Spontaneous pattern formation in Turing systems

Manel Vila Vidal
Facultat de Física, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain.

Abstract: We give a general description of pattern forming systems and describe the linear stability analysis that allows to determine whether a system in a uniform state will spontaneously evolve to a patterned state. Such an analysis is performed on Turing systems and conditions for pattern formation are derived. As an example of a Turing system, we consider the Brusselator model, for which a variety of patterns are found numerically for different values of the bifurcation parameters.

I. INTRODUCTION

A quick look around us reveals that, far from being uniform, the world we live in exhibits a complex structure: galaxies, stars, convection cells on the sun's surface, sand dunes in the desert, the electric impulses through the heart, the Earth as a whole... Clearly all these systems are not in equilibrium, because systems in equilibrium exhibit no structure whatsoever.

The study of pattern forming systems is still quite young. Analytical methods have recently been developed [1–3], and research at an experimental level is also being carried out, but still a lot remains to be done.

The aim of this undergraduate thesis is to describe briefly the theoretical background for understanding such systems and to introduce some of the analytical methods used to study them. In order to get some insight into these techniques we will discuss the Turing model. Although first proposed in 1952 as a model for morphogenesis [4, 5], many examples of it have been found in other fields [7] such as chemistry [6], optics [8, 9], biology [10, 11] or the study of quantum fluids [12, 13].

II. CONCEPTUAL FRAMEWORK

Let us consider a system whose dynamics may be described with a system of m (nonlinear) partial differential equations

$$\frac{\partial \boldsymbol{u}(\boldsymbol{x},t)}{\partial t} = f\left(\boldsymbol{u}, \frac{\partial \boldsymbol{u}}{\partial x_i}, \frac{\partial^2 \boldsymbol{u}}{\partial x_i^2}, \ldots, p\right) \qquad (1)$$

where $\boldsymbol{x} \in \mathbb{R}^n$ $(n = 1, 2, 3)$ is a vector in space, $\boldsymbol{u}(\boldsymbol{x}, t) = (u_1(\boldsymbol{x}, t), \ldots, u_m(\boldsymbol{x}, t))$ encodes the state of the system and f is a certain function of $\boldsymbol{u}$, its spatial derivatives and one or more control parameters. For the sake of simplicity, let us assume the presence of only one control parameter p, which we can freely tune.

As a starting point, we assume the system to exhibit no structure, i.e., to be in a time-independent spatially-uniform base solution $\boldsymbol{u} = \boldsymbol{u}_b$. We assume this solution to be stable, in the sense that any small perturbations would be damped after a certain transient time. By experimentally increasing (or decreasing) the value of p we may reach a critical value p_c above which the uniform solution $\boldsymbol{u}_b$ becomes unstable to small perturbations, and the system may evolve to a new state. A pattern is said to form if $\boldsymbol{u}$ exhibits a structured dependence on $\boldsymbol{x}$.

A. The role of boundaries

As we are looking for patterns arising naturally from uniform states, it is suitable to consider translationally invariant systems in the extended directions and minimise the effect of boundaries. To attain such an idealisation we can consider infinitely wide systems or periodc boundary conditions in the extended directions. The latter is chosen for mathematical simplicity.

III. LINEAR STABILITY ANALYSIS

It is our goal to be able to determine under which conditions patterns will form, that is to say, to determine the critical value p_c. Our starting point will be the uniform solution u_b around which we will perform a linear stability analysis.

For every t and for every $j \in \{1, \ldots, m\}$, u_j is periodic in each spatial direction (let us say 2π-periodic for simplicity). Therefore if we denote the set of 2π-periodic functions in every spatial direction with P, we can conclude that as time varies u_j evolves in P, and $\boldsymbol{u}$ evolves in $P \otimes \mathbb{R}^n$. It is known that P is a Hilbert space and that it is spanned by the countably infinite basis

$$\{e^{i\boldsymbol{q}\boldsymbol{x}}\}_{\boldsymbol{q}\in\mathbb{Z}^n}, \qquad (2)$$

and $P \otimes \mathbb{R}^n$ is spanned by

$$\{\vec{e}_j e^{i\boldsymbol{q}\boldsymbol{x}}\}_{\boldsymbol{q}\in\mathbb{Z}^n, j=1,\ldots,m}, \qquad (3)$$

where $\{\vec{e_j}\}$ is the canonical basis in $\mathbb{R}^m$. We may then write the Fourier series

$$u_j(t) = \sum_{\boldsymbol{q}\in\mathbb{Z}^n} a^j_{\boldsymbol{q}}(t) e^{i\boldsymbol{q}\boldsymbol{x}}, \qquad (4)$$

which virtually allows to rewrite (1) as a countably infinite system of ODEs in the variables

$\{a_{\boldsymbol{q}}^j(t)\}_{\boldsymbol{q}\in\mathbb{Z}^n, j=1,\ldots,m}$. In practice, however, this may be very difficult or even impossible to do due to f being nonlinear. However, we can still take advantage of the ideas stated above. Let $\mathcal{L}$ be the linearization of f about the base state $\boldsymbol{u}_b$, which is obtained by performing a Taylor expansion around the base state and retaining only linear terms in u_i and its spatial derivatives. As usual in finite-dimensional dynamics, we must solve the eigenvalue problem for $\mathcal{L}$:

$$\mathcal{L}[\boldsymbol{u}] = \sigma \boldsymbol{u}. \tag{5}$$

Eigenvectors with $\mathrm{Re}(\sigma) > 0$ will determine unstable directions and eigenvectors with $\mathrm{Re}(\sigma) < 0$ will be stable.

Here we may still take advantage of another fact. Consider the following subspace of P:

$$H_{\boldsymbol{q}} = \langle \vec{e}_j e^{i\boldsymbol{q}\boldsymbol{x}}, j = 1, \ldots, m\rangle, \tag{6}$$

where $\langle\cdot\rangle$ means *spanned by.* It is clear, since $\mathcal{L}$ is a linear operator on P, that $H_{\boldsymbol{q}}$ is invariant under $\mathcal{L}$. Therefore we may solve the eigenvalue problem in each subspace independently. This highly simplifies our study, since no different Fourier modes need to be mixed to solve the problem exhaustively.

Let us now take $\boldsymbol{u} \in H_{\boldsymbol{q}}$, that is $\boldsymbol{u} = \boldsymbol{u}_0 e^{i\boldsymbol{q}\boldsymbol{x}}$, for $\boldsymbol{u}_0 \in \mathbb{R}^m$, and consider $\mathcal{L}[\boldsymbol{u}_0 e^{i\boldsymbol{q}\boldsymbol{x}}] = \mathcal{L}_{\boldsymbol{q}}[\boldsymbol{u}_0] e^{i\boldsymbol{q}\boldsymbol{x}}$, where $\mathcal{L}_{\boldsymbol{q}}$ is the corresponding linear operator on $\mathbb{R}^m$. We must solve the eigenvalue problem

$$\mathcal{L}_{\boldsymbol{q}}[\boldsymbol{u}_0] = \sigma \boldsymbol{u}_0, \tag{7}$$

which, for every $\boldsymbol{q}$, yields at most m different eigenvalues $\sigma_{\boldsymbol{q}}$ and eigenvectors $\boldsymbol{u}_{0\boldsymbol{q}}$. The functional relation between $\sigma_{\boldsymbol{q}}$ and $\boldsymbol{q}$ is the so-called dispersion relation[1]: $\sigma_{\boldsymbol{q}} = \sigma(\boldsymbol{q})$ and in fact there is a different dispersion relation for every value of the control parameter p. In figure 1 three possible examples of such a dispersion relation are shown.

If $\mathrm{Re}(\sigma(\boldsymbol{q})) < 0$ for every $\boldsymbol{q}$ then $\boldsymbol{u}_b$ is stable. But for a certain value $p = p_c$, $\mathrm{Re}(\sigma(\boldsymbol{q}))$ may cross 0 and become positive for some values of $\boldsymbol{q}$ as p is further increased. A bifurcation has occurred. The value of $\boldsymbol{q}$ for which $\mathrm{Re}(\sigma(\boldsymbol{q}))$ first becomes positive is called the critical wave vector and will be denoted by $\boldsymbol{q}_c$.

Furthermore, if p is only slightly above the threshold value p_c, only a small range of wave vectors around $\boldsymbol{q}_c$ will have $\mathrm{Re}(\sigma(\boldsymbol{q})) > 0$. Let us call $\boldsymbol{q}_m$ the wave vector for which $\mathrm{Re}(\sigma(\boldsymbol{q}))$ has its maximum value (which may not necessarily be $\boldsymbol{q}_c$ itself). If the system is exposed to a perturbation[2], after a transient time only the Fourier modes with $\mathrm{Re}(\sigma(\boldsymbol{q})) > 0$ will survive. The dynamics of the linearised problem will then be dominated by $\boldsymbol{q}_m$, that will evolve as

$$\boldsymbol{u}_{0\boldsymbol{q}_m} e^{\sigma_{\boldsymbol{q}_m} t} e^{i\boldsymbol{q}_m \boldsymbol{x}}. \tag{8}$$

This mode varies periodically in $\boldsymbol{x}$. The length $\lambda = \frac{2\pi}{q_m}$ determines the characteristic scale of the pattern. It is exponentially growing in time with a growth rate of $\mathrm{Re}(\sigma_{\boldsymbol{q}_m})$. Furthermore, if $\omega_m = \mathrm{Im}(\sigma_{\boldsymbol{q}_m}) = 0$, the pattern will only grow in time, but if $\omega_m \neq 0$ the growing pattern will be modulated by oscillations of period $T = \frac{2\pi}{\omega_m}$.

A. Types of instabilities

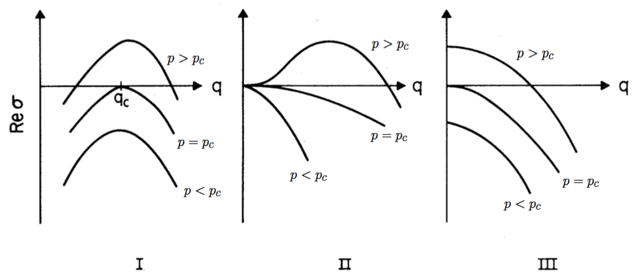

FIG. 1: Schematic representation of the linear growth rate as a function of the wave vector around the threshold value p_c. Classification of instabilities. Source: [2]

A first classification is based on whether the maximum growth rate passes through zero at a zero or a non zero value of the wave number. Figure 1 is self-explanatory. Note that in the type-III instability patterns with very large length scale develop since $\boldsymbol{q}_c = 0$, which corresponds to an infinitely long wavelength. Note also that above p_c the uniform system is unstable over a band of wave numbers. The growing non-dominating modes will appear as spatial modulations of the main mode. Additionally an instability can be stationary ($\omega_m = 0$), denoted by -s, or oscillatory ($\omega_m \neq 0$), denoted by -o.

B. The importance of nonlinearities

It is worth noting that stable uniform solutions are controled by the linear terms of the system. Thus such solutions hide the rich complexity of the system being studied. The linear analysis performed in this section shows that when the uniform solution becomes unstable, a certain mode will grow exponentially in time. It is then, when this mode is sufficiently large, that the nonlinearities of the system come into action by stopping the growth. The mode has saturated and a stable pattern may have formed.

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[1] It must be carefully observed that not all the values of $\boldsymbol{q}$ are allowed. However, if the function is L-periodic, each component of $\boldsymbol{q}$ can take values $\frac{2\pi d}{L}$ for $d \in \mathbb{Z}$ and if L is large enough (as in our examples), $\boldsymbol{q}$ may be considered to be continuous, rather than discrete.

[2] Real systems are permanently exposed to fluctuations due to the non-existence of a perfect isolation. A random fluctuation may be decomposed in a superposition of the different Fourier modes.

IV. TURING INSTABILITY

In [4], Turing proposed a mathematical model of the growing embryo, in which two chemical substances (called morphogens) with stabilising reaction kinetics can form spatial patterns autonomously when diffusion (which is thought of as smoothening spatial differences) is added! Cells would then differentiate depending on the concentration of the morphogens, thus resulting in biological structures such as fingers or the spotted or striped skins of fishes or zebras. Nowadays such patterns are named after Turing and although there is no biological evidence [5] of his model, diffusion-driven instability was shown to be true for chemical systems and it provides a general theoretical framework for many disciplines.

Consider a reaction-diffusion system consisting of two chemicals with concentrations u and v in one dimension[3]:

$$\begin{aligned} \partial_t u_1 &= f(u_1, u_2) + D_1 \partial_x^2 u_1, \\ \partial_t u_2 &= g(u_1, u_2) + D_2 \partial_x^2 u_2, \end{aligned} \tag{9}$$

where f and g are the reaction rates and D_1, D_2, the diffusion coefficients. The system is assumed to have a uniform solution $\boldsymbol{u}_b = (u_{1b}, u_{2b})$, which is stable in the absence of diffusion. Small perturbations $\boldsymbol{\delta u}_b = (\delta u_1, \delta u_2)$ around it are governed by the linearized equation

$$\partial_t \boldsymbol{\delta u} = \boldsymbol{A} \boldsymbol{\delta u} + \boldsymbol{D} \partial_x^2 \boldsymbol{\delta u} \tag{10}$$

where $\boldsymbol{A} = \begin{pmatrix} f_1 & f_2 \\ g_1 & g_2 \end{pmatrix} = \begin{pmatrix} \partial_{u_1} f & \partial_{u_2} f \\ \partial_{u_1} g & \partial_{u_2} g \end{pmatrix} |_{\boldsymbol{u}=\boldsymbol{u_b}}$, and $\boldsymbol{D} = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}$. If a perturbation of the form $\boldsymbol{\delta u} = \boldsymbol{\delta u}_{0q} e^{\sigma_q t} e^{iqx}$ is introduced in (10) we obtain the eigenvalue problem $\boldsymbol{A}_q \boldsymbol{\delta u}_{0q} = \sigma_q \boldsymbol{\delta u}_{0q}$, with $\boldsymbol{A}_q = \boldsymbol{A} - q^2 \boldsymbol{D}$, which yields the dispersion relation

$$\sigma_{q1,2} = \frac{1}{2} \operatorname{tr} \boldsymbol{A}_q \pm \frac{1}{2} \sqrt{(\operatorname{tr} \boldsymbol{A}_q)^2 - 4 \det \boldsymbol{A}_q}, \tag{11}$$

For each q if the real part of at least one of the σ_q is positive the corresponding mode will be unstable, otherwise it will be stable. Figure 2 shows the regions of stability in the $\operatorname{tr} \boldsymbol{A}_q - \det \boldsymbol{A}_q$ plane, with

$$\begin{aligned} \operatorname{tr} \boldsymbol{A}_q &= \operatorname{tr} \boldsymbol{A} - (D_1 + D_2) q^2, \\ \det \boldsymbol{A}_q &= \det \boldsymbol{A} - (f_1 D_2 + g_2 D_1) q^2 + D_1 D_2 q^4 \end{aligned} \tag{12, 13}$$

For the uniform solution to be stable if diffusion is 0:

$$\begin{aligned} \operatorname{tr} \boldsymbol{A} &= f_1 + g_2 < 0, \\ \det \boldsymbol{A} &= f_1 g_2 - f_2 g_1 > 0 \end{aligned} \tag{14, 15}$$

The former implies that $\operatorname{tr} \boldsymbol{A}_q < \operatorname{tr} \boldsymbol{A} < 0$. The right half of figure 2 is therefore prohibited and no oscillatory

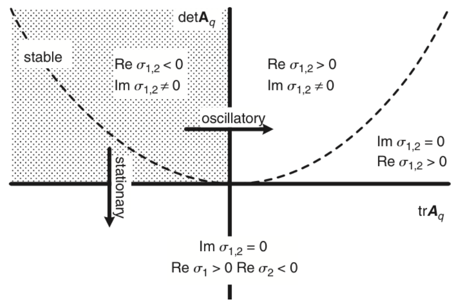


FIG. 2: Stability regions for a fixed q in the $\operatorname{tr} \boldsymbol{A}_q - \det \boldsymbol{A}_q$ plane. Source: [1]

patterns will develop. However, a stationary pattern may develop if the minimum value of $\det \boldsymbol{A}_q$ is negative. This minimum value is attained at $q_c^2 = \frac{D_1 g_2 + D_2 f_1}{2 D_1 D_2}$ and the value of the determinant is $\det \boldsymbol{A}_{q_c} = \det \boldsymbol{A} - D_1 D_2 q_c^4$, which is negative if

$$\boxed{D_1 g_2 + D_2 f_1 > 2\sqrt{D_1 D_2 (f_1 g_2 - f_2 g_1)}} \tag{16}$$

Condition (16) must be satisfied for a Turing pattern to form. Together with (14) and (15) they imply that $f_1 > 0$ and $g_2 < 0$, which means that an increase of u_1 over the uniform state induces its own production while u_2 inhibits its own production. We might call them activator and inhibitor, respectively.

Also, $f_2 g_1 < 0$. If $f_2 < 0$ and $g_1 > 0$, u_1 is a global activator and u_2 a global inhibitor. Additionally, from (16), $D_2/D_1 >> (-g_2)/f_1 > 1$, so that the inhibitor diffuses much faster than the activator. The expression "local activation with long-range inhibition" was coined in 1972 by Gierer and Meinhardt [14] for this property, which plays a key role in Turing patterns. If u_1 is locally increased over u_{1b}, the local production of u_1 and u_2 will be enhanced. The inhibitor will diffuse much faster to the surrounding areas, thus inhibiting the production of both. A pattern will form. The spatial variation of u_2 will be smoother than that of u_1 and maxima of both will be colocalised. If $f_2 > 0$ and $g_1 < 0$, a similar reasoning can be applied to see that in the resulting pattern maxima of u_1 and minima of u_2 will be colocalised.

V. BRUSSELATOR MODEL

Consider the following reaction-diffusion model in two dimensions:

$$\begin{aligned} \partial_t u &= a - (b+1) u + u^2 v + D_u \nabla^2 u, \\ \partial_t v &= b u - u^2 v + D_v \nabla^2 v, \end{aligned} \tag{17}$$

with $a, b, D_u, D_v > 0$. This model is known as the Brusselator [6], which is a portmanteau of oscillator and Brussels, where it was first proposed by Prigogine [3].

We consider $D_v = 10$ and $a = 3$ to be fixed and take b to be the bifurcation parameter as a function of D_u. A

[3] For $n \geq 2$, ∂_x^2 is replaced by ∇^2. The results are the same since the dispersion relation involves only q^2, which becomes $|\boldsymbol{q}|^2$.

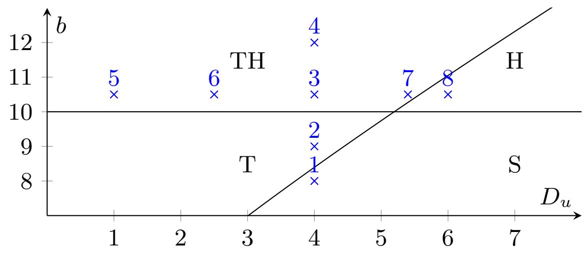


FIG. 3: Bifurcation diagram for the Brusselator model for $a = 3, D_v = 10$. Hopf bifurcation: $b_H = 1 + a^2$, Turing bifurcation: $b_T = (1 + a\sqrt{D_u/D_v})^2$.

uniform solution exists for $(u, v) = (a, b/a)$. The matrix for the linear stability analysis (10) is $\boldsymbol{A} = \begin{pmatrix} b-1 & a^2 \\ -b & -a^2 \end{pmatrix}$.

From (16) the condition for a Turing bifurcation is

$$b > b_T = (1 + a\sqrt{D_u/D_v})^2 \tag{18}$$

In the previous section we considered the system to be stable in the absence of diffusion, which yielded equations (14) and (15). If these conditions is removed, oscillatory patterns may arise if some $\boldsymbol{q}$ enters the right half-plane in figure 2, i.e., if tr $\boldsymbol{A_q}$ becomes positive for some $\boldsymbol{q}$. But tr $\boldsymbol{A_q}$ is a parabola (12) with its maximum at $\boldsymbol{q} = 0$, which means that only instabilities of type-III-o may arise, i.e., uniform oscillations around the uniform stationary state. This is a Hopf bifurcation and the condition can be derived from tr $\boldsymbol{A}_0 =$ tr $\boldsymbol{A} = 0$:

$$b > b_H = 1 + a^2 \tag{19}$$

As now only two parameters are considered we can do a bifurcation diagram (figure 3), on which some points have been selected for further study. Four regions are indentified in this diagram. In S the uniform state is stable. In T, the uniform state becomes unstable in front of Turing instabilities. Region H is unstable in front of Hopf instabilities. In domain TH both Hopf (for $\boldsymbol{q} = 0$) and Turing instabilities (for $\boldsymbol{q} \neq 0$) can occur. In figure 4 we have plotted the growing rate (Re($\sigma_{\boldsymbol{q}}$)) as a function of $\boldsymbol{q}^2$ for points 1, 2, 3 and 4 along $D_u = 4$ in figure 3. Point 1 is clearly stable, point 2 is Turing-unstable and points 3 and 4 are in the TH domain, but the Turing mode dominates over Hopf. This has been checked on a computer simulation, performed on a square of size 128×128 with periodic boundary conditions.

A simulation has also been performed for points 5, 6, 3, 7 and 8 on the line $b = 10.5$. The growing rate and the behaviour after a transient time are shown in figure 5. Again, 5 and 6 are also in the domain TH, but the Turing instability dominates (figure 5a). This is checked in the simulations. Even in point 7 a stationary pattern is obtained. Note that for $D_u = 1$ (figure 5*b*) a very organised lattice of maxima-spots is created. As we increase D_u the diameter of this spots increases (figure 5*c*) until they finally collide destroying the spotted pattern and forming a labyrinth-type pattern (figure 5*d*). Then a

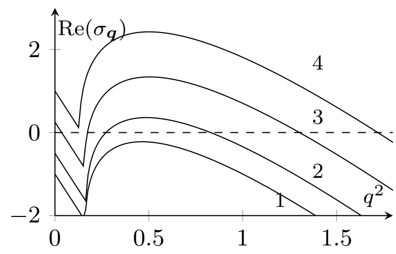


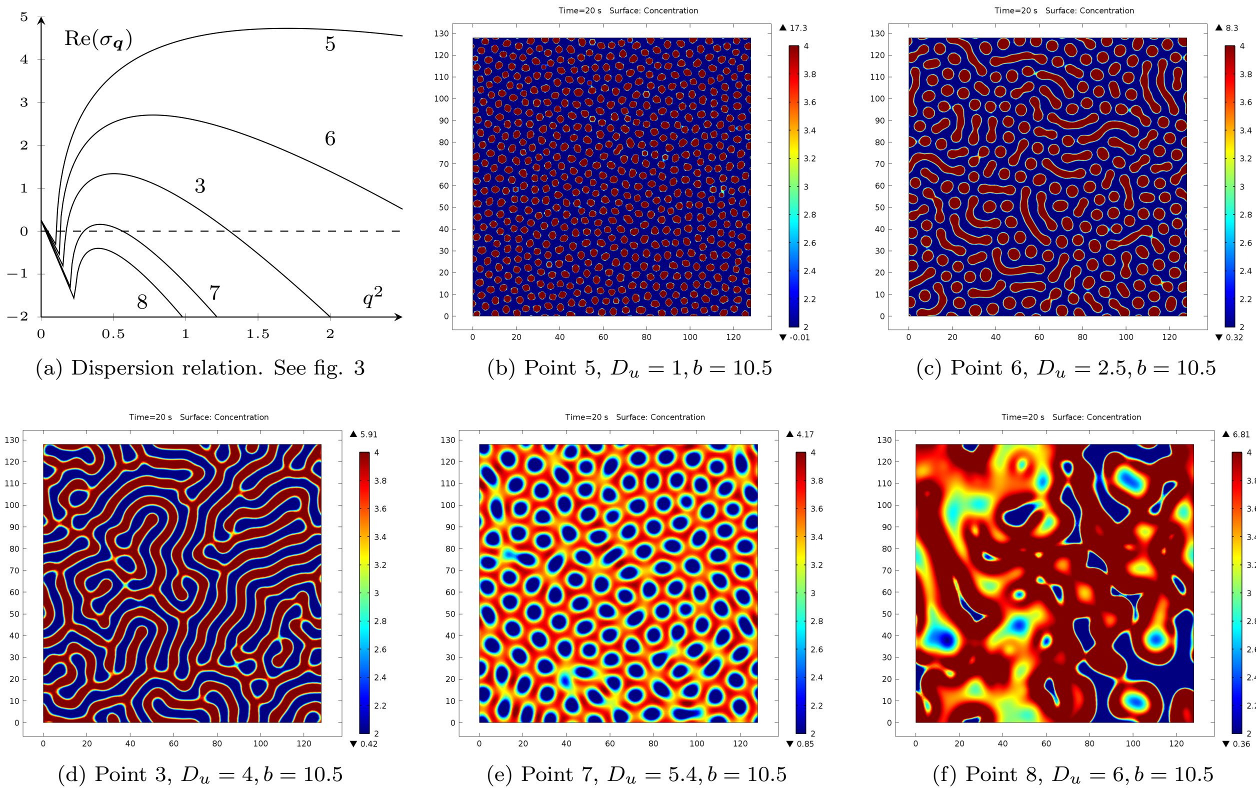
FIG. 4: Dispersion relation for points in fig. 3

spotted pattern is formed again (figure 5*e*), but the spots are minima of concentration. Point 8 is expected to exhibit uniform oscillations, but neither periodic nor uniform behaviour is observed. However if examined carefully a background oscillation with period $T \approx 2$ is seen. This is in accordance with what was predicted at the end of section III: $\omega = \mathrm{Im}(\sigma_0) = \sqrt{4 \det \boldsymbol{A} - (\mathrm{tr}\, \boldsymbol{A})^2}/2 = \sqrt{36 - b^2 - 100 + 20b}/2 \approx 3$, where equation (11) and $a = 3$ have been used. We have also checked that the frequency of the oscillations does not depend on D_u.

Another important observation can be made. Consider for example point 3. In figure 5a we can see that the maximum value of the growth rate is attained at $|\boldsymbol{q}| \approx 0.7$, which, as deduced at the end of section III yields a characteristic length of $\lambda \approx 9$, which is also a fairly good approximation. The same can be checked for point 7. On the other hand as D_u is decreased the maximum of the growth rate is attained at larger values of $\boldsymbol{q}^2$ and the characteristic scale of the pattern should decrease, which accords perfectly well with the numerical simulation.

VI. CONCLUSIONS

- Pattern formation analysis may be applied to any research field. Rather than a new discipline, it is a new perspective under which any system should be considered again to discover new properties.
- Turing systems show how the interaction of two stabilising processes can result into an unstable situation. This is a good example of an emerging property, which results in the formation of a self-sustained pattern.
- The Brusselator model is quite simple and yet we have seen that it exhibits a rich set of solutions. Linear stability analysis has proven to be a very powerful tool, for it can predict not only whether a pattern will form, but also some characteristic features of the forming pattern.
- Linear stability analysis cannot predict the specific shape of the pattern and some solutions are not in accordance with what the theory would predict. A more advanced tool can be derived. The so-called amplitude equation retains the information of non-linear terms and can do more accurate predictions.



(a) Dispersion relation. See fig. 3

(b) Point 5, $D_u = 1, b = 10.5$

(c) Point 6, $D_u = 2.5, b = 10.5$

(d) Point 3, $D_u = 4, b = 10.5$

(e) Point 7, $D_u = 5.4, b = 10.5$

(f) Point 8, $D_u = 6, b = 10.5$

FIG. 5: Dispersion relation and patterns obtained in the Brusselator model for $b = 10.5$ and $D_u = 1, 2.5, 4, 5.4, 6$.

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