Spirals and targets in reaction-diffusion systems

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The existence of spirals and targets is common in reaction diffusion systems of excitable dynamics. I present a multiple scale perturbation analysis to show the existence of all these patterns near a Hopf bifurcation boundary in a Turing type reaction-diffusion system.

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In two-dimensional reaction-diffusion systems, rotationally symmetric patterns, known as targets or sinks, and a generalization of them with broken circular symmetry, i.e., spirals are being investigated experimentally as well as theoretically [1] in many nonlinear systems. The Belousov-Zabotinsky reaction is a well investigated excitable reaction-diffusion system that shows all these patterns [2–4]. Spirals are characteristic patterns in slime mold aggregates [5–8] and are an important observation in cardiac arrythmias [9] as well. Targets and spirals, which are generally found to form around some defects, precede some defect mediated chaos, commonly known as spiral defect chaos [10,11]. All these have made the study of the origin and stability [12] of these patterns a subject of renewed interest. In this paper the existence of spirals and targets is reported in the Gierer-Meinhardt (GM) model, representing a reaction-diffusion system for biological pattern formation. Here I work near a Hopf bifurcation boundary which separates the Turing state and a homogeneous steady state from a homogeneous oscillatory state. The GM model represents a Turing type reaction-diffusion system, which to my knowledge, has not been investigated analytically for the existence of targets and spirals.

In general, an investigation of targets in a system starts with the inclusion of an additive inhomogeneity in the phase equation followed by a Cole-Hopf transformation that gives the equation the shape of a linear Schrödinger equation. The target is a bound state of the Schrödinger equation; it then remains to obtain the appropriate form of the inhomogeneity from a suitable potential. This type of approach has made it particularly controversial, whether intrinsic targets exist in the vicinity of an oscillatory state or not. There is an explicit solution for spirals in the λ-ω system due to Hagan [13]. The λ-ω system in simpler cases has the structure of a complex Ginzberg-Landau equation without an imaginary part in the coefficient of ∇^2. In his analysis, Hagan was of the opinion that a spiral of a single branch will only persist if the higher order spirals are unstable. It is also important to note that the spirals obtained in these way are characterized by a quadratic dispersion relation. Complex Ginzberg-Landau type amplitude equations and eikonal equations [1], developed from the curling up of a line defect, are standard approaches with which to show spiral patterns. In what follows, we arrive at a linear amplitude equation from the solvability criterion applied at first order in a perturbation expansion of the GM model using multiple scales. It is shown subsequently that a general solution of a spiral exists for that amplitude equation in a region of phase space where a homogeneous oscillatory state is stable. Targets and stars are shown to be special cases. These things occur without any externally imposed local inhomogeity. The other part of the result is obtained by imposing an inhomogeneous distribution on the removal rate of the interacting species; in the asymptotic region this gives incoming spirals and targets with particular wave numbers.

It was Turing who first showed that the interaction of two substances, say A and B, with differerent diffusion rates can cause steady patterns to form. Two basic properties that account for the formation of pattern in a Turing system are local self enhancement and long range inhibition. Local enhancement causes inhomogenieties to grow and long range inhibition confines that effect if the antagonist is taken to be fast diffusing. The two species A and B constitute a reaction-diffusion system [14], known as the GM model:

$$\frac{\partial A}{\partial t}=D_a\nabla^2A+\rho_a\frac{A^2}{(1+k_aA^2)B}-\mu_aA+\sigma_a, \tag{1}$$

$$\frac{\partial B}{\partial t}=D_b\nabla^2B+\rho_bA^2-\mu_bB+\sigma_b. \tag{2}$$

Here D_a and D_b are diffusion constants such that $D_b \gg D_a$ (the condition for formation of a Turing pattern), σ_a and σ_b are the basic production terms, and μ_a and μ_b are removal rates. All of these parameters are real and positive. The natural pattern formation requires $\mu_a \ll \mu_b$ to make an autocatalytic local amplification of A effective to form steady patterns [14]. In the above mentioned model, ρ_a and ρ_b are cross reaction coefficients; k_a is a saturation constant, which actually plays a role in determining the shape of the pattern, and is also real and positive.

The model is simplified by setting $k_a=\sigma_B=0$, to make an analytic treatment more easy without any loss of the qualitative nature of the result. Then a change of scale as $\overline{t}=\mu_at$, $\overline{l}=\sqrt{\mu_a/D_a}l$, $a=(\mu_a\rho_b/\mu_b\rho_a)A$, and $b=(\mu_a^2\rho_b/\mu_b\rho_a^2)B$ allows us to reach the following set of equations [14]:

$$\frac{\partial a}{\partial \overline{t}}=\overline{\nabla}^2a+\frac{a^2}{b}-a+\sigma, \tag{3}$$

$$\frac{\partial b}{\partial \overline{t}}=\overline{\nabla}^2b+\mu(a^2-b). \tag{4}$$

Here $D=D_a/D_b$, $\mu=\mu_a/\mu_b$, $\sigma=\rho_b\sigma_a/\mu_b\rho_a$, and $\overline{\nabla}^2$ is the Laplacian operator in a changed length scale. The steady homogeneous fixed points of the above mentioned equations are $a_0=(1+\sigma)$ and $b_0=(1+\sigma)^2$.

The scales of variables A and B are now changed such that the fixed point is at the origin. Here I introduce $r=r_0+\epsilon r_1$, $\overline{t}=t_0+\epsilon\tau$, and $\theta=\epsilon^{1/2}\vartheta$. The order parameters in multiple scales are expanded as

$$A=\epsilon A_1+\epsilon^2 A_2+---, \tag{5}$$

$$B=\epsilon B_1+\epsilon^2 B_2+---, \tag{6}$$

where $\epsilon<1$. Now, in multiple scales, I find, to $O(\epsilon)$,

$$\begin{pmatrix} \frac{\partial}{\partial t_0}-D\left[\frac{1}{r_0}\frac{\partial}{\partial r_0}r_0\frac{\partial}{\partial r_0}+\frac{1}{r_0^2}\frac{\partial^2}{\partial\theta^2}\right]-\frac{1-\sigma}{1+\sigma} & \frac{1}{(1+\sigma)^2} \\ -2\mu(1+\sigma) & \frac{\partial}{\partial t_0}-\left[\frac{1}{r_0}\frac{\partial}{\partial r_0}r_0\frac{\partial}{\partial r_0}+\frac{1}{r_0^2}\frac{\partial^2}{\partial\theta^2}\right]+\mu \end{pmatrix} \times\begin{pmatrix} A_1 \\ B_1\end{pmatrix}=0. \tag{7}$$

Equation (17) has a solution of the form

$$\begin{pmatrix} A_1 \\ B_1\end{pmatrix}=A(r_1,\vartheta,\tau)\begin{pmatrix} a_1 \\ b_1\end{pmatrix}e^{\alpha t_0}, \tag{8}$$

where α is given by

$$\alpha=\frac{\frac{1-\sigma}{1+\sigma}-\mu}{2}\pm\frac{1}{2}\left[\left(\frac{1-\sigma}{1+\sigma}+\mu\right)^2-\frac{8\mu}{1+\sigma}\right]^{1/2}. \tag{9}$$

The real part of α grows when $\mu<(1-\sigma)/(1+\sigma)$, which is the boundary that separates a Turing patterned region and a steady homogeneous state from the homogeneous oscillatory state, as shown in Refs. [14,15] i.e., the Hopf-bifurcation boundary for the system. Figure 1 shows the phase diagram obtained from the linear stability analysis [14,15]. Now, since $\sigma<1$ for the growth of a solution, an oscillatory instability is created somewhere above the boundary $\mu_0=(1-\sigma)/(1+\sigma)$, but the solution grows below this line.

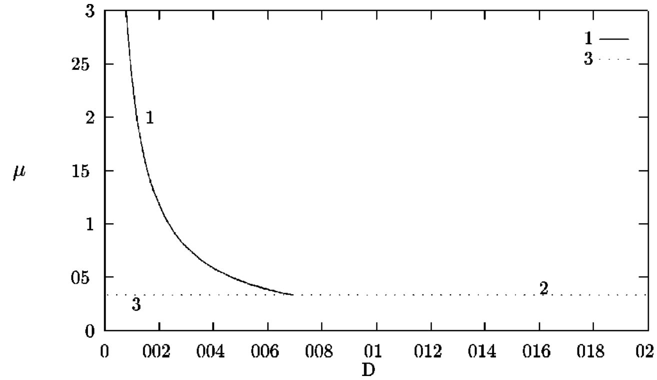

FIG. 1. Phase diagram as obtained from a linear stability analysis of the model [Eqs. (3) and (4)] in μ-D space. The lines marked 1 and 3 enclose the stationary patterned state, where the region over the line marked 2 is steady homogeneous. In this figure the dotted horizontal line is the boundary $\mu=\mu_0$, below which a steady oscillatory state exists. The perturbation analysis has been done about the line $\mu=\mu_0$.

The explicit form of the oscillatory solution in $O(\epsilon)$ is

$$\begin{pmatrix} A_1 \\ B_1\end{pmatrix}=A(r_1,\vartheta,\tau)\begin{pmatrix} \alpha+\mu \\ 2\mu[1+\sigma]\end{pmatrix}e^{\alpha t_0}+\text{c.c.}, \tag{10}$$

where, at the boundary, $\mu=\mu_0=(1-\sigma)/(1+\sigma)$ and $\alpha=in=[i/(1+\sigma)][2(1-\sigma)-(1-\sigma)^2]^{1/2}$.

Let us try to solve the equation at the next order i.e., at $O(\epsilon^2)$, keeping $\mu=\mu_0$ with an $O(\epsilon)$ variation μ_1 such that $\mu=\mu_0+\epsilon\mu_1$ where μ_1 can be a function of space and time. So, in $O(\epsilon^2)$,

$$L\begin{pmatrix} A_2 \\ B_2\end{pmatrix}=\begin{pmatrix} \left[-\frac{\partial}{\partial\tau}+\frac{1}{r_0}\frac{\partial}{\partial r_0}r_0\frac{\partial}{\partial r_1}+\frac{1}{r_0^2}\frac{\partial^2}{\partial\vartheta^2}\right] & 0 \\ 2\mu_1(1+\sigma) & \left[-\frac{\partial}{\partial\tau}+\frac{1}{r_0}\frac{\partial}{\partial r_0}r_0\frac{\partial}{\partial r_1}+\frac{1}{r_0^2}\frac{\partial^2}{\partial\vartheta^2}\right]-\mu_1 \end{pmatrix}\begin{pmatrix} A_1 \\ B_1\end{pmatrix}+(\text{nonlinear terms}). \tag{11}$$

Now, since the operator L has eigenstates with zero eigenvalues, the solvability criterion applied to Eq. (11) results in an amplitude equation

$$\frac{\partial A}{\partial\tau}=\frac{1}{r_0}\frac{\partial A}{\partial r_1}+\frac{1}{r_0^2}\frac{\partial^2 A}{\partial\vartheta^2}-\frac{4n^2\mu_1(1+\sigma)^2(1-\sigma)}{f(\sigma)^2-4n^2(1-\sigma^2)^2}A -i\frac{2n\mu_1 f(\sigma)(1+\sigma)}{f(\sigma)^2-4n^2(1-\sigma^2)^2}A, \tag{12}$$

where $f(\sigma)=[(1-\sigma)^2-2(1-\sigma)-n^2(1+\sigma)^2]=-2(1-\sigma)(1+\sigma)$.

Thus $f(\sigma)$ is negative for $0<\sigma<1$. Now, coming back to the original scale, Eq. (12) takes the shape

$$\frac{\partial A}{\partial t}=\frac{1}{r}\frac{\partial A}{\partial r}+\frac{1}{r^2}\frac{\partial^2 A}{\partial\theta^2}-\epsilon\frac{4n^2\mu_1(1+\sigma)^2(1-\sigma)}{f(\sigma)^2-4n^2(1-\sigma^2)^2}A +i\epsilon\frac{4n\mu_1(1+\sigma)^2(1-\sigma)}{f(\sigma)^2-4n^2(1-\sigma^2)^2}A. \tag{13}$$

Equation (13) has a general solution in the form of a spiral, with and without any space vatiation in μ_1, and solutions for the star, target, sink, etc. exist as special cases of that solution under varied conditions, as shown in the following.

Let us try a solution of the form

$$A=e^{\gamma t}\overline{A}(r)e^{i(\omega t+\psi(r)+m\theta)}, \tag{14}$$

which is the general solution of a spiral, where m is a real number known as a spiral number, and γ is the time rate of growth. Now, inserting this into Eq. (13) and equating the imaginary and real parts, respectively, we obtain

$$\frac{\partial\psi(r)}{\partial r}=\left[\epsilon\frac{4n\mu_1(1+\sigma)^2(1-\sigma)}{D}-\omega\right]r \tag{15}$$

and

$$\frac{1}{\overline{A}(r)}\frac{\partial\overline{A}(r)}{\partial r}=\left[\gamma+\epsilon\frac{4n^2\mu_1(1+\sigma)^2(1-\sigma)}{D}\right]r+\frac{m^2}{r}. \tag{16}$$

Equation (16) can be rewritten as

$$\gamma=\frac{1}{r\overline{A}(r)}\frac{\partial\overline{A}(r)}{\partial r}-\epsilon\frac{4n^2\mu_1(1+\sigma)^2(1-\sigma)}{D}-\frac{m^2}{r^2}. \tag{17}$$

From the above equation it is clear that an intrinsic spiral will grow for negative μ_1, i.e., the solution will grow below the line $\mu=\mu_0$ where a homogeneous oscillatory state exists. Numerical analysis reveals the existence of patterns with spatiotemporal variations due to nonlinear effects in the above mentioned region of phase space [14]. Integrating Eqs. (15) and (16),

$$\psi(r)=\frac{1}{2}\left[\epsilon\frac{4n\mu_1(1+\sigma)^2(1-\sigma)}{D}-\omega\right]r^2+N \tag{18}$$

and

$$\overline{A}(r)=Mr^p\exp\left(\frac{1}{2}\left[\gamma+\epsilon\frac{4n^2\mu_1(1+\sigma)^2(1-\sigma)}{D}\right]r^2\right), \tag{19}$$

where $D=f(\sigma)^2-4n^2(1-\sigma^2)^2=4(1-\sigma)^2(1+\sigma)^2[1-(1-\sigma)/(1+\sigma)]$, $p=m^2$ is a number, and N and M are arbitrary constants.

Equations (18) and (19) indicate the existence of an oscillatory solution as well as a steady solution. Since the exponent in Eq. (19) can always be made negative, keeping γ positive, and e^{-r^2} is a faster decaying function than r^p, the amplitude will not diverge at infinity. Equations (18) and (19) also indicate that though steady spirals and targets are possible solutions, there must be a solution which represents an oscillatory star when $\psi(r)$ is set to zero. The oscillation frequency $\omega=\epsilon([4n\mu_1(1+\sigma)^2(1-\sigma)]/D)$.

The form of $\psi(r)$ suggests that oscillations along the radius will be closer and closer as r grows, and consequently will be averaged out to make the system homogeneous at large r. An intrinsic target will result if we set $m=o$ in Eq. (16). On the other hand, we will obtain an intrinsic oscillating star with an oscillation frequency $\omega=\epsilon([4n\mu_1(1+\sigma)^2(1-\sigma)]/D)$, since in this case $\psi(r)$ is set to zero. These patterns are called intrinsic, since μ_1 is taken to be uniform in space.

It is interesting to observe that a spatial variation of μ_1 like $\mu_1=Pr/(Q+r)$, where P and Q are arbitrary constants, can, in the asymptotic region (i.e., $r\gg Q$), make $\psi(r)$ a linear function of r and can give some values to other constants as well. In the asymptotic region, as defined above, we can approximate μ_1 as $\mu_1=P-PQ/r$, so from Eqs. (15) and (16) it is obvious that if the oscillation frequency ω is set equal to $\epsilon([4n\mu_1(1+\sigma)^2(1-\sigma)P]/D)$, then

$$\psi(r)=-\epsilon\frac{4n\mu_1(1+\sigma)^2(1-\sigma)PQ}{D}r. \tag{20}$$

Thus an incoming target solution may exist with an amplitude

$$\overline{A}(r)=e^{Cr}, \tag{21}$$

where $C=\epsilon([4n^2(1+\sigma)^2(1-\sigma)PQ]/D)$, with a growth rate $\gamma=-\epsilon([4n^2P(1+\sigma)^2(1-\sigma)]/D)$. Now to make γ positive, we have to make P negative; on the other hand, depending upon the sign of Q, the target is an incoming or outgoing one.

A similar type of analysis shows that if we take another term in the expansion of μ_1 in the asymptotic region, $\mu_1=P-PQ/r+PQ^2/2r^2$, and a selection of spiral number

$$m^2=-\epsilon\frac{4n^2(1+\sigma)^2(1-\sigma)PQ^2}{D}=-\epsilon\frac{PQ^2}{2\sigma} \tag{22}$$

results in a spiral. Now to make m^2, a positive number P should be made negative. However, that, on the other hand, would change the growth rate to $+ve$. Thus this type of spiral can only be incoming with $Q<0$ to avoid any exponential growth of the amplitude.

In conclusion, the existence of intrinsic spirals and targets in a region of phase space where an oscillatory solution is stable is a most important observation. This is due not only to the fact that such a model (the GM model), representing biological systems, provides an interesting analytical prediction, but also because it predicts the generation of intrinsic spiral and target instabilities. There is a large question of whether spirals or targets can form intrinsically in a system or not. It has mostly been seen that these patterns form around some local inhomogeneity. In the present work it was shown that such instabilities can indeed develop without any local perturbation. In the present work, since the spirals are obtained in the next higher order from those of targets, in the expansion of inhomogeneous μ_1 spirals should form in a region closer to the origin than the region in space where incoming targets or shocks are formed. The spirals and targets, as obtained from a linear Schrödinger equation type phase equation, are characterized by a quadratic dispersion relation [1]; however, in the present results the dispersion relation is linear. Nothing can be said about whether spirals of higher number m will be unstable or not. Here, from Eq. (21), we see that, to make m large we have to make PQ^2 large. A large P and Q, in turn, will not only make the amplitude $\overline{A}(r)$ fall faster but will also push the region of validity for the asymptotic solution further away from the origin. It can also be argued that since the result comes on a large θ scale, lower spiral numbers would be preferable.

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