Why Turing mechanism is an obstacle to stationary periodic patterns in bounded reaction-diffusion media with advection

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Formation of stationary periodic patterns is paramount to many chemical, biological, physical, and ecological media. One of the most subtle mechanisms was suggested by Turing, who highlighted the applicability of isotropic reaction-diffusion dynamics with at least two diffusing fields. However, on finite domains with the presence of a symmetry breaking differential advection, two diffusing fields are rather disadvantageous to formation of stationary periodic patterns. We show that the criterion to stationary periodic patterns in Turing type models requires non-periodic boundary conditions and tuning of two parameters (a co-dimension-2 bifurcation in space) whereas in systems with one diffusing field (non-Turing) the bifurcation is of co-dimension 1 and thus easier to satisfy. We demonstrate this general result using spatial dynamics methods and direct numerical simulations of the canonical FitzHugh-Nagumo model.

Alan Turing in his seminal work on morphogenesis,1 had postulated a generic mechanism for which stationary periodic patterns (SPP) arise spontaneously out of a uniform steady state once a critical parameter value is exceeded. A minimal model that exhibits such an instability constitutes a local autocatalytic activation and a long range inhibition, hence reaction-diffusion (RD) type media:2

\[ \text{Le} \frac{\partial u}{\partial t} = f(u, v) + \frac{\partial^2 u}{\partial x^2}, \quad (1a) \]
\[ \frac{\partial v}{\partial t} = g(u, v) + D \frac{\partial^2 v}{\partial x^2}, \quad (1b) \]

where \( D, \text{Le} > 1 \) are the diffusion and the time scale ratios, respectively. The mechanism proposed by Turing, known also as a finite wave number instability, was generalized since then and found to occur in variety of natural phenomena,2 and in particular was found to be plausible in chemical and biological systems.3

However, RD type media are physically bounded and naturally exposed to external forcing, for example due to influx of flow4 or imposed electrical field.5 The modification of eqn (1) is done by inclusion of gradient terms imposing a unidirectional advective flow and thus a spatial symmetry breaking. Such reaction-diffusion-advection (RDA) media have been used in many contexts.4,6 In particular, in the context of SPP formation it was found that the differential advection removes the Turing's constrain between the activator-inhibitor diffusion ratios, \( D > 1 \), indicating robustness in the emergence of SPP.4 The latter were demonstrated experimentally and through computations employing mostly linear theory on infinite domains and numerical simulations.4,7 While Turing's mechanism gives rise to SPP in systems described by eqn (1), it was found as not effective when a differential advection is added,8 even though SPP have been observed in RDA systems with a single diffusing field.4,9 The theoretical basis about the conditions why and when such SPP are expected is missing, partially due to the nonlinear (large perturbations) effects of convective instabilities and boundary conditions (BCs).2,10 Thus, it is natural to ask how such a symmetry breaking flow destroys the already present SPP (due to Turing), and what is the theoretical basis of such phenomena.

In recent studies of SPP with \( D = 0 \), to which we refer here as ‘non-Turing’ models, we showed using dynamical systems methods the origin and the asymptotic properties of both travelling waves and SPP on finite domains.11 In this communication, we extend the theoretical framework due to the wide realization of the Turing mechanism. We exploit the simplicity of a canonical FitzHugh-Nagumo model to show the resulting spatiotemporal dynamics, when a Turing instability is subjected to a differential advection. Employing linear theory and ideas from nonlinear spatial bifurcations,13 we explain why Turing instability is not a favorable cast to obtain SPP, and suggest a distinct condition under which SPP can be expected. The condition corresponds to a co-dimension-2 bifurcation as opposed to co-dimension-1 bifurcations in non-Turing models. Since the criterion corresponds to a spatial instability it may arise in variety of RDA models, for example physico-chemical and vegetation patterns.4,6 Consequently, RD non-Turing models, having only one diffusing substance12 [e.g. \( D = 0 \) in eqn (1)], are fundamentally distinct and more robust to yield SPP, as has been already observed in ref. 4.

To demonstrate the impact of a differential advection on the Turing mechanism, we exploit a canonical FitzHugh-Nagumo model12 with advective terms

\[ f(u, v) = u - u^3 + v - s \frac{\partial u}{\partial x}, \quad (1c) \]
\[ g(u, v) = -u - \beta v - s \frac{\partial v}{\partial x}, \quad (1d) \]

where \( s > 0 \) indicates a unidirectional flow from \( x = 0 \) to \( x = L \). Such a system was widely employed to study the basic features of reaction diffusion type media.2 For the sake of simplicity, we are using a re-scaled form that allows both positive and negative values for \( u \) and \( v \).
Without a loss of generality, we assume here a simplified version of the traditionally (in chemical reactors) employed symmetry breaking Danckwerts BCs: \[ u(x,0) = (u_0,0) \text{ at } x = 0, \]
\[ \left( \frac{\partial u}{\partial x}, \frac{\partial v}{\partial x} \right) = (0,0) \text{ at } x = L, \]
where \( L \) is the domain size and \( u_0 = 0.1 \) (the value of \( u_0 \) is not significant). Evidently, such BCs do not in general support uniform solutions to (1). It has been shown that in non-Turing models such BCs select under certain conditions stationary patterns even though the primary instability is of a finite wavenumber Hopf\textsuperscript{9,12} type, i.e., to traveling waves. Nevertheless, properties of the forming patterns, traveling or stationary, were deduced from looking at the asymptotic model equations on periodic domains, adapting ideas from spatial dynamics.\textsuperscript{11} Thus, in what follows we exploit the spatial bifurcation theory to analyze system (1), while using direct numerical integrations to confirm the performed asymptotic analysis.

Our analysis begins with temporal stability of uniform solutions on an infinite domain. For positive \( \beta \) values, system (1) admits a trivial solution, and bistability (a pitchfork bifurcation) if \( \beta > \beta_h = 1 \)
\[ \left( \frac{u^e}{v^e} \right) = \left( \pm \frac{1}{\sqrt{1-\beta}} \right), \]
but in what follows, we consider only the monostable regime (see Fig. 1). Linear stability analysis (\( \varepsilon \ll 1 \)) about the trivial state to periodic perturbations,\textsuperscript{2}
\[ \left( \frac{u}{v} \right) = \varepsilon \left( \frac{u_k}{v_k} \right) e^{i \sigma x + i \omega t} + \text{c.c.} + \mathcal{O}(\varepsilon^2), \]

yields after insertion of (4) into (1) and collecting up to a linear order in \( \varepsilon \), two dispersion relations
\[ \sigma^+ (k) = \frac{b^- + i k sp^+ - a^- k^2 \pm \sqrt{1 - 4 Le \gamma^+ \gamma^-}}{2 Le}, \]
where \( k > 0 \) is a wavenumber, \( \sigma \) is a complex growth rate, c.c. stands for complex conjugated, and \( \gamma^\pm \equiv iksp^- + a^- k^2 + b^- \pm 1, a^- \equiv DL \leq 1, b^- \equiv 1 \pm \beta Ge, p^\pm \equiv Le \pm 1; \) the superscripts \( \pm \) correspond to the respective on the right hand side.

In the absence of advective terms (\( s = 0 \)), and for \( \beta = \beta_H \) and \( D = D_c \), \( \sigma^+ (k) \) admits a co-dimension-2 Hopf-Turing instability\textsuperscript{14} (see top inset in Fig. 1), where
\[ \beta_H = \frac{Le}{1}, \]
\[ D_c = 2 + 2 \sqrt{1 - \beta - \beta}, \]
and the Turing mode for which \( \text{Re}[\sigma^+(k_c)] = 0 \), is
\[ k_c^2 = \frac{a^- - 2 \sqrt{D}}{\sqrt{Da^+}}, \]
For \( \beta_H < \beta < \beta_s \), \( \text{Re}[\sigma^+(0)] < 0 \) and \( \text{Im} [\sigma^+(0)] > 0 \), where
\[ \beta_s = \beta_H \pm \frac{Le}{1}, \]
while for \( \beta_s < \beta < \beta_b \), \( \text{Im}[\sigma^+(0)] = 0 \), as shown in the top inset in Fig. 1.

Advection contributes to \( \sigma^+ (k) \) by making the growth rate to be complex and having a finite band of \( \text{Re}[\sigma^+(k)] \) to be positive, implying a linear instability of the trivial state. For the present we neglect the contribution of the advection in vicinity \( \beta \lesssim \beta_H \), that is \( k \ll 1 \), and focus on the regime around \( \beta_s \), as shown in the bottom inset in Fig. 1. Notably, above \( 2 \beta_s \), the dispersion relation has a qualitatively similar form as in non-Turing RDA models that is with \( D = 0 \).\textsuperscript{11} Naturally, with periodic BCs, the trivial state becomes unstable to traveling waves, not shown here. Surprisingly, with non-periodic BCs of (2) type, traveling waves emerge only if additionally \( D > D_c \) is satisfied, as demonstrated in Fig. 2 (left panel). Hence, the formation of traveling waves requires tuning of two parameters, \( D \) and \( s \). The latter manifests the impact of Turing instability.
mechanism: if the Turing threshold $D = D_c$ is not exceeded (before setting $s > 0$), the infinitesimal perturbations are swept from the domain, due to the convective instability, leaving the trivial steady state behind.

Consequently, for $D > D_c$ and $s > 0$ traveling waves are being regenerated near the left boundary, as shown in Fig. 2 (right panel). This behavior is distinct since non-periodic BC (2) in non-Turing type models break the translational symmetry and by that select stationary structures. Here, once $D_c$ is exceeded, the periodic Turing solutions that was present for $s = 0$, drifts due to the advection. The latter makes the behavior distinct from a finite wavenumber Hopf bifurcation which is a signature of non-Turing models. Particularly, the formation of SPP in Turing type models (i.e. with at least two diffusing fields) is also distinct: the emergence of SPP patterns is not subjected to the condition that is known to address.

To understand the asymptotic properties of SPP, we wish to study their existence. We do so by rewriting eqn (1), using a time independent co-moving coordinate transformation $\xi = x - ct$, as a set of four ordinary differential equations (ODEs):

$$\frac{du}{d\xi} = w, \quad \frac{dw}{d\xi} = (s - cLe)w - u + u^3 - v, \quad \frac{dv}{d\xi} = h, \quad \frac{dh}{d\xi} = \frac{(s - c)h + u + \beta v}{D}. \quad (11d)$$

Such an approach allows us to view the spatial coordinate $x$ as a time-like variable, through which periodic solutions emerge via Hopf bifurcations (in space), for more details we refer the reader to ref. 11. Following dynamical systems methods, the solutions’ properties and the onsets of the distinct Hopf bifurcations can be revealed by eigenvalue inspection, and since $(u, v, w, h)^T \propto \exp(\mu \xi)$, eqn (11) admits four spatial eigenvalues, where the superscript $T$ stands for transpose. We note that here temporal stability calculations are not addressed.

As a result, at the Turing onset, $\beta u < \beta < \beta^T$, $D = D_c$ ($s = 0$), the four eigenvalues are imaginary and of double multiplicity corresponding to the reversible Hopf bifurcation. Above $D_c$, the eigenvalues split and form a quartet of complex conjugated two pairs, in the $(\text{Re}[\mu], \text{Im}[\mu])$ plane. As $s \to s_{SH} > 0$, the real part of a complex conjugated pair (with $\text{Re}[\mu] < 0$) vanishes so that the pair becomes imaginary at $s = s_{SH}$. The latter is identical to the condition (10), as shown in Fig. 3(left panel). As in the non-Turing model, increase in $s$ (with $c = 0$) results in a spatial supercritical bifurcation to periodic solutions, see middle panel in Fig. 3. However, here above $s = s_{SH}$, direct numerical integration of eqn (1) with BCs (2), does not show SPP even though the translational symmetry is indeed broken (right panel in Fig. 3).

The reason is that in a four component ODE, with $s = s_{SH}$ and $D > D_c$, there is a presence of an additional complex conjugate pair with $\text{Re}[\mu] > 0$ implying the existence of other type of asymptotic periodic solutions, such as traveling waves. Namely, the Turing mechanism (or its analogue reversible Hopf) excludes the simple formation of a spatial Hopf bifurcation as appears in the non-Turing models.

A similar bifurcation structure also persists once we vary $\beta$ or $D$, while keeping $s = s_{SH}$ fixed. In Fig. 4(left panel), we describe the behavior under changing $\beta$ while qualitatively similar results are also obtained for $D$. Note that the spatial bifurcation is in the opposite directions as compared to Fig. 3(middle panel), indicating that all the eigenvalues have $\text{Re}[\mu] > 0$ for $\beta < \beta_c$, respectively. The uniform trivial state under such conditions is linearly unstable due to $s > 0$. Consequently, direct numerical simulations support again the fact that SPP can not be formed and instead travelling waves emerge, see right panel in Fig. 4.

Finally, we left with a question about the origin or a criterion for which SPP can emerge in bounded RDA media.

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Fig. 3 Left panel: Dispersion relation of the trivial state [see eqn (5)] at $s = s_{SH} \approx 1.357$, where the solid (dashed) line represents the real (imaginary) part. Note that $\text{Re}[\sigma^+(k)] = \text{Im}[\sigma^+(k)] = 0$, i.e. eqn (10), is satisfied at $k = k_{SH} \approx 0.4$. The inset shows a schematic configuration of the spatial eigenvalues. Middle panel: Bifurcation diagram for stationary periodic solutions plotted in terms of the maximal amplitude of $u(\xi)$ (solid line), computed via eqn (11) on periodic domains with a simultaneous variation of $s$ and $\lambda$, while keeping $c = 0$. Right panel: Space-time plot above $s_{SH}$ (see Fig. 2 for details). Other parameters: $\text{Le} = 100$, $\beta = \beta_c$, $D = D_c + 0.5$. 

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produce SPP. While in non-Turing models the spatial bifurcation is of co-dimension-1, in Turing-type models the bifurcation becomes of co-dimension-2 (i.e. tuning of two parameters to reach an onset). As such, this theoretical outcome explains why stationary periodic patterns are easily destroyed by advective flow in RD type media\(^8\) and moreover allows for a distinct vista to look into and design practical applications, such as discussed in ref. 4–6.

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References

16. The numerical continuation was performed using the AUTO package\(^1\) by two parameter variation (\(s, l\)) starting from the onset at which \(s = s_{SH}\) and \(l = \lambda_{SH} = 2\pi k_{SH}\), while all other parameters fixed.