

Physical interactions enable energy-efficient Turing patterns

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Patterns are ubiquitous in nature, but how they form is often unclear. Turing developed a seminal theory to explain patterns based on reactions that counteract the equalizing tendency of diffusion. These reactions require continuous energy input since the system otherwise would proceed to equilibrium, but what systems are energy-efficient is currently unclear. To address this question, we introduce a thermodynamically consistent model of a Turing system. We reveal that repulsive interactions between the stereotypical activator and inhibitor reduce energy requirements significantly. Interestingly, efficient patterns occur for weak activity, albeit at reduced amplitude. Our results suggest that physical interactions might be central in forming natural patterns.

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Nature is full of interesting patterns, including nanocrystals [1], complex tissues [2], and geophysical phenomena [3]. One prominent model to explain such patterns goes back to Alan Turing [4], who showed that patterns emerge spontaneously in mixtures of diffusing and reacting chemicals. These *Turing patterns* form when a locally self-enhancing activator is counterbalanced by a faster-diffusing inhibitor that suppresses production globally [5,6]. Turing patterns require energy input, since diffusion would equalize all profiles in a closed system. In biological systems, this energy input can come in the form of ATP molecules that are hydrolyzed to ADP to drive reactions. Other patterns might rely on external energy input, e.g., light, vibrations, or wind. However, the standard description of patterns, based on reaction-diffusion equations, does not explicitly include any energy input, which precludes a detailed analysis. In particular, that approach cannot identify energy-efficient patterns.

In this Letter, we introduce a thermodynamically consistent description of pattern formation inspired by Turing. In this model, diffusive and reactive fluxes are driven by chemical potentials, which allows a natural inclusion of physical interactions between components. Such physical interactions can facilitate patterns [7], and they are inevitable in biological systems, in particular, inside cells, where strong interactions lead to phase separation [8–11]. We here show that interactions can lower the energy demands of creating patterns.

To build our model, we consider a mixture of an activator A and an inhibitor I described by the respective volume fractions $\phi_A(\mathbf{r}, t)$ and $\phi_I(\mathbf{r}, t)$. The remaining fraction, $\phi_S = 1 - \phi_A - \phi_I$, accounts for a solvent component S . Their dynamics are

governed by partial differential equations [7],

$$\partial_t \phi_i = \nabla \cdot (D_i \phi_i \nabla \bar{\mu}_i) + s_i^p + s_i^d, \quad i = A, I, \quad (1)$$

which comprises diffusive fluxes (first term on the right) and source terms s_i^p and s_i^d , which, respectively, describe the production and degradation of components $i = A, I$. The diffusive fluxes are proportional to the diffusivities D_i , where we focus on the case of large solvent mobility (Sec. S3 in the Supplemental Material [12]). These diffusive and reactive fluxes are driven by differences in the nondimensional exchange chemical potentials, $\bar{\mu}_i = (v/k_B T) \delta F / \delta \phi_i$, where $k_B T$ is the relevant energy scale and v denotes the molecular volume, which we take to be the same for all components. The behavior of the molecules is governed by the free energy F , and we consider a minimal model,

$$F[\phi_A, \phi_I] = \frac{k_B T}{v} \int \left[\phi_A \ln \phi_A + \phi_I \ln \phi_I + \phi_S \ln \phi_S + \chi \phi_A \phi_I + \frac{w^2}{2} (|\nabla \phi_A|^2 + |\nabla \phi_I|^2) \right] dV, \quad (2)$$

which describes a nonideal, incompressible, and isothermal ternary fluid of species A , I , and S . The first line in Eq. (2) accounts for translational entropies of all components, which drives normal diffusion. The term proportional to the Flory parameter χ accounts for potential physical interactions between activator A and inhibitor I , whereas we assume that the solvent S interacts with neither A nor I . Finally, the last term penalizes interfaces, which will then exhibit a typical width w . This free energy, known as Flory-Huggins free energy [13–15], describes attraction between A and I for negative χ , whereas the two species repel each other for positive χ . In particular, without reactions ($s_i^p = s_i^d = 0$) and for equal average fraction $\bar{\phi}$ of A and I , minimizing F implies that A would phase separate from I if $\chi > \bar{\phi}^{-1}$ [7]. In contrast, $\chi = 0$ corresponds to the ideal diffusion commonly discussed for Turing patterns.

Turing patterns require nonlinear reactions involving the activator A and inhibitor I . To analyze the energetics of our model, we choose thermodynamically consistent rate laws

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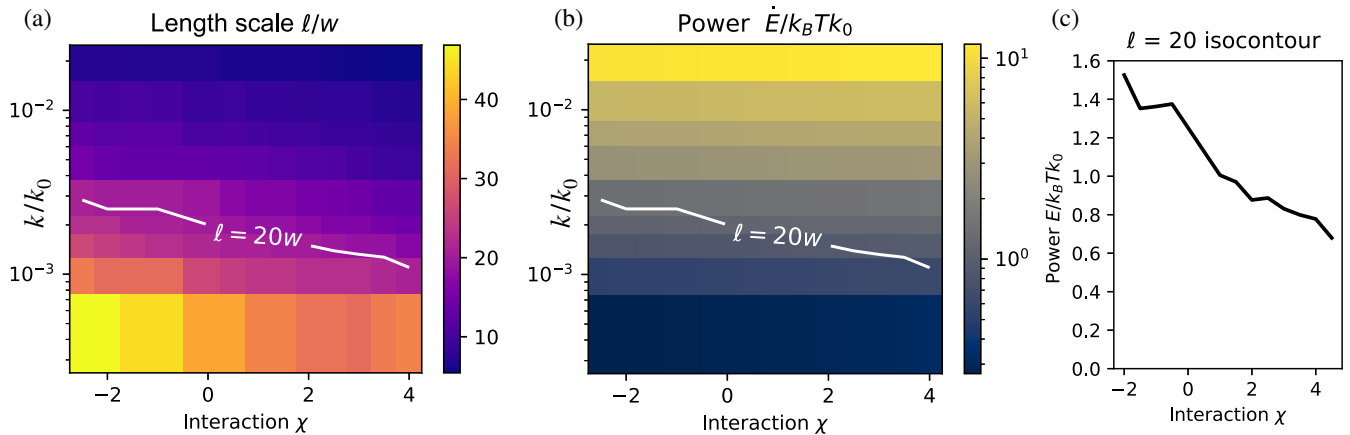


FIG. 1. Physical interactions reduce power requirements of Turing patterns. (a) Pattern length scale ℓ determined from the number of peaks in the stationary profile $\phi_A(x)$ in a finite system as a function of interaction parameter χ and reaction rate k . (b) Power $\dot{E}$ given by Eq. (4) as a function of χ and k . (c) $\dot{E}$ as a function of χ along the isocontour for $\ell = 20w$ [white lines in panels (a) and (b)]. (a)–(c) Model parameters are $\Delta\mu = 5$, $h = 5$, $D_I/D_A = 10$, $\phi_0 = 0.2$, and $k_0 = D_A/w^2$. Simulations were performed on periodic grids of size $L = 2000w$.

inspired by transition state theory [16–21]. In brief, for a general reaction $X \rightleftharpoons Y$, the net reaction flux s comprises two parts, $s = s_{\rightarrow} - s_{\leftarrow}$, stemming from the two directions in which the reaction can run. These fluxes must obey a local detailed balance condition, $s_{\rightarrow}/s_{\leftarrow} = \exp[(\bar{\mu}_X - \bar{\mu}_Y)/k_B T]$, whereas absolute rates depend on kinetic details. We use this freedom to express production and degradation of species $i = A, I$ as

$$s_i^p = k \frac{2\phi_0}{1 + (\phi_I/\phi_A)^h} [e^{\Delta\mu} - e^{\bar{\mu}_i}], \quad (3a)$$

$$s_i^d = k\phi_i [e^{-\bar{\mu}_i} - e^{\Delta\mu}], \quad (3b)$$

where the square brackets ensure the thermodynamic constraint of local detailed balance, while the prefactors encode details of the kinetics. The thermodynamic part involves the exchange chemical potentials $\bar{\mu}_i$, which capture the energy required to convert solvent into species i . To ensure that the system does not simply reduce to thermodynamic equilibrium, we also include a nondimensional chemical potential difference $\Delta\mu$, which describes a chemical driving force, e.g., provided by fuel that is kept available through a particle reservoir. For $\Delta\mu = 0$, the system obeys passive dynamics and relaxes toward equilibrium, which is characterized by $\bar{\mu}_i = 0$, so that production and degradation cease separately ($s_i^p = s_i^d = 0$) and patterns cannot be maintained. To form patterns, we choose a nontrivial kinetic prefactor, where k is a rate constant determining the overall speed of the reactions, ϕ_0 controls the average amount of A and I in the system, and the Hill coefficient h quantifies the nonlinearity in the production term [22], which biases production to regions where $\phi_A > \phi_I$. The form of the kinetic prefactor was chosen such that Eq. (3) reduces to our previous model [7] in the limit of a strongly driven system ($\Delta\mu \rightarrow \infty$ with $k \rightarrow ke^{-\Delta\mu}$). We thus expect regular patterns for sufficiently strong driving force $\Delta\mu$, provided the other parameters (particularly h , ϕ_0 , D_I/D_A , and χ) are suitably picked.

We analyze the dynamics given by Eqs. (1)–(3) using numerical simulations and find patterns of various length scales as a function of χ and k [Fig. 1(a)]. In particular, the observed

length scale increases with decreasing k , but it varies only weakly with χ , consistent with previous results [7].

We leverage our thermodynamically consistent model to determine the energetic costs of maintaining a periodic pattern. Energy is injected via the chemical driving force $\Delta\mu$ described by Eq. (3) and dissipated via diffusive and reactive fluxes. In stationary state, energy injection balances dissipation (Sec. S4 in the Supplemental Material [12]), allowing us to focus on the rate of injected energy,

$$\dot{E} = \frac{1}{V} \sum_{i=A,I} \int (s_i^p - s_i^d) \Delta\mu dV, \quad (4)$$

which is the power required to maintain the pattern. Figure 1(b) shows that $\dot{E}$ increases strongly with larger reaction rate k , whereas the interaction χ has a weaker effect. Combining Figs. 1(a) and 1(b), we find that patterns with longer periods ℓ are less expensive, presumably because they require a weaker drive to counteract the equalizing tendency of diffusion.

Our model permits multiple parameter sets that lead to the same pattern length scale ℓ . Are some of these parameters energetically favourable? To analyze this in detail, we next determine the power $\dot{E}$ at fixed pattern period ℓ . Figure 1(c) shows that $\dot{E}$ generally decreases with increasing χ along the isocontour of fixed ℓ , which we also observe for other parameters (Fig. S1 in the Supplemental Material [12]). Taken together, this indicates that repulsion between the activator A and the inhibitor I can lower the required energy input to maintain a pattern of a given period ℓ .

To understand why physical repulsion can lower the required power $\dot{E}$, we analyze patterns in detail. Physical attraction could help amplifying patterns, which would imply larger amplitudes, but the activator amplitude increases only slightly with the interaction strength χ and is independent of the reaction rate k [Fig. 2(a)]. In contrast to the activator, the amplitude of the inhibitor is vanishingly small, except for very large χ [Fig. 2(b)]. In particular, the inhibitor profile is almost flat without interactions [$\chi = 0$; Fig. 2(c)], while the activator A shows pronounced variations. This shape is consistent with

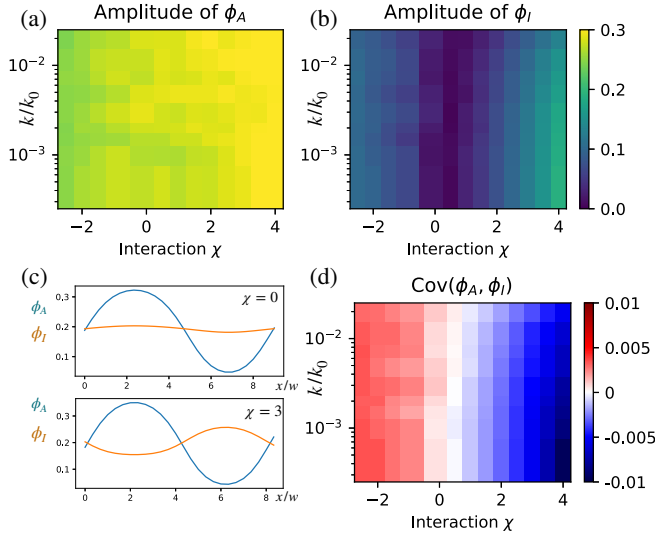


FIG. 2. Interactions induce anticorrelation between activator and inhibitor. Amplitude $\max(\phi_i) - \min(\phi_i)$ of activator profile ϕ_A [panel (a)] and inhibitor profile ϕ_I [panel (b)] for the data in Fig. 1. (c) Activator profile ϕ_A (blue) and inhibitor profile ϕ_I (orange) as a function of space x for two interaction parameters χ . (d) Covariance $\langle \phi_A \phi_I \rangle - \langle \phi_A \rangle \langle \phi_I \rangle$ for the data in Fig. 1.

the stereotypical mechanism of “local activation and global inhibition”, which underlies Turing patterns [5,6]. However, this qualitative behavior deviates for larger interactions, where both species show significant variations [Fig. 2(c)]. In particular, the profiles are now anticorrelated, whereas they are slightly correlated for $\chi = 0$. Indeed, the covariance between A and I becomes more negative for larger χ [Fig. 2(d)], suggesting that anticorrelated patterns are associated with a lower cost.

We next examine how anticorrelated patterns can emerge and why they can lower the cost $\dot{E}$ by analyzing the system for weak repulsive interactions ($|\chi| < 5$), where phase separation is absent [7]. Assuming small variations of the profiles, we linearize the diffusion term in Eq. (1), to obtain

$$\partial_t \phi_i = D_{ij} \nabla^2 \phi_j + s_i^p + s_i^d, \quad (5)$$

where the reaction terms are still given by Eq. (3), and we introduced the constant diffusivity matrix

$$D_{ij} = \begin{pmatrix} D_A(1 + \psi) & D_A(\psi + \chi \phi_*) \\ D_I(\psi + \chi \phi_*) & D_I(1 + \psi) \end{pmatrix}, \quad (6)$$

with $\psi = \phi_*/(1 - 2\phi_*)$. Here, ϕ_* denotes the concentration in the homogeneous steady state, which we obtain from the condition $s_i^p + s_i^d = 0$, using $\phi_A = \phi_I = \phi_*$ and the associated chemical potentials. Numerical simulations of Eq. (5) reproduce the essential features of the patterns of the full model (Fig. S3 in the Supplemental Material [12]), suggesting that the simplified model captures all essential features.

The diffusivity matrix D_{ij} of the simplified model given by Eq. (6) reveals that the interaction parameter χ amplifies cross-diffusion since χ only appears in the off-diagonal terms. In systems without interactions ($\chi = 0$) and $\psi \ll 1$, D_{ij} is essentially diagonal, implying that the flux of each species is governed predominantly by its own concentration gradient. In

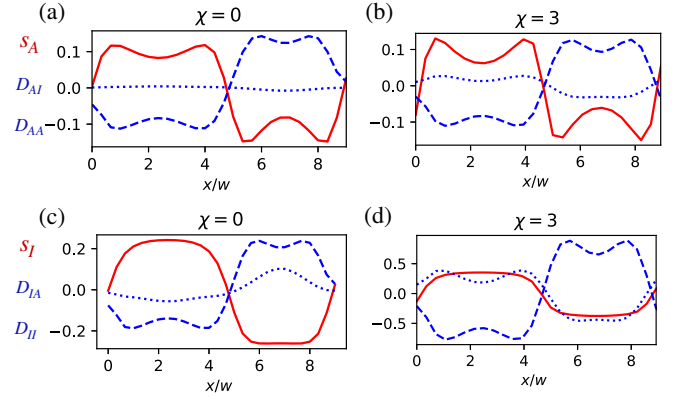


FIG. 3. Cross-diffusion aids pattern formation. Spatial profiles of the three terms on the right-hand side of Eq. (7) for the activator (upper row) and inhibitor (lower row) as a function of space x for two interaction parameters χ for the data in Fig. 1, $k = 0.01$. The equalizing self-diffusion (blue dashed lines) is often opposed by cross-diffusion (blue dotted lines) and the reactions (red lines).

contrast, if $\chi \approx \phi_*^{-1}$, the off-diagonal terms are comparable to the diagonal terms, implying strong coupling of the diffusion of the two species, suggesting that this cross-diffusion could explain the reduced cost. However, large χ also influence the chemical potentials, and thus the reaction fluxes given by Eq. (3), which might also explain the reduced cost. To test this alternative hypothesis, we next consider the limits $\Delta\mu \rightarrow \infty$ and $h \rightarrow \infty$, where the reaction fluxes reduce to piecewise constant functions, which only depend on k , ϕ_0 , and ϕ_i , but are independent of χ . This case can be solved analytically (Sec. S3 in the Supplemental Material [12]), and the resulting profiles are consistent with numerical simulations of Eq. (5) (Fig. S4 in the Supplemental Material [12]). We thus conclude that the influence of χ onto the reaction rates is negligible, and instead cross-diffusion is the major factor allowing to form patterns at reduced cost.

To understand how cross-diffusion affects patterns, it is instructive to write Eq. (5) as

$$\partial_t \phi_i = D_{iA} \nabla^2 \phi_A + D_{iI} \nabla^2 \phi_I + s_i, \quad (7)$$

for $i = A, I$ with the total reaction flux $s_i = s_i^p + s_i^d$. Analyzing the three terms on the right-hand side individually confirms that cross-diffusion is essentially absent without interactions [$\chi = 0$; Fig. 3(a)], implying that self-diffusion must balance reactions in the stationary state. In contrast, strong interactions [$\chi = 3$; Fig. 3(b)] lead to significant cross-diffusion, which is correlated with the reaction flux. Consequently, the equalizing self-diffusion is opposed by cross-diffusion and the reaction flux, allowing for a weaker reaction flux [and thus lower cost $\dot{E}$; see Eq. (4) and Sec. S4 in the Supplemental Material [12] to maintain similar profiles. Essentially, cross-diffusion, driven by the repulsion between activator and inhibitor, tends to separate the two components, which aids pattern formation.

So far, we have shown that interactions aid pattern formation for a particular driving force ($\Delta\mu = 5$), and our thermodynamically consistent model implies vanishing patterns for vanishing drive ($\Delta\mu = 0$). To understand the

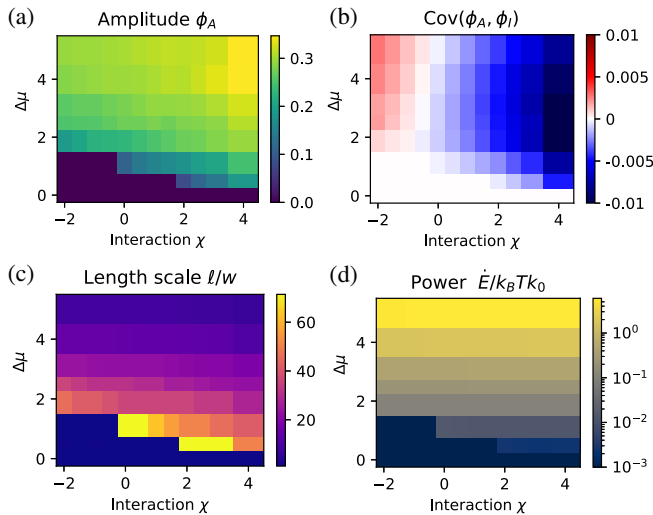


FIG. 4. Weak drive leads to efficient patterns with small amplitudes. Activator amplitude ($\max(\phi_A) - \min(\phi_A)$) [panel (a)], covariance between activator and inhibitor ($\langle \phi_A \phi_I \rangle - \langle \phi_A \rangle \langle \phi_I \rangle$) [panel (b)], pattern length scale ℓ [panel (c)], and power $\dot{E}$ [Eq. (4); panel (d)] as functions of interaction χ and chemical driving force $\Delta\mu$. Simulation parameters are $k = 0.01 k_0$, $h = 8$, $D_I/D_A = 15$, $\phi_0 = 0.2$, and $k_0 = D_A/w^2$. Simulations were performed on periodic grids of size $L = 2000w$.

detailed influence of $\Delta\mu$, we next consider fixed reaction rates k since this value has little influence on the amplitudes and covariance of profiles (Fig. 2). Figure 4 shows that there is a minimal value of $\Delta\mu$ required for pattern formation. This minimal value decreases with increasing interaction strength χ , consistent with our result that repulsive interactions aid pattern formation. If $\Delta\mu$ is sufficiently large, it has little influence on the amplitude, covariance, and pattern length scale [Figs. 2(a)–2(c)], similar to the influence of k . However, larger $\Delta\mu$ strongly increase the power $\dot{E}$ [Fig. 2(d)], suggesting that there is an optimal value for $\Delta\mu$ that minimizes $\dot{E}$ for a given length scale ℓ . Our data suggest that this optimal value is close to the threshold value for pattern formation. Indeed, we find that smaller $\Delta\mu$ leads to larger average composition ϕ_* (Fig. S6 in the Supplemental Material [12]), implying larger ψ , and thus larger cross-diffusion [Eq. (6)]. This effect also

explains the weak anticorrelation between A and I that we observe for small $\Delta\mu$ even at $\chi = 0$ [Fig. 2(b)]. Taken together, the increased cross-diffusion at small $\Delta\mu$ explains why pattern formation requires only small powers $\dot{E}$ [Fig. 2(d)], but it comes at the cost of a reduced pattern amplitude [Fig. 2(a) and Sec. S2 in the Supplemental Material [12]].

In summary, we have introduced a thermodynamically consistent model of a pattern-forming mixture of an activator and an inhibitor. We found that repulsion between the components significantly reduced the energy required to maintain patterns, indicating that such physical interactions are crucial for pattern formation. Essentially, the physical repulsion separates the inhibitor from the activator, which manifests in significant cross-diffusion. Cross-diffusion has been identified as a key factor in many pattern-forming systems [23–31], but the nonlinearities that eventually lead to phase separation amplify the effect. In contrast to standard Turing patterns, where molecules are produced in a restricted zone (local activation) and degraded everywhere (global inhibition), repulsion allows to concentrate the inhibitor (local inhibition), and thus anticorrelated patterns.

More generally, our analysis shows that the heterogeneous distribution of molecules, which is key for pattern formation, involves multiple processes. Traditional reaction-diffusion models emphasize nonlinear chemical reactions to create localized zones, but we showed that nonlinear diffusive fluxes originating from physical interactions can play similar roles. Since this diffusion does not require energy input, and dissipation mainly takes place via reactions in our case and other examples [32], it can lower the overall power required to maintain patterns. Taken to the extreme, one can then use the physical interactions to produce droplets and use chemical reactions to modify their behavior. Such chemically active droplets indeed exhibit pattern formation [20,21,33–38], and it will be interesting to explore the rich physics of reacting nonideal systems.

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Data availability. The data that support the findings of this Letter are openly available [39].

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