Permeation Instabilities in Active Polar Gels
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We present a theory of active, permeating, polar gels, based on a two-fluid model. An active relative force between the gel components creates a steady-state current. We analyze its stability, while considering two polar coupling terms to the relative current: a permeation-deformation term, which describes network deformation by the solvent flow, and a permeation-alignment term, which describes the alignment of the polarization field by the network deformation and flow. Novel instability mechanisms emerge at finite wave vectors, suggesting the formation of periodic domains and mesophases. Our results can be used to determine the physical conditions required for various types of multicellular migration across tissues.

\[ f_p = (1 - \phi)^2 \left[ \frac{1}{2} K (\nabla p)^2 + K_d \nabla \cdot p \right] - \frac{1}{2} h_{||} p^2. \] (1)

It accounts for distortions of the polarization field around a fully polarized state [10, 11]. In Eq. (1), \( K \) is the Frank constant in the single-constant approximation and \( K_d \) is a polar splay coefficient, while \( h_{||} \) is a Lagrange multiplier to ensure that \( p^2 = 1 \). The polar splay term, \((1 - \phi)^2 K_d \nabla \cdot p\), is the only polar term in the free energy. It plays an important role in our theory because of its coupling to the concentration; otherwise, it reduces to a boundary term. The coupling is considered to scale as \((1 - \phi)^2\), because the free energy originates from solvent-solvent interaction.

The gel is active. It is constantly driven out of equilibrium by the input of a fixed energy-density, \( \Delta \mu \) that corresponds, for example, to the chemical-potential difference between ATP and its hydrolysis products [12, 13].

We describe the dynamics of the concentration, polarization, and strain within a hydrodynamic framework. The network moves with a velocity \( v^n \) and the solvent with a velocity \( v^s \), corresponding to a center-of-mass (COM) velocity, \( v = \phi v^n + (1 - \phi) v^s \), and a relative current, \( J = \phi (1 - \phi) (v^n - v^s) \). We have assumed, for simplicity, the same molecular mass for both components.

The dynamics of the concentration are determined from the continuity equation, \( \partial_t \phi + \nabla \cdot (\phi v^n) = 0 \). For the polarization and network configuration, we derive in the Supplemental Material (SM) [14] the following, minimal...
constitutive relations:

\[ \left( \partial_t + v^s \cdot \nabla \right) p = \frac{1}{\tau_1} h + p \cdot \nabla v^s + \lambda J, \]

\[ \left( \partial_t + v^n \cdot \nabla \right) B = -\frac{1}{\tau} \frac{\partial B}{\partial t} : \sigma^{el} + B \nabla v^n + (\nabla v^n)^T B \]

\[ + \frac{1}{2} \xi \left( Jp + pJ \right). \]

In Eq. (2), \( \gamma_1 \) is the rotational viscosity, \( h = -\delta F/\delta p \) is the solvent orientational field, and the second term in the right-hand side (RHS) is a convective term [15–18]. In Eq. (3), \( \tau \) is a viscoelastic relaxation time and \( \sigma^{el} \) is the elastic (Kirchhoff) stress [16]. It is given by \( \sigma^{el} = -2H^B B \), where \( H^B = -\delta F/\delta B \) is the network molecular field. The next two terms in Eq. (3) are convective terms [15].

The last terms in RHS of Eqs. (2) and (3) are reactive couplings allowed by the polar symmetry. We refer to \( \lambda \) as the permeation-alignment parameter. It couples the polarization rate with the relative current. We refer to \( \xi \) as the permeation-deformation parameter. It couples the network strain-rate with the relative current. Both \( \lambda \) and \( \xi \) have units of inverse length. They are central to our work, and we give a heuristic description of their roles in Fig. 1a. In the absence of polarization and for a linear elastic stress-strain relation, Eq. (3) reduces to the upper-convected Maxwell equation [19].

Onsager’s reciprocal relations infer reciprocal, reactive couplings involving \( \lambda \) and \( \xi \) in the constitutive equation for the relative current, \( J \). As in the two-fluid model, friction due to the relative current acts as a relative force between the components. Therefore, the new permeation couplings are concurrent with new relative forces between the gel components [14],

\[ f^{rel} = \frac{1}{\gamma} J - \phi (1 - \phi) \left( \lambda h + \xi H^B \cdot p + \nu \Delta \mu p \right). \]

Here we included an active relative force \( \sim \nu \Delta \mu \), where \( \nu \) has units of inverse length, which results in an active relative current.

Overall, the force-balance equations for the two components read

\[ f^n - \phi \nabla \delta P = f^{rel}, \]

\[ f^s - (1 - \phi) \nabla \delta P = -f^{rel}, \]

where \( f^n \) and \( f^s \) are the forces acting on the network and solvent, respectively, and \( \delta P \) is a pressure difference that enforces incompressibility [14]. Equation (5) reduces to a standard two-fluid model [20] in the absence of activity and polarization. As the new relative forces do not include any derivatives, as opposed to the stress and pressure terms, they are especially important in the limit of small wave vectors.

The forces acting on each of the components are [14]

\[ f^n_\alpha = \partial_\beta \sigma^{el}_{\alpha \beta} - \delta \partial_\alpha \mu - H^B_{\beta \gamma} \partial_\alpha B_{\gamma \beta}, \]

\[ f^s_\alpha = \partial_\beta \left[ 2\eta_s v^s_{\alpha \beta} - h_s \rho_\beta + (1 - \phi) \zeta \Delta \mu Q_{\alpha \beta} \right] - h_s \partial_\alpha \rho_\beta. \]

In Eq. (6), the second term in RHS is the osmotic pressure gradient with \( \mu = \delta F/\delta \phi \) being the relative chemical potential, and the last term originates in the Ericksen stress of the gel. In Eq. (7), \( \eta_s \) is the solvent viscosity and \( v^s_{\alpha \beta} = \left( \partial_\alpha v^s_\beta + \partial_\beta v^s_\alpha \right)/2 \) is the solvent strain rate. The next term is the stress due to polarization rotations and the last term in the parenthesis is an active stress, proportional to the nematic tensor, \( Q \), and solvent concentration. The last term in RHS also originates in the Ericksen stress. These equations satisfy Onsager reciprocity with the convective terms in Eqs. (2) and (3).

**FIG. 1:** (Color online) Heuristic description of a polar solvent (green, polarization indicated by a black arrow) and a viscoelastic network (purple). (a) Reactive, polar couplings for \( J_0 < 0 \); permeation-deformation coupling, where the network becomes more aligned (\( \xi < 0 \)) or less aligned (\( \xi > 0 \)) with the relative current and network polarization, and permeation-alignment coupling, where the solvent becomes aligned against (\( \lambda < 0 \)) or in the direction of the relative current (\( \lambda > 0 \)). (b) The system is unstable for \( \xi = \lambda = 0 \) and \( J_0 K_d < 0 \), where the relative current brings the polar solvent closer together and increases its concentration.

**Linear stability analysis.** We examine the linear stability of the steady state with respect to perturbations with a growth rate \( s \) and wave vector \( q \), of the form \( \exp(st + iq \cdot r) \). The steady state is homogeneous, \( \phi = \phi_0 \), \( p = p^0 = \hat{x} \), and \( B = B^0 \), with a relative current driven by the active relative force, given by \( J^0 = J_0 p^0 \) with \( J_0 = \gamma \phi_0 (1 - \phi_0) \nu \Delta \mu \). The system is stable if Re\( s < 0 \) for all the eigenvalues of the linear system. The details of the analysis are found in the SM [14].

For simplicity and in order to highlight new instabilities that result from the polar couplings, we focus on a 2-dimensional system with wave vectors perpendicular to the steady-state polarization, \( q = q y \) [21–23]. We consider the strain-free energy, \( f_B = G\phi \text{Tr}(B - \ln B) / 2 \), corresponding to Gaussian polymer chains [24–26], where \( G\phi \) is the shear modulus, and \( f_{Bp} = 0 \).

In the hydrodynamic limit, we consider small wave vectors and solve for the growth rate up to quadratic order
in q, s ≃ s_0 + iuq - Dq^2, where s_0 is a relaxation rate, u a velocity, and D a diffusion coefficient. In the opposite, large-q limit, the system is always stable [14].

First, we analyze the stability for \( \lambda = \xi = 0 \). The uniform steady-state has no deformation (isotropic network), \( B_{0\alpha\beta}^0 = \delta_{0\alpha\beta} \). There are two purely hydrodynamic modes with \( s_0 = 0 \), which correspond to linear combinations of \( p^1 \) and \( \phi^1 \) for \( q = 0 \). Their velocity is given by \( u = \pm \sqrt{2|J_0 p_p|/|\tau_p (1 - \phi_0)|} \), where \( I_p = K/K_d \) is a polarization length-scale, which may be negative, and \( \tau_p = q^2/\eta_p \) is a relaxation time associated with the angular diffusion coefficient, \( D_p = (1 - \phi_0)^2 K/\gamma_1 \). The velocity is imaginary for \( J_0 K_d < 0 \), in which case the growth rate is positive. This instability can be understood intuitively; the polar splay aligns the solvent molecules towards each other, while the active relative current brings them closer together, as is illustrated in Fig. 1b.

The quadratic correction is given by \( D = (D_p + D_d + D_\phi)/2 \), where \( D_d = \gamma \phi_0 (1 - \phi_0)/\chi \) is the osmotic diffusion coefficient, with \( 1/\chi = \partial^2 f_\phi / \partial \phi^2 \) being the inverse osmotic compressibility. The active term, \( D_\phi = \phi \gamma d \Delta \mu/2 \), originates in the concentration dependence of the active stress. The active stress varies with the concentration, resulting in a relative current that modifies the concentration further. For sufficiently negative active stresses, the quadratic correction vanishes and then becomes negative. The critical active stress when this occurs is \( \xi_0 \Delta \mu = -2 (D_p + D_d) / (\gamma \phi_0) \).

The system is unstable for a combination of an imaginary \( u \) and negative \( D \), where the growth rate is positive and increases with \( q \). As the system is stable for large wavenumbers, this instability persists only up to a finite \( q \), and there exists a most unstable wave vector, \( q^* \), with a fastest growth rate, \( s^* \). For an imaginary velocity, \( u = |u| i \), and positive quadratic coefficient, \( D > 0 \), they are found analytically as \( q^2 = \eta s^*/2D \) and \( s^* = |u|^2/4D \). If the velocity \( u \) is real, a vanishing diffusion constant \( (D = 0) \) infers traveling waves (Hopf bifurcation). Beyond this threshold, for \( D < 0 \), the concentration-polarization instability is oscillating in time, and the values of \( q^* \) and \( s^* \) can be calculated numerically. The linear stability analysis for \( \xi = \lambda = 0 \) is summarized in Fig. 2a. Note that in the passive limit \( (\Delta \mu = 0) \), the linear term vanishes \((u = 0)\), and the system is unstable for \( 4\chi K_d^2 > K \) [11]. We assume that 

\[ 4 \chi K_d^2 < K \text{ hereafter.} \]

Next, we perform the linear stability analysis for \( \xi \neq 0 \) and \( \lambda \neq 0 \). In addition to a polarization-concentration instability, we demonstrate a possible strain instability. The eigenvector of this instability reduces to a strain component for \( q = 0 \) \( (B_{xy} \text{ for } \xi \neq 0 \text{ and } B_{yy} \text{ for } \lambda \neq 0) \), and its growth rate is \( s = s_0 - Dq^2 \text{ with } s_0 < 0 \). As the growth rate is negative for both small and large \( q \) values in this case, a numerical calculation of \( s(q) \) is required to verify the instability for intermediate \( q \) values.

Permeation deformation \( (\lambda = 0, \xi \neq 0) \). The permeation-deformation coupling, combined with the active relative current, deforms the network in the steady state, \( B_{0\alpha\beta}^0 = \delta_{0\alpha\beta} + \xi J_0 \tau_p \phi_0 \). The network is more (less) aligned with the flowing solvent for \( \xi J_0 > 0 \) \((\xi J_0 < 0)\). The network also expands (contracts) for \( \xi J_0 > 0 \) \((\xi J_0 < 0)\). As \( B_{0\alpha\beta} \) is a positive-definite tensor, a steady state exists only for \( \xi J_0 \tau > -1 \). We assume a small value of \( \xi J_0 \tau \) and expand our results to linear order in \( \xi J_0 \tau \). The permeation-deformation coupling retains the possible polarization-concentration instability to linear order in \( q \), with \( u = \pm \sqrt{2|J_0 + J_\xi| \tau / |\tau_p (1 - \phi_0)|} \). Compared to our previous result, note the additional active relative-current term, \( J_\xi = \xi \gamma \phi_0 (1 - \phi_0)^2 \chi \Delta \mu \eta_n/2 (\eta_n + \eta_n) \), where \( \eta_n = G \phi_0 \tau \) is the network viscosity. This current originates in the active stress, which strains the network, and induces a relative current due to the permeation-deformation coupling. An instability occurs for \( (J_0 + J_\xi) K_d < 0 \).

The diffusion coefficient is given by \( D = (D_p + D_d + D_\phi + D_\chi)/2 \), with \( D_\chi = -2 \eta_s \tau_p J_\xi / |(1 - \phi_0)(\eta_n + \eta_n)/\tau_p| \), it can be either positive or negative, depending on the sign of \( J_\xi K_d \). The mechanism driving the instability can be understood by considering a small concentration fluctuation. The polar-splay term results in a polarization rotation that strains the network, due to the active stress. The permeation-deformation coupling then induces a relative current that modifies the concentration. The feedback can be either positive or negative.

The permeation-deformation coupling may lead to a shear-strain instability as well. The shear strain relaxes at \( q = 0 \) with a rate \( s_0 = -(1 + \eta_n/\eta_n)/\tau \). The linear correction vanishes, while the diffusion coefficient is given by \( D = D_B - D_\chi \), where \( D_B = G \chi / (1 - \phi_0) \) is the strain diffusion coefficient, due to permeation. This infers a possible instability for \( D_\chi > D_B \). The mechanism driving the instability is as follows: a shear strain induces a relative current, due to permeation deformation. The resulting concentration gradient rotates the polarization due to the polar splay term, and the resulting active stress shears the network further. This feedback can be either positive or negative.

The linear stability analysis in the presence of permeation deformation is summarized in Fig. 2b. As the instabilities are mainly related to network deformations, stability can be achieved by reducing strain. This is possible either by a strong suppression (large \( G \) with fixed \( \tau \)) or fast relaxation (small \( \tau \) for fixed \( G \)).

Permeation alignment \( (\xi = 0, \lambda \neq 0) \). We study the stability up to linear order in \( \lambda \) [14]. The network is isotropic in the steady-state with \( B_{0\alpha\beta}^0 = \delta_{0\alpha\beta} \). The polarization-concentration velocity is \( u = \pm \sqrt{2|J_p \tau_p (1 - \phi_0) + \chi (D_\phi + D_\chi)} \). The second term in the parenthesis is independent of polar splay; as the polarization rotates, it exerts an active relative force,
which leads to a relative current. The permeation-alignment coupling then rotates the polarization further. An instability to linear order in \( q \) occurs when the argument of the square root is negative.

The diffusion coefficient is given by

\[
D = (D_p + D_\phi + D_\zeta)/2, \quad \text{with} \quad D_\phi = 2\lambda D\phi \left[ \left( \frac{\eta_s}{1-\phi_0} \right)^2 + \frac{\eta_n}{\phi_0^2} \right] J_0 + 2\phi_0 (1-\phi_0)^2 K_d \]

It can be either positive or negative and includes contributions from two mechanisms: any polarization fluctuation causes both an active relative force \( \sim J_0 \) (first mechanism) and a concentration gradient through the polar-splay coupling \( \sim K_d \) (second mechanism). Both induce a relative current that rotates the polarization, due to the permeation-alignment coupling. This feedback can be either positive or negative.

The permeation-alignment coupling can result in an instability for the elongation strain, \( B_{yy} \). The growth rate relaxes for \( q = 0 \) as \( s_0 = -1/\tau \). The linear correction vanishes, while the diffusion coefficient is given by

\[
D = (1 - \lambda \tau J_0) D_B. \]

In order to understand the \( \lambda \) term, consider a fluctuation in \( B_{yy} \). The resulting stress induces a relative current that rotates the polarization by permeation alignment. The active relative force then modifies the relative current that further strains the network by convection.

The linear stability analysis in the presence of permeation alignment is summarized in Fig. 2c. As the instabilities are mainly related to the relative current in the \( y \)-direction, stability can be achieved by lowering the pressure gradient. This is possible by lowering the solvent and network viscosities, which induce smaller pressures.

**Discussion.** In this Letter, we have reported finite-wavelength instabilities that result from polar couplings to the relative current between a viscoelastic network and active, polar fluid. This implies possible mesophases and periodic domains with continuous flow patterns [11, 28, 29]. The permeation couplings may also modify known instabilities in ordered, active nematics [17, 18, 22], close to the isotropic-polar transition [30], and in the shape of active permeating sheets [31].

Our theory can be used to describe cell migration in tissue. Cells often migrate collectively in a fluid-like manner with weak and short-lived mutual adhesions (“multicellular streaming” [3, 32]). In a coarse-grained view, this can be regarded as permeation of an active, polar fluid in a viscoelastic network. Our analysis suggests the required physical conditions for migrating cells to traverse a tissue homogeneously (a stable, flowing steady-state), as opposed to migration in strands or local cell movement in confined domains (finite-\( q \) instabilities).

The novel ingredients of our theory describe in this context the forces exerted between cells and, for example, the extra-cellular matrix (ECM), including matrix deformation [33, 34]. The cross-talk between migrating cells and the ECM is called “dynamic reciprocity”, and it is considered important to embryonic development, tissue regeneration, and metastasis [35–37]. Our work thus provides a new, hydrodynamic framework to describe “dynamic reciprocity” during collective migration. We investigate this application further in a separate study [27].

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See Supplemental Material at [URL will be inserted by publisher] for the derivation of Eqs. (2)-(7) and the details of the calculations presented in the Letter.

The convective terms in Eqs. (2) and (3) correspond to Lie derivatives [14]. There are other possible choices of convective terms [14]. A similar and more general constitutive equation for one-component, nematic gels is used in Refs. [17, 18].

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