partial t}$ are the rates of change (over time) of a, b.

Δ_a, Δ_b are the Laplacians of a, b, defined $\Delta_a = \nabla \cdot \nabla a = \sum_i \frac{\partial^2 a}{\partial x_i^2}$ over spatial dimensions x_i.

a is activator concentration, and b is inhibitor concentration.

$s, s_a, r_a, r_b, D_a, D_b, b_a$ are real-valued parameters. s weights the rate of autocatalysis due to presence of a. b_a represents an external influx of a. s_a controls when a saturates. r_a, r_b weight the self-inhibition of a, b. D_a, D_b weight the diffusion of a, b.

Here, the activator self-catalyzes at a superlinear rate, but saturates at a threshold concentration. So cells must 'dump' inhibitor into neighbors to become active, and the system stabilizes once activator is

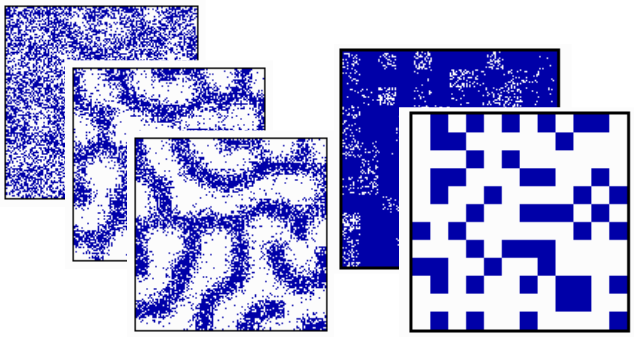

Figure 2: Sample output of stripe formation model, with and without diffusion. (via Meinhardt's webpage.)

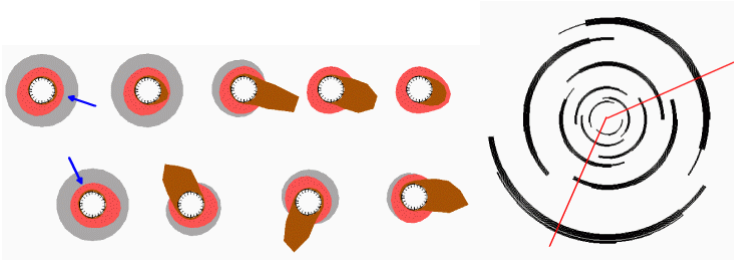

Figure 3: Sample output of leaf formation model due to Meinhardt, H., Koch, A.J. and Bernasconi, G (1998).

concentrated in some cells but not others (in a suitable pattern). If activator does not diffuse, the two types of cell appear (with fixed ratio) in clumps. If activator does not saturate, a single spot is formed.

The exact positioning of clumps and stripes appears to depend on the source density (which initiates activator and inhibitor production), which should be distributed uniformly but at random. Sensitivity to initial conditions in this regard (i.e. chaotic behavior) suggests why individuals of a given species tend to vary in their exact coat pattern, due to very slight differences in development.

We might also consider helical leaf arrangements, i.e. spiral patterns about a sealed central tube, which do not arise if only a single inhibitor is present. It turns out that a system lacking memory can only produce oscillation between one side and the other (i.e. a 180° angle). So to model this structure, Meinhardt and collaborators introduced a long-duration inhibitor to a spatial model of periodic initiation. They found that the angular spacing did converge to the golden angle (137°) for a wide variety of parameters, as has been observed anecdotally, albeit for unspecified reasons.

References: Meinhardt H and Gierer A (2012), "Theoretical aspects of pattern formation and neuronal development". Max-Planck-Campus Tübingen.
http://www.eb.tuebingen.mpg.de/de/forschung/emeriti/hans-meinhardt/home.html

2.3 Morphogenesis

How do limbs know where to form? The genome contains highly-conserved homeobox (Hox) regions, laid out along the chromosome in the same arrangement as the corresponding body segments along the spinal cord (Meyers 2008). In terms of developmental biology, morphogenesis occurs according to the transcription factors present, e.g., the products of Hox (homeobox) genes, PAX (paired box) genes, and the BMPs (bone morphogenetic proteins a.k.a. cytokines, metabologens). Transcription factors activate suites of genes, leading to cell differentiation. By swapping in a different Hox gene at a given location, the development of an inappropriate segment can be induced, such as legs in place of the antennae of a fruitfly.

But how are the Hox genes associated with such specific regions? Their activation is tied to what is termed a segmental clock.

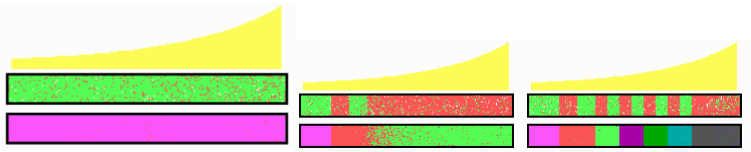

Figure 4: Sample output of somite formation model due to Meinhardt (1982).

Consider an oscillating system where A inhibits A but encourages P, whilst P inhibits P but encourages A. If the entire space consists of cells in a single state, the oscillation occurs in time, as the space flips back and forth. But if there is an A-P border anywhere in the space, the oscillations occur over space, forming a pattern that is stable in time. [img: gradient / A-P / segment]

Meinhardt argues that in the presence of a concentration gradient (of some morphogen), this initial border can be formed at some threshold concentration, triggering the pattern to develop. Moreover, every A/P cycle is able to increment some form of counter, activating the subsequent Hox gene.

References: Myers, P. (2008) Hox genes in development: The Hox code. Nature Education 1(1):2, http://scienceblogs.com/pharyngula/2007/09/the_hox_code.php

Meinhardt and Gierer (2012).

3 Signals to Other Individuals

3.1 Coloration

Primates are highly visual for mammals, but in terms of color perception, birds are well ahead of us. Moreover, this is reflected in their richly varied plumage, which has a correspondingly elaborate evolutionary history - including the development of structural colors, and a surprising amount of avian color space (accounting for their tetrachromacy) which goes unexploited (Stoddard and Prum, 2011).

Activator-inhibitor dynamics between sonic hedgehog (Shh) and bone morphogenetic protein 2 (Bmp2) are involved in feather patterning. The evolution of this system upon the surface of a tube suffices to explain the formation of barb rid-ges in chick natal down feathers (Harris et. al. 2005). Related dynamical systems presumably account for the formation of various other structures, including the depositing of pigment.

Pigments used in feathers include melanins (black, reddish browns, pale yellows), carotenoids (bright red, orange, yellow - acquired from plants), and porphyrins (pink, browns, reds, greens - these fluoresce red under UV). Melanins, at least, have non-signalling utility as structural reinforcement ("All About Birds: Color", 2007).

However, the modification of feathers for signalling reaches an extreme in birds such as the peacock, whose iridescent feathers (variations of which are present on pigeons, cuckoo-rollers, hummingbirds, and many others) are so colored due to their structure, not pigment. Iridescence is achieved via diffraction grating and micro-prisms. Bright blue, as seen on jays, bluebirds, and buntings, is achieved via deformed matrices and light scattering.

Other organisms that develop structural coloration include butterflies (via diffraction grating, photonic crystals, and selective mirrors), sea mice (via crystal fibres), marble berries (via spiral coils), and color-changing cephalopods (via reflectin in their chromatophores). Broadly speaking, the optics behind these methods tend to involve highly regular mirrored or meshlike structures at the microscopic scale. An article hosted by the American Society for Photobiology goes into various examples with much greater depth (Ball 2012).

References: [Wikipedia article on 'structural coloration'.]

Stoddard MC and Prum RO (2011). "How colorful are birds? Evolution of the avian plumage color gamut". Behavioral Ecology 22 (5): 1042-1052. doi: 10.1093/beheco/arr088

Harris MP, Williamson S, Fallon JF, Meinhardt H, Prum RO (2005). PNAS vol. 102 no. 33 11734-11739. doi: 10.1073/pnas.0500781102

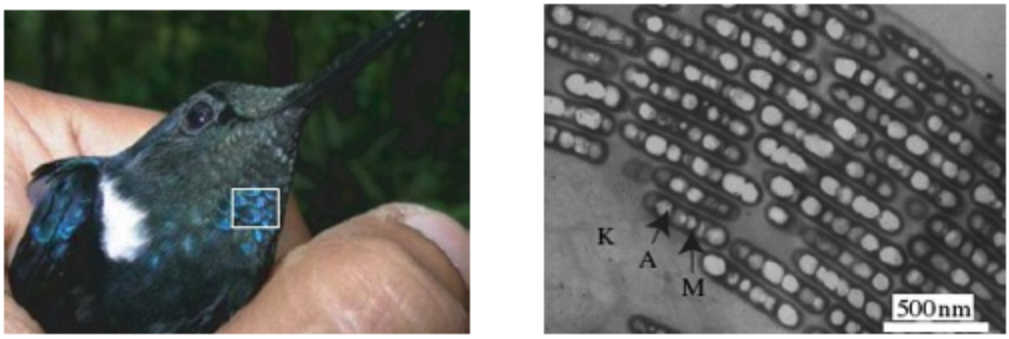

Figure 5: Platelets of melanin punctuated with air holes function as a photonic crystal, producing the iridescent blue on the Black Inca hummingbird. K=keratin, A=air, M=melanin. (From Shawkey et al., 2009, via Ball, 2012.)

(2007) "All About Birds: Color". Cornell Lab of Ornithology.
www.birds.cornell.edu/AllAboutBirds/studying/feathers/color/document_view

Ball P (2012). "Nature's Fantastical Palette: Color from Structure". American Society for Photobiology.
http://www.photobiology.info/Ball.html

3.2 Teeth and horns

Why do other primates have fangs? How do they arise? In primates, the size of the canine teeth is correlated with the degree of male-male competition (Boyd and Silk, 2000). As a chimpanzee, showing one's upper teeth in a smile is a form of intimidation ("Chimpanzee smiles", 2013). Signalling dominance is less costly than fighting to express it.

Mammalian teeth are specialized, and hard to replace. Their shape is produced by the addition of cusps during the bell stage (following the bud and cap stages), which form the various crest patterns seen in mammalian heterodonty (Jernvall and Thesleff, 2012). But tooth shape is determined earlier, based on the number of roots, which arise from the epithelial diaphragm cells (MacPherson 2003).

Changing topics, we see great variety in the horns (and analogously, tusks) of various species living in the same locale. Only in a few cases (musk oxen, moose) are the horns are useful for defense against predators. Rather, they are often suited to competing with same-sex conspecifics using the head and neck, the legs being preoccupied by bearing weight (Geist 1966). This occurs not only against male rivals for mates, but occasionally against female rivals for food (Robinson and Kruuk, 2007).

As to the developmental mechanisms behind such ritualized weapons, curving horns could perhaps be produced by unequal elongation on outside & inside. Spiralling horns could be produced by 'orienting' systems of differential equations as described by Meinhardt, in which the maximum continually escapes to an adjacent position.

References:

Boyd R and Silk JB (2000). "How Humans Evolved - Part 2: Primate Behavior and Ecology - Primate Mating Systems". W.W. Norton & Company, Inc.
http://www.wwnorton.com/college/anthro/bioanth/ch7/chap7.htm

(2013). "Chimpanzee smiles". Chimpanzee Sanctuary Northwest.
http://www.chimpsanctuarynw.org/blog/2013/09/chimpanzee-smiles/

Jernvall J and Thesleff I (2012). "Tooth shape formation and tooth renewal: evolving with the same signals". Development 139, 3487-3497. doi: 10.1242/dev.085084

MacPherson BR (2003?). "Oral Histology - Module 3: Tooth Development - 40. Determination of Root Shape". University of Kentucky College of Medicine (a personal site hosted by the institution).
http://www.uky.edu/~brmacp/oralhist/module3/lab/oh3main.htm

Geist V (1966). "The Evolution of Horn-Like Organs". Behaviour Vol. 27, No. 3/4, pp. 175-214.
http://www.jstor.org/stable/4533157

Robinson MR, Kruuk LEB (2007). "Function of weaponry in females: the use of horns in intrasexual competition for resources in female Soay sheep". Biol. Lett.: 2007 3 651-654. doi: 10.1098/rsbl.2007.0278

3.3 Symbolic reasoning

Language is a particularly rich source of patterned signals, elaborating upon the unpatterned signals of symbols arbitrarily associated with meaning (evidence already of a rich learning capability). Once sufficient intergenerational bandwidth is available to transmit substantial memetic information, cultural evolution seems to kick off in earnest, and in general proceeds far more rapidly than biological evolution. But to go into detail would require a deeper foray into linguistics.

4 Addtl' Cases of Self-Organization

4.1 Flocking

Once, the passenger pigeon blotted out the skies of North America, forming grand murmurations of billions of birds. Starlings, which still exist, do the same behavior in a different (non-migratory) context. Remarkably, even as the group's direction changes rapidly, none of the birds bump into one another.

How computationally difficult is flocking, anyways? Helpfully, the computation requires only local information (i.e. not the entire state of the system, which could be very large). Ultimately, by brute force or otherwise, computers can simulate flocking by substantial numbers of agents - including crowds of humans, which is useful in the visual arts and building design.

Algorithm 3 Flocking algorithm, as per Shiffman.

Let a boid's maximum velocity be 1, so that normalization produces vectors of said length.
For every boid b,

alignment = (normalized average of neighbors' velocities) - (own normalized velocity)

separation = weighted average (by proximity) of vectors pointing away from too-close neighbors

cohesion = normalization of ((average of neighbors' locations) - (own location))

Cap the length of each of these three vectors (to limit steering force), and sum them with arbitrary weighting. We add the result to the acceleration of b.

It turns out that self-propelled, light-activated particles (in colloidal suspension) can flock, too. In this case, physics is doing the computation. In the absence of hematite-exciting blue light, diffusion predominates. But light causes the asymmetrical particles to self-propel, by releasing a chemical cloud from the corner of a hematite cube exposed outside a polymer sphere.

References: Shiffman, D (2012). "The Nature of Code". Ch.6. (self-published).
http://natureofcode.com/book/chapter-6-autonomous-agents/

Palacci J, et. al. (2014). "Light-activated self-propelled colloids" Phil. Trans. R. Soc. A: 2014 372 20130372. doi: 10.1098/rsta.2013.0372
alternative link: http://www.sciencemag.org.proxy.cc.uic.edu/content/339/6122/936.full

4.2 Fractals in bacterial colonies

Consider the growth of a bacterial colony as it forages for nutrients. Under certain conditions, this process produces fractal shapes. How?

Figure 6: "Gardens-in-a-Petri". (Ben-Jacob and Levine, 2006)
Via 'pruned.blogspot.com/2006/02/more-gardens-in-petri.html'.

Algorithm 4 A reaction-diffucusion model of bacterial colony growth by Lacasta et. al.

$$\begin{aligned} \frac{\partial b}{\partial \tau} &= \nabla D_b \nabla b + \theta f(b,n) \\ \frac{\partial n}{\partial \tau} &= D_n \nabla^2 n - f(b,n) \end{aligned}$$

$b(\tau, \vec{r})$ is the density of bacteria. $n(\tau, \vec{r})$ is the concentration of nutrient. τ represents time, and $\vec{r}$ represents space.

∇, the gradient operator, is defined $\nabla a = \sum_i \frac{\partial a}{\partial r_i}$. (Recall using it to define the Laplacian.)

f describes the consumption of nutrient by bacteria, and is defined $f(b,n) = \frac{knb}{(1+\gamma' n)}$, where k is the intrinsic consumption rate and γ' controls saturation (satiation).

D_b, D_n are diffusion coefficients. θ is a parameter describing bacterial efficiency.

When nutrient concentration is low and agar concentration is high (softening the agar surface, hence raising the bacterial diffusion coefficient, i.e. b's rate of diffusion), Lacasta et. al. found that actual *Bacilus subtilis* colonies developed a ramified (branching) structure, roughly as per the diffusion-limited aggregation (DLA) model.

Although DLA does produce Brownian trees, which are a kind of fractal, it is not clear how this might account for, say, the spiralling elements of the patterns produced by the researchers at Tel-Aviv University. These researchers have proposed that chemically-mediated signalling between the bacteria may be responsible for more complex growth patterns (Frame et. al., 2015).

References: Lacasta AM, Cantalapiedra IR, Auguet CE, Peñaranda A, and Ramírez-Piscina L (1999). "Modeling of spatiotemporal patterns in bacterial colonies". Phys. Rev. E 59, 7036.
http://journals.aps.org.proxy.cc.uic.edu/pre/abstract/10.1103/PhysRevE.59.7036

Johnson KR (2006). DLA Cluster (photograph). Wikimedia Commons. (Released under Creative Commons Attribution-Share Alike 3.0 Generic.)
http://commons.wikimedia.org/wiki/File:DLA_Cluster.JPG

Frame, Mandelbrot, and Neger (2015). Course notes on Fractal Geometry, section 5G, third link.
http://classes.yale.edu/fractals/

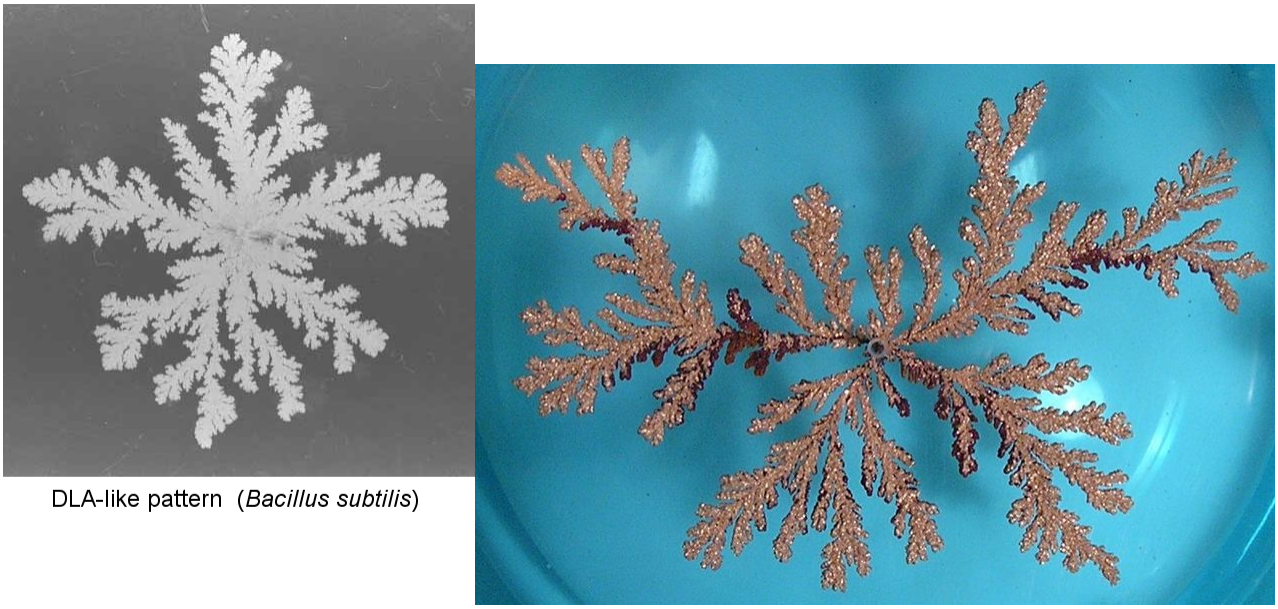

Figure 7: Left: Bacterial colony with ramified structure. (Lacasta et. al. 1999) Right: DLA cluster formed from copper. (Johnson 2006)

5 Conclusion

From these examples, we argue that mechanisms of pattern formation are greatly diverse, and well-modelled by mathematical & computational techniques. Our interest arises because arbitrary patterns can function as signals, and therefore play a social role.

'Signals to other societies' was originally slated as an additional section, including tribalism (exemplified by the asabiya model of empire rise-and-fall) and social stratification (exemplified by the Sugarscape agent-based societal model). The dearth of ecological models (with social components) in 'signals to other individuals' should also be addressed.

Aside from their role in signalling, the developmental mechanisms here discussed are interesting in such contexts as material science and computer graphics.