Permeation Instabilities in Active Polar Gels

Ram M. Adar[1,2,3,*] and Jean-François Joanny[1,2,3]

[1]*Collège de France, 11 place Marcelin Berthelot, 75005 Paris, France*
[2]*Laboratoire Physico-Chimie Curie, Institut Curie, Centre de Recherche,*
Paris Sciences et Lettres Research University, Centre National de la Recherche Scientifique, 75005 Paris, France
[3]*Université Pierre et Marie Curie, Sorbonne Universités, 75248 Paris, France*

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.

Introduction.—Active materials are driven out of equilibrium by a constant consumption of energy at the microscopic level, which is converted into forces and motion [1]. These include, among others, biological objects on different scales, ranging from active motors, to living cells, and even groups of animals. A useful framework for the study of active matter is hydrodynamics. Similarly to continuum theories of liquid crystals [2], it describes macroscopic physical properties and flows, relying on conservation laws and symmetries. It also provides an efficient language to distinguish between active materials, based on their composition, orientational order, and rheological properties.

The biological motivation to our physical theory is multicellular migration. Connective tissues are made of cells in a complex extracellular environment, which often has a viscoelastic behavior [3]. Cells may migrate collectively in tissues in a fluidlike manner [4]. We propose that the tissue can be regarded, therefore, as an active, permeating, gel with the cells acting as a solvent. We further focus on a *polar* solvent, relevant to cells with spindlelike shapes or a defined direction. While active, permeating, polar gels have been studied in other contexts in the past [5–9], these studies remain at a general level, without interpreting the new Onsager transport coefficients of the theory, or clarifying the nature of the interaction between the two gel components.

Our new theory is formulated in a systematic way as a two-fluid model. It identifies the internal forces of each component and the interaction forces between components, which orient the solvent ("permeation alignment") and deform the network ("permeation deformation"). These mechanisms drive novel, finite-wavelength instabilities, unique to active, permeating polar gels. Our theory opens

an avenue to study interactions between cells and their environment during multicellular migration.

Theory.—We consider a two-component gel, composed of an active, polar solvent (s) and a viscoelastic network (n). The polarization field is given by the unit vector $\boldsymbol{p}$. The network configuration is described by the left Cauchy-Green strain tensor $\boldsymbol{B} = \boldsymbol{E}\boldsymbol{E}^T$, where $\boldsymbol{E}$ is the deformation gradient tensor. We consider the network component to be viscoelastic; elastic at short times and flowing at long times. It has a volume fraction ϕ and the solvent $1 - \phi$. The gel is assumed to be incompressible.

The free energy of the gel can be decomposed into $F = \int d\boldsymbol{r}(f_p + f_B + f_{Bp} + f_\phi)$, where f_p is the polarization free-energy density, f_B is the elastic free-energy density, f_{Bp} is a strain-polarization coupling term, and f_ϕ is the mixing free-energy density. The polarization contribution is given by

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

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 $h_\parallel$ is a Lagrange multiplier to ensure that $\boldsymbol{p}^2 = 1$. The polar splay term, $(1 - \phi)^2 K_d \nabla \cdot \boldsymbol{p}$, 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 adenosine triphosphate 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 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 specific 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 [14] the following, minimal constitutive relations:

$$(\partial_t + v^s \cdot \nabla)p = \frac{1}{\gamma_1}h + p \cdot \nabla v^s + \lambda J, \qquad (2)$$

$$(\partial_t + v^n \cdot \nabla)B = -\frac{1}{\tau}\frac{\partial B}{\partial \sigma^{\text{el}}} : \sigma^{\text{el}} + B\nabla v^n + (\nabla v^n)^T B$$
$$+ \frac{1}{2}\xi(Jp + pJ). \qquad (3)$$

In Eq. (2), γ_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), τ is a viscoelastic relaxation time and σ^{el} is the elastic (Kirchhoff) stress [16]. It is given by $\sigma^{\text{el}} = -2H^B B$, 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 λ as the *permeation-alignment* parameter. It couples the polarization rate with the relative current. We refer to ξ as the *permeation-deformation* parameter. It couples the network strain-rate with the relative current. Both λ and ξ have units of inverse length. They are central to our work, and we give a heuristic description of their roles in Fig. 1(a). 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 λ and ξ 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],

$$f^{\text{rel}} = \frac{1}{\gamma}J - \phi(1 - \phi)(\lambda h + \xi H^B \cdot p + \nu\Delta\mu p). \qquad (4)$$

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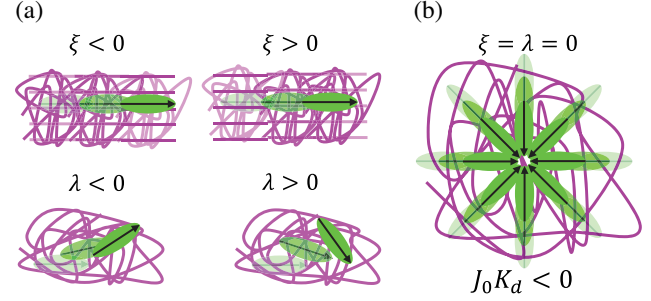

FIG. 1. Heuristic description of a polar solvent (green, polarization indicated by a black arrow) and a viscoelastic network (purple). (a) Reactive, polar couplings for $J_0 < 0$; permeation-deformation coupling, where the network becomes more aligned ($\xi < 0$) or less aligned ($\xi > 0$) with the relative current and solvent 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.

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

$$f^n - \phi\nabla\delta P = f^{\text{rel}},$$
$$f^s - (1 - \phi)\nabla\delta P = -f^{\text{rel}}, \qquad (5)$$

where f^n and f^s are the forces acting on the network and solvent, respectively, and δP 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]

$$f^n_\alpha = \partial_\beta \sigma^{\text{el}}_{\alpha\beta} - \phi\partial_\alpha\bar{\mu} - H^B_{\beta\gamma}\partial_\alpha B_{\gamma\beta}, \qquad (6)$$

$$f^s_\alpha = \partial_\beta[2\eta_s v^s_{\alpha\beta} - h_\alpha p_\beta + (1 - \phi)\zeta\Delta\mu Q_{\alpha\beta}] - h_\beta\partial_\alpha p_\beta. \qquad (7)$$

In Eq. (6), the second term in rhs is the osmotic pressure gradient with $\bar{\mu} = \delta F/\delta\phi$ being the relative chemical potential, and the last term originates in the Ericksen stress of the gel. In Eq. (7), η_s is the solvent viscosity and $v^s_{\alpha\beta} = (\partial_\alpha v^s_\beta + \partial_\beta v^s_\alpha)/2$ 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).

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

$\exp(st + i\boldsymbol{q} \cdot \boldsymbol{r})$. The steady state is homogeneous, $\phi = \phi_0$, $\boldsymbol{p} = \boldsymbol{p}^0 = \hat{x}$, and $\boldsymbol{B} = \boldsymbol{B}^0$, with a relative current driven by the active relative force, given by $\boldsymbol{J}^0 = J_0 \boldsymbol{p}^0$ with $J_0 = \gamma\phi_0(1 - \phi_0)\nu\Delta\mu$. The system is stable if $\mathrm{Re}\, s < 0$ for all the eigenvalues of the linear system. The details of the analysis are found in the Supplemental Material [14]. For simplicity and in order to highlight new instabilities that result from the polar couplings, we focus on a two-dimensional system with wave vectors perpendicular to the steady-state polarization, $\boldsymbol{q} = q\hat{y}$ [21–23]. We consider the strain free energy, $f_B = G\phi\mathrm{Tr}(\boldsymbol{B} - \ln\boldsymbol{B})/2$, 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, $s \simeq s_0 + iuq - Dq^2$, 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), $B^0_{\alpha\beta} = \delta_{\alpha\beta}$. There are two purely hydrodynamic modes with $s_0 = 0$, which correspond to linear combinations of p^1 and ϕ^1 for $q = 0$. Their velocity is given by $u = \pm\sqrt{2J_0 l_p/[\tau_p(1 - \phi_0)]}$, where $l_p = K/K_d$ is a polarization length scale, which may be negative, and $\tau_p = l_p^2/D_p$ 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 toward each other, while the active relative current brings them closer together, as is illustrated in Fig. 1(b).

The quadratic correction is given by $D = (D_p + D_\phi + D_\zeta)/2$, where $D_\phi = \gamma\phi_0(1 - \phi_0)/\chi$ is the osmotic diffusion coefficient, with $1/\chi = \partial^2 f_\phi/\partial\phi^2$ being the inverse osmotic compressibility. The active term, $D_\zeta = \phi_0\gamma\zeta\Delta\mu/2$, 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 $\zeta_c\Delta\mu = -2(D_p + D_\phi)/(\gamma\phi_0)$.

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 wave vectors, 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, $u = i|u|$, and positive quadratic coefficient, $D > 0$, they are found analytically as $q^* = |u|/2D$ 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. 2(a). 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 $4\chi K_d^2 < K$ 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
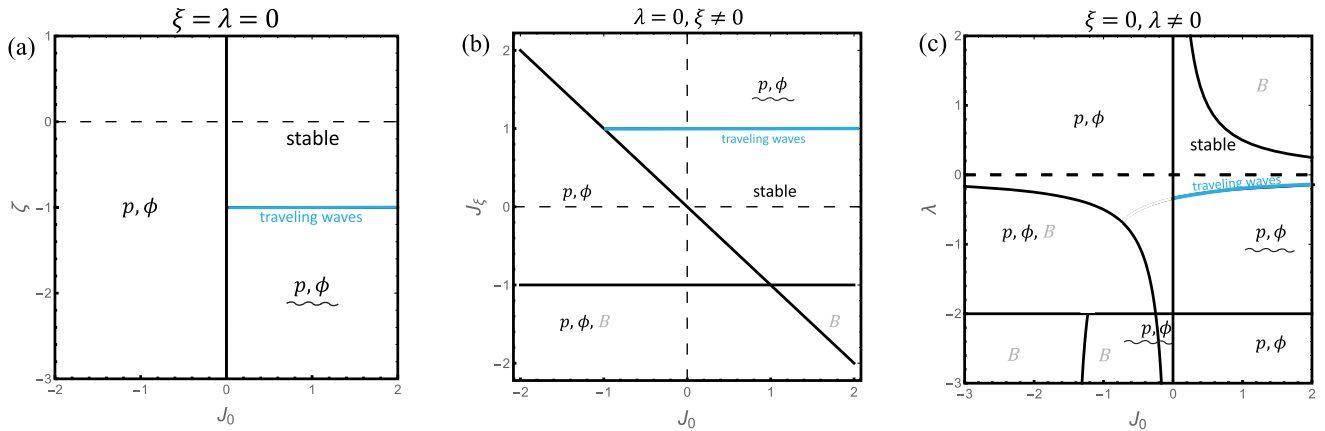

FIG. 2. Linear stability diagrams for active, permeating, polar gels. Polarization, concentration, and possible strain instabilities are denoted by p, ϕ, and gray B, respectively. Waves indicate instabilities that oscillate in time. J_0 is written in units of $(1 - \phi_0)l_p/\tau_p$. (a) Stability diagram for $\xi = \lambda = 0$. The value $2(D_p + D_\phi) = \gamma\phi_0\Delta\mu$ is used. (b) Stability diagram for $\lambda = 0$, $\xi \neq 0$ with J_ξ written in units of $(1 - \phi_0)l_p/\tau_p$. The values $1 + (D_\phi + D_\zeta)/D_p = D_B/D_p = 2\eta_s\tau/(\eta_s + \eta_n)\tau_p$ are used. (c) Stability diagram for $\xi = 0$, $\lambda \neq 0$ with λ written in units of $1/(1 - \phi_0)l_p$. The values $D_p = D_\phi + D_\zeta$, $4\gamma_1/(1 - \phi_0) = 3[\eta_s/(1 - \phi_0)^2 + \eta_n/\phi_0^2]$, $2\phi_0\gamma_1\gamma = 3(1 - \phi_0)l_p^2$, and $\tau = 2\tau_p$ are used.

component for $q = 0$ (B_{xy} for $\xi \neq 0$ and B_{yy} for $\lambda \neq 0$), and its growth rate is $s = s_0 - Dq^2$ 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, $B_{\alpha\beta}^0 = \delta_{\alpha\beta} + \xi J_0 \tau p_\alpha^0 p_\beta^0$. 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 $B_{\alpha\beta}$ 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 ξ [14].

The permeation-deformation coupling retains the possible polarization-concentration instability to linear order in q, with $u = \pm\sqrt{2(J_0 + J_\xi)l_p/[\tau_p(1 - \phi_0)]}$. Compared to our previous result, note the additional active relative-current term, $J_\xi = \xi\gamma\phi_0(1 - \phi_0)^2\zeta\Delta\mu\eta_n/[2(\eta_s + \eta_n)]$, 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 $D = (D_p + D_\phi + D_\zeta + D_\xi)/2$, with $D_\xi = -2\eta_s\tau l_p J_\xi/[(1 - \phi_0)(\eta_s + \eta_n)\tau_p]$, 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 $s_0 = -(1 + \eta_n/\eta_s)/\tau$. The linear correction vanishes, while the diffusion coefficient is given by $D = D_B - D_\xi$, where $D_B = G\gamma/(1 - \phi_0)$ is the strain diffusion coefficient, due to permeation. This infers a possible instability for $D_\xi > D_B$. 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. 2(b). 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 τ) or fast relaxation (small τ for fixed G).

Permeation alignment $(\xi = 0, \lambda \neq 0)$.—We study the stability up to linear order in λ [14]. The network is isotropic in the steady state with $B_{\alpha\beta}^0 = \delta_{\alpha\beta}$. The polarization-concentration velocity is $u = \pm\sqrt{[2l_p/\tau_p(1 - \phi_0) + \lambda(D_\phi + D_\zeta)]J_0}$. 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 $D = (D_p + D_\phi + D_\zeta + D_\lambda)/2$, with $D_\lambda = 2\lambda D_\phi\chi\{[\eta_s/(1 - \phi_0)^2 + \eta_n/\phi_0^2]J_0 + 2\phi_0(1 - \phi_0)^2K_d\}$. 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 λ 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. 2(c). 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 [11,27,28]. The permeation couplings may also modify known instabilities in ordered, active nematics [17,18,22], close to the isotropic-polar transition [29], and in the shape of active permeating sheets [30].

Our theory can be used to describe cell migration in tissues. Cells often migrate collectively in a fluidlike manner with weak and short-lived mutual adhesions ("multicellular streaming" [4,31]). 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 extracellular matrix (ECM), including matrix deformation [32,33]. 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 [34–36]. Our work thus provides a new, hydrodynamic framework to describe dynamic reciprocity during collective migration. We investigate this application further in a separate study [37].

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[*]ram.adar@college-de-france.fr

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