Composition based on the talk of

-Pattern formation-

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Content

1. Introduction on pattern formation

This elaboration of my talk on pattern formation tries to cope the basic concepts of the Turings model (A.M. Turing, 1952) on pattern formation, which are partial differential equations describing the reaction and diffusion behaviour of chemicals. It will introduce the concept of the breakdown of a former homogenous and symetrical system, what Turing calls himself the breakdown of a prepattern. Therefore it will deal with the mathematical terms of stability analysis of a so called stationary state. Under particular circumstances such stable systems are capable of generating stationary patterns of finite characteristic wave lengths even if the system starts from arbitrary initial conditions. What Turing showed is that this characteristic behaviour of the system is determined intrinsically by the reaction rates and by its diffusion rates and not by external constraints. Alan M. Turing investigated the chemical basis of morphogenesis and showed that the coupling of nonlinear kinetics with diffusion may lead to spatial differentiation, i.e. to structures denoted later as Turing patterns. Turing patterns have been shown to have counterparts in natural systems and therefore could be a plausible way to model the mechanicsm of biological growth(Gierer & Meinhardt, 1972).

2. Instability-breakdown of symmetry and homogeneity

Turing's inspiration were natural phenomena, such as gastrulation, describing the early phase in the development of an animal embryos or phylotaxis the growth of plants. Natural Systems exhibit an amazing diversity in both living and non living systems. Trees and plants growing from a single seed can show extremly complex organization. Also the complex development of mammals starting from a single fertilized egg cell. Such systems although originally quite homogenous develop a pattern due to an instability of the homogeneous equilibrium, triggered of by random disturbances. Turing proposed that the mathematical model describing a system of spontanously spreading and reacting chemicals, so called morphogens could give rise to stable stationary concentration patterns of fixed wavelength, while an additional driving force like diffusion might have relevance in describing the growth of a biological form. In order to understand the concepts of a driving force breaking the symmetry, a very demonstrative example can be used.
A metal stripe being thin and wide, is fixed on a peace of wood with a certain weight attached. If we snip with the finger against the strip, small virbations occur, but the stripe returns in its orignial stable state (standing straight). The attached weight can be moved along the vertical axes of the stripe. It is easy to imagine, if the weight is moved upwards the vertical axes, there is a certain height h_c, where the metal stripe standing straight (former steady state) is spontanously bend in one of the directions of the two of its thiner axes. For illustration see figure 1.

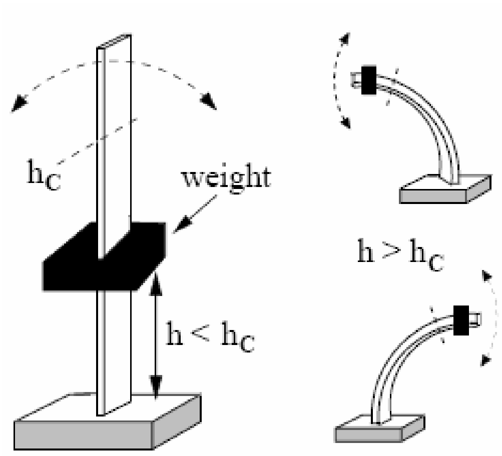

Figure 1 A metal stripe undergoing a spontaneous symmetry breaking, after the attached weight is moved upwards a certain threshold. This example is used to clarify the concept of a driving force(e.g. gravity) inducing a system to loose its stability.

So the driving force in this case is the gravity affecting the system. The small perturbations within the system Turing had in mind are in this case small vibrations of the metal stripe, that have a effect on the stability of the system, if gravity is present. But if gravity is absent those small forces have no influence on the stability of system itself, the metal strip is not even bend. Turing investigated this local instabilities using a reaction-diffusion system, where the small vibrations on the metal stripe are descibed by small perturbation in the concentration of two chemical substances called morphogens and a set of chemical reactions between the morphogens, and the physical laws of diffusion being the driving force on the system inducing a new globally stable pattern.
In this system a new structure emerges during development, a localized high concentration of a morphogen is first formed, while in turn it initiates the determination and differentiation of that particular area (a area of instability), so spatial differences are generated from quite homogeneous conditions.
In this case the morphogen distribution may be considered as the pre- or primary pattern which precedes the structure to be formed. A prepattern can determine more than on structure, if the morphogen is not used for an all or none decision, a long ranging signal exists which can spread out from a small group of cells the "organizing region".
To simplify the idea of reaction kinetics Turing used the analog example of the world of "the cannibals (C) and the missionaries (M) (J. Swintons, 2004). He was setting up following rules using partial differential equations to describe the growth rate of the systems components. Missionaries and cannibals live on the island. Missionaries are all celibate and thus dependent on the recruitment of the outer world as its members gradually die.
Cannibals also die, but can also reproduce, so that the population naturally increases. However when two missionaries meet a cannibal, the cannibal is converted to missionary status. This tension between production and transformation means that a balance is reached when both populations are mixed together. If this balance is disturbed by a small amount of noise, the tension will act to restore the balance: the system is stable.

3. Stability of a stationary state

The concentration over time of missionaries and cannibals is formalized by equation I and II, where *a* is the growth rate of the missionaries, the growth rate of the cannibals is expressed by the parameter *b*. The expression M square times C expresses the "kinetic" rule that if 2 missionaries meet on cannibal a missionary is recruited, therefore this term is added to the equation expressing the missionary concentration und subtracted from the equation expressing the cannibal change of concentration at time t. A more general form is given by equation *III* with the vector w (M,C) of the concentration coefficients over time t and a function F expressing the reaction kinetics f(M,C), g(M,C) and θ representing the parameter set.

$$(I)\ \frac{\mathrm{d}M}{\mathrm{d}t} = a - M + M^2 C$$
$$(II)\ \frac{\mathrm{d}C}{\mathrm{d}t} = b - M^2 C$$
$$(III)\ \frac{\mathrm{d}w}{\mathrm{d}t} = F\left(w,\theta\right)$$

The concept of stability is intuitive: If we disturb the system by a small perturbation a stable system evolves to the stable stationary state when time $t \rightarrow \infty$.
Stationary states are determined by setting F (w_o, θ) = 0, and stability analysis can be performed by looking at the properties of the eigenvalues of the Jacobian Matrix A.

$$A = \begin{pmatrix} \partial f_M & \partial f_C \\ \partial g_M & \partial g_C \end{pmatrix}$$

A is given by .the partial derivatives of the functions of the reaction kinetics f and g. In the case of our example of the "*Missionaries and the Cannibals*" we obtain the eigenvalues
$\lambda_1 = -0.499 + i\ 0.866$
$\lambda_2 = -0.499 + i\ -0.866$
by setting the parameters *a* and *b* of equation *I* and *II* equal to 1. If one or more real parts of the eigenvalues λ_i are positiv the system gets unstable. We get a stable steady state at 2.5 missionaries by 1 cannibal since the real part of the complex eigenvalue a<0. So we know now that Island is in a stable state and it is resistent to small pertubations. But since Turing was concerned with the onset of instabilty he added the concept of diffusion to the equations of the reaction kinetics. Achiving a system with local instabilities, but globaly stable. To understand the switch between unstable and stable states, the concept of bifurcation is introduced. In the example of the metalstripe with the adjustable weight, the point of bifurcation is the height h_c, where the stable steady state is bifurcating into two possible stable steady states (see figure 2 B).

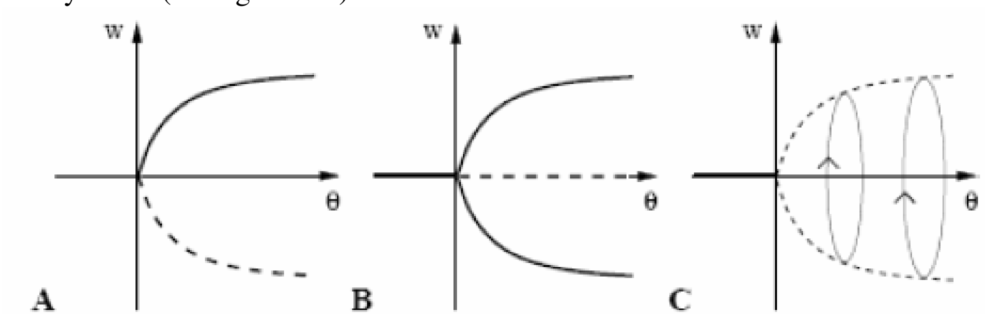

Figure 2 Saddle Node Bifurcation, B Supercritical Pitchfork Bifurcation, C Hopfbifurcation are reached by propagating the bifurcation parameter θ. (Dotted and straight lines indicate unstable and stable states)

4. Diffusion enhances and suppresses induced local instability

Now an extended chemical system is discussed, where diffusion enables the transport of matter and represents the only kind of spatial coupling. An inhomgenous distribution of concentration of the species M leads to a flux J which is proportional to the diffusion-gradient $J = -D \nabla M$ of the missionaries in our example. Fick's second law simplifies to the diffusion equation since it is assumed that D is not space dependend we obtain the diffusion equation $\frac{\partial M}{\partial t} = D \nabla^2 M$, which is added to the term of the reaction kinetics.

$$(I)\ \frac{dM}{dt} = a - M + M^2 C + dD \nabla^2 M$$
$$(II)\ \frac{dC}{dt} = b - M^2 C + D \nabla^2 C$$
$$(III)\ \frac{dw}{dt} = F(w, \theta) + D \nabla^2 w$$

Equation 3 In III the D denotes the matri x with the diffusion coeffients

In the example of the cannibals and missionaries Turing described the process of diffusion. with the picture of the two populations, instead of mixing completely together, are spread out in a thin ring around the rather narrow beach of the island. Now individuals react (that is, reproduce or convert) only with their immediate neighbours, but they also move around at random in a diffusive way. Moreover the members of the two populations move at different speeds: the missionaries have bicycles and move faster, denoted by *d* in equation I.. This is enough to destabilize the system. If there is at any point a small excess of cannibals, say, then this will be followed by excess 'production' of more cannibals, and then of more missionaries (since they have more targets for conversion). Without the spatial dimension the extra production of missionaries would in turn reduce the cannibal excess and the system would return to balance. But because the missionary excess is transported away more quickly, a pattern develops in which there is a near excess of cannibals and a far excess of missionaries. Moreover the distance between these zones of relative excess is determined by the interaction between the reaction and the diffusion: a length scale, which is what is required for the emergence of pattern from non-pattern, has emerged from the dynamics.
The important point here is that the diffusion rates of the two reactans have to differ, so that a spatio-temporal pattern evolves.

The pattern which evolves by adding the different diffusion rates to the term of the raction kinetics of the populations has a certain wave length depending on the parameters of the reaction-diffusion system. a characteristic polynom of this diffusion-reaction system. $\left(J - \lambda I - k^2 D\right) \times w_0 = 0$, w_0 being the vektor of the initial condtions $f(M_0, C_o)$ at the equilibrium and D the matrix with the diffusion parameters. For k =0 the influence of the diffusion term disappears, but the stability of the reaction-diffusion has to be investigated by varying k. The dispersion-relation can be described with $\lambda(k) = \lambda\left(k^2\right)\cdot$ where *k* is the wave vector number and λ is the growth rate. This relation can predict the unstable wave numbers. The dispersion analysis looks for the wave number of unstable modes k_c.

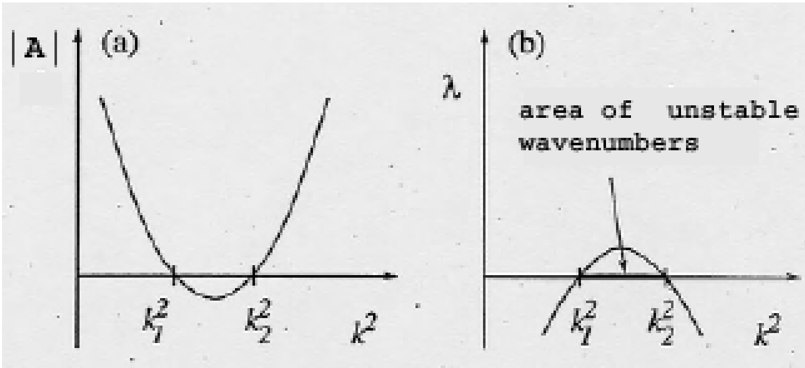

Figure 3 (a) is the determinant of the Jacobi Matrix of our diffusion reaction system, with respect to the wavenumber k, b) describes the area of unstable wavenumbers with respect to the dispersion relation λ(k)

5. Examination of Pattern Development

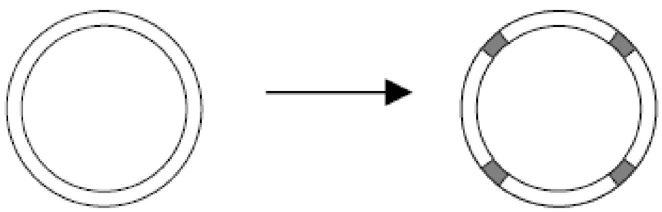

Figure 4 This ring represents the emergence of a pattern on the system. the black parts on the right hand side can be seen as high cannibal concentrations, with k-mode = 4

This simple description of the Turing instability explains where a characteristic length scale emerges, but things are a little more complicated. For example, given that all waves of the maximal wavenumber will be growing at an equal rate, and that perturbations are equally likely to occur at all places round the ring, the model can't predict the phase of the pattern: that is it might say there will be four troughs around the ring but it can't say (figure 4) where they will begin.
It explains that the number of waves k on the system are dependend on the parameters of the diffusion-reaction system. Another complexity is that the simple model predicts that patterns will go on growing forever: in order to prevent this we have to change the conditions after a while. These and other questions made it necessary for Turing to introduce the notion of 'cooking', this is simply increasing the dispersion relation, so that the system moves from having no unstable mode, to having a stable one. In two dimensions, what happens to the dispersion relation? For a one dimensional lattice, we saw that patterns on rings could be described by wavenumbers. Thus the analogue in two-dimensions of the dispersion-relation is the dispersion plot (Figure 3).

The asumptions which lead to a stable steady state in the absence of diffusion are:
$- f_M + g_C < 0; f_M g_C - f_C g_M > 0$;

The wavenumber of unstable steady states can be obtained by

$$k_c^2 = \frac{D_M f_C + D_C g_M}{2 D_C D_M} = \sqrt{\frac{f_C g_M - f_M g_C}{D_M D_C}}$$

it yields for the stationary stable state to be unstable in presence of diffusion processes additional rules have to hold

- $f_M > 0$, $g_C < 0$
- $D_M > D_C$
- $(f_M D_C + g_M D_M)^2 > D_M D_C (f_M g_C + f_C g_M)$

(Hu-Script, 2000)

5. Summary and Outlook

Turing showed in his paper 1952 that diffusion can produce homogeneous spatial patterns. Instability induced by diffusion is called a Turing instability, which leads to a new Turing pattern, if the constraints of the dispersion relation hold and effect the real part of the Jacobian matrix $Re\{\lambda(k)\} > 0$ of the reaction-diffusion system.
The linear analysis predicts which wave numbers become unstable in the system, but does not give any insight into symmetries that might arise as a result of nonlinear coupling of the unstable wave modes. Typically, Turing systems (and also many other physical systems) exhibit stripes and hexagonally arranged spots, but also other morphologies such as rhombic arrays and labyrinthine patterns have been observed in two dimensions (Kapral and Showalter, 1995). The question is wether complex pattern can evolve out of a reaction-diffusion system descibed by Turing. An activator inhibitor system is conceivable (Koch-Meinhardt, 1994) with an short range activator (high diffusion rate) and a longe range inhibitor (low diffusion rate).This does describe the nature of a chemical system, although other systems are imaginable where a negativ concentration could last. Numerical simulations on the Gray–Scott Model revealed a variety of spatio- temporal patterns (J.E. Pearson,1993).

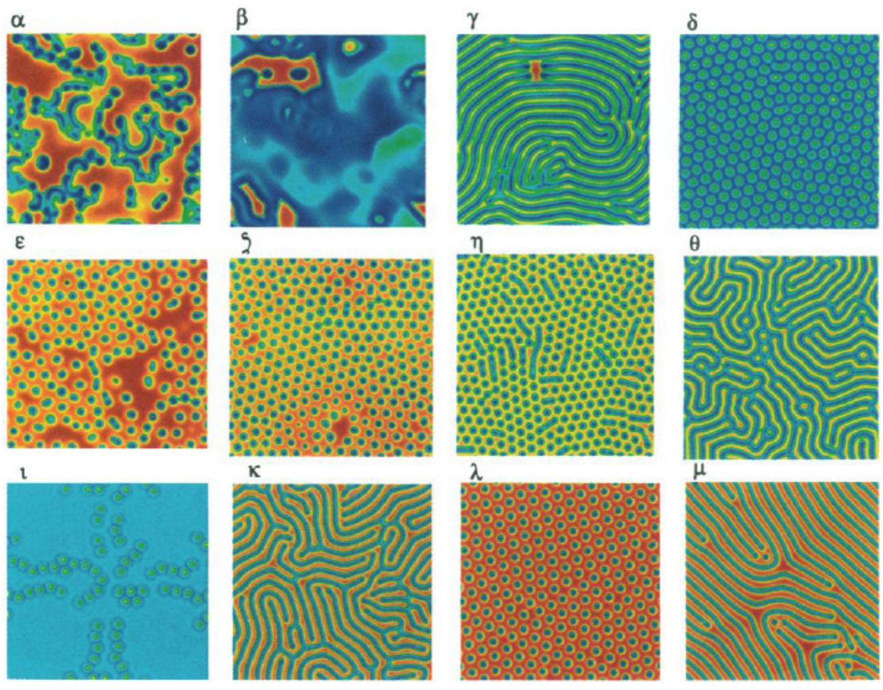

Figure 5 Gray-Scott Model developing a great variety of patterns, based on Tourings diffusion reaction system.

6. Sources

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