

Temperature of an active nematic

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We employ a hydrodynamic framework for active matter coupled to an environment to study the local temperature of an active nematic, assuming proximity to thermal equilibrium. We show that, due to the mechanosensitivity of fuel consumption, linearized temperature correlations in a homogeneous active nematic steady state remain unaffected by activity. However, we demonstrate that local shearing and twisting cause a confined active nematic undergoing a spontaneous flow transition to develop a distinctive inhomogeneous temperature profile, serving as a thermal signature of activity.

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Introduction. Active matter consists of microscopic, fuel-consuming agents, enabling it to exhibit macroscopic behavior that is distinct from ordinary passive matter. In particular, when active matter admits a continuum hydrodynamic description for collective transport, it possesses the remarkable ability to circumvent various constraints that govern passive systems, arising from the local second law of thermodynamics, Onsager's reciprocity relations, and fluctuation-dissipation theorems (FDTs).

The transport phenomena in active matter become particularly striking when some form of spontaneous order is present, such as in nematic liquid crystals, which exhibit spontaneous rotational order [1,2]. Active nematics constitute one of the most widely studied classes of active matter, from both experimental and theoretical perspectives [3–7]. In particular, they exhibit distinctive turbulent states that do not arise in ordinary passive nematics [8–11]. Active nematics are realized in a variety of physical systems, such as bacterial populations [12–15], microtubule-motor protein mixtures [16,17], swarming sperm cells [18], and epithelial cells [4,19,20]. Hydrodynamics provides a promising theoretical framework for describing active nematics, wherein the hydrodynamic theory of ordinary passive nematics [21] is extended to incorporate the effects of fuel consumption [22–25].

Hydrodynamics describes the near-equilibrium macroscopic behavior of a varied classes of physical systems. It governs the evolution of collective variables, such as energy, momentum, and mass, as well as Goldstone modes of

spontaneously broken symmetries [26]. A central assumption of hydrodynamics is local thermal equilibrium, which breaks down in the presence of microscopic active agents that drive the system away from equilibrium. However, when active effects remain reasonably small and comparable to the local gradients away from thermal equilibrium, activity can be introduced perturbatively within the hydrodynamic framework [27–29].

Extending the framework of hydrodynamics to active matter requires accounting for the fuel-consuming processes inherent to active agents, which collectively serve as a local energy source supporting activity [28]. As such, fuel consumption leads to a continuous buildup of energy in the system, preventing it from reaching a stable steady state. Consequently, such a framework inevitably cannot make long-time predictions for temperature. To address this issue, one must recognize that active matter is defined not only by the presence of fuel-consuming agents but also by its ability to dissipate excess energy into the environment.

In earlier work, we incorporated this idea into the hydrodynamics of active matter by allowing the system to exchange of energy and entropy with an environment at a fixed temperature T_E [30]. This restores the balance of energy, thereby allowing for nonequilibrium steady states maintained at a temperature above T_E . The loss of entropy to the environment also modifies the local second law of thermodynamics, making it possible for active matter to acquire unique transport properties that are not present in passive systems [30].

The conversion of chemical energy to kinetic energy sources the energy balance equation of the fluid, and Onsager reciprocity dictates that this sourcing of energy is *mechanosensitive*, i.e., sensitive to the state of the system [23,28,31,32]. We show that, as a consequence, linear temperature correlations in a homogeneous active nematic steady state are entirely agnostic of activity, which is unlike the density correlator in dry active matter [33–35]. Nonetheless, temperature dynamics exhibit nontrivial active signatures when the nematic enters an inhomogeneous state induced

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by activity. To study this, we compute the local temperature profile of an active nematic in a confined geometry close to the spontaneous flow transition [36]. We unravel an interesting qualitative interplay between the local temperature profile and the length scale of energy relaxation to the environment [37]. Our work provides compelling evidence of how the hydrodynamic framework can enable us to understand the thermal characteristics of active matter.

Passive hydrodynamics. To set the stage, let us begin with a passive two-dimensional incompressible fluid. The hydrodynamic variables consist of the conserved energy density ϵ and momentum density π^i , with $i, j, \dots \in \{x, y\}$ denoting spatial indices. Correspondingly, we have the conservation equations

$$\partial_t \epsilon + \partial_i \epsilon^i = 0, \quad \partial_t \pi^i - \partial_j t^{ij} = 0, \quad (1)$$

where ϵ^i and t^{ij} denote the energy flux and stress tensor, respectively. Incompressibility requires $\partial_i v^i = 0$, where $v^i = \pi^i / \rho_0$ is the fluid velocity and ρ_0 is the constant mass density. Identifying the comoving energy density $\varepsilon = \epsilon - \frac{1}{2} \rho_0 v^2$ and flux $\varepsilon^i = \epsilon^i + \frac{1}{2} \rho_0 v^2 v^i + t^{ij} v_j$, the constitutive equations for the passive fluid are given by

$$\varepsilon^i = \varepsilon v^i + \varepsilon_{\text{nhs}}^i, \quad t^{ij} = -\pi^i v^j - p \delta^{ij} + t_{\text{nhs}}^{ij}. \quad (2)$$

Here, p and T are the local fluid pressure and temperature, while $\varepsilon_{\text{nhs}}^i$ and t_{nhs}^{ij} denote the dissipative fluxes.

To fix the dissipative constitutive relations, let us consider the dissipation rate of the fluid $\Theta \equiv \partial_t s + \partial_i s^i$, where s is the entropy density and $T s^i = T s v^i + \varepsilon_{\text{nhs}}^i$ is the heat flux. Using thermodynamic identities and conservation equations, we find

$$T \Theta = -\frac{1}{T} \varepsilon_{\text{nhs}}^i \partial_i T + t_{\text{nhs}}^{ij} u_{ij}, \quad (3)$$

where $u_{ij} = \frac{1}{2}(\partial_i v_j + \partial_j v_i)$ is the fluid shear tensor. Since the dissipation rate should be locally non-negative, the nonhydrostatic fluxes must take the form

$$\varepsilon_{\text{nhs}}^i = -\kappa \partial^i T + \xi_{\text{nhs}}^i, \quad t_{\text{nhs}}^{ij} = 2\eta u^{ij} + \xi_{\text{nhs}}^{ij}, \quad (4)$$

where κ and η are the thermal conductivity and viscosity of the fluid, respectively. Requiring $\Theta \geq 0$ leads to the second-law constraints $\kappa, \eta \geq 0$.

We have also included the stochastic fluxes ξ 's in Eq. (4) to account for thermal fluctuations [38–41]. These are defined to have zero mean, $\langle \xi(x, t) \rangle = 0$, but nonzero short-ranged variance $\langle \xi(x, t) \xi(x', t') \rangle \propto \delta^{(2)}(x - x') \delta(t - t')$. In local thermal equilibrium, the magnitude of the variance is fixed by FDT in terms of the dissipative transport coefficients κ and η (see the Supplemental Material [42] for a review).

We can use this hydrodynamic model to derive the temperature dynamics on a passive incompressible fluid. Ignoring stochastic noise, we have [43]

$$c_v \frac{d}{dt} T - \partial_i (\kappa \partial^i T) = 2\eta (u_{ij})^2, \quad (5)$$

where $d/dt = \partial_t + v^i \partial_i$ is the material derivative along the fluid and $c_v = \partial \epsilon / \partial T$ is the heat capacity. At linearized order, temperature fluctuations decouple and exhibit diffusional dispersion relations $\omega = -i D_\epsilon k^2$, where $D_\epsilon = \kappa / c_v$ is the energy diffusion coefficient and ω, k^i are the frequency and wave vector of linearized perturbations. More generally, however,

inhomogeneous shearing of the fluid velocity affects temperature via nonlinear interactions.

Hydrodynamics with fuel consumption. We now introduce fuel consumption into our hydrodynamic model, which provides the energy source needed for supporting activity [28]. As we formalized in Ref. [30], for such models to admit an active steady state maintained at a fixed temperature, we need to also allow for an outflow of energy to the environment. In the present case, the environment may model a fixed substrate on which the two-dimensional active nematic lies. These ingredients are summarized in the energy balance equation [44]

$$\partial_t \epsilon + \partial_i \epsilon^i = r_F \Delta \mu - r_E k_B T_E, \quad (6)$$

where we have introduced the fuel reaction rate r_F and heat loss rate r_E , together with the corresponding chemical potential difference $\Delta \mu$ and environment temperature T_E . Throughout this work, we will assume $\Delta \mu$ and T_E to be constant and positive.

We can again employ the second law of thermodynamics to determine the form of the rates $r_{F,E}$. In the presence of energy outflow to the environment, the dissipation rate Θ is no longer necessarily non-negative. However, the total dissipation rate $\Theta_{\text{tot}} = \Theta + k_B r_E$, which also includes entropy loss to the environment, should still be non-negative [30]. We find

$$T \Theta_{\text{tot}} = r_F \Delta \mu + r_E k_B \Delta T - \frac{1}{T} \varepsilon_{\text{nhs}}^i \partial_i T + t_{\text{nhs}}^{ij} u_{ij}, \quad (7)$$

which leads to the constitutive relations for the rates

$$r_F = \gamma_F \Delta \mu + \xi_F, \quad r_E = \gamma_E k_B \Delta T + \xi_E. \quad (8)$$

Here, $\Delta T = T - T_E$ is the temperature differential between the system and the environment, $\gamma_{F,E}$ are some coefficients that control the respective rates, while $\xi_{F,E}$ represent the associated stochastic noise. Requiring $\Theta_{\text{tot}} \geq 0$ enforces the constraints $\gamma_F, \gamma_E \geq 0$, in addition to $\kappa, \eta \geq 0$.

Plugging the rates (8) back into the energy balance equation (6), we can derive the temperature dynamics

$$c_v \frac{d}{dt} T - \partial_i (\kappa \partial^i T) + c_v \Gamma_\epsilon \delta T = 2\eta (u_{ij})^2, \quad (9)$$

where $\Gamma_\epsilon = k_B^2 T_E \gamma_E / c_v$ and $\delta T = T - T_0$, with

$$T_0 = T_E \left(1 + \frac{\gamma_F}{\gamma_E} \frac{\Delta \mu^2}{k_B^2 T_E^2} \right). \quad (10)$$

It follows that the fluid only admits a steady-state solution at temperature T_0 . Note that $T_0 \geq T_E$ in the presence of fuel consumption, regardless of the sign of $\Delta \mu$, for any $\gamma_{F,E} \geq 0$ consistent with entropy production, whereas $T_0 = T_E$ when the fuel is turned off. Further note that obtaining the steady-state temperature T_0 is more involved when the coefficients $\gamma_{F,E}$ are allowed to depend on the system or environment temperature. In this work, we will assume all hydrodynamic coefficients to be temperature independent for simplicity. A steady-state solution like in Eq. (10) does not exist when coupling to environment is absent, i.e., when $\gamma_E \rightarrow 0$, and leads to a steady growth of energy and temperature [28].

Since energy is not conserved, linearized temperature fluctuations near the steady state relax at characteristic timescale $2\pi / \Gamma_\epsilon$, with dispersion relations $\omega = -i \Gamma_\epsilon - i D_\epsilon k^2$. We can

also identify the characteristic length scale $L_\epsilon = 2\pi\sqrt{D_\epsilon/\Gamma_\epsilon}$ at which the temperature fluctuations decay.

FDT only applies to systems fluctuating around thermal equilibrium and, as such, cannot be used in a nonequilibrium steady state. Nonetheless, we can tune the system close to thermal equilibrium by turning off the fuel source and then use FDT to calibrate the noise variances (see Ref. [33,45]). We find (see the Supplemental Material [42])

$$\begin{aligned}\langle \xi_F(x, t) \xi_F(x', t') \rangle &= 2k_B T_0 \gamma_F \delta^{(2)}(x - x') \delta(t - t'), \\ \langle \xi_E(x, t) \xi_E(x', t') \rangle &= 2k_B T_0 \gamma_E \delta^{(2)}(x - x') \delta(t - t').\end{aligned}\quad (11)$$

Active nematics. The effect of fuel consumption has been somewhat trivial in our hydrodynamic model thus far. The temperature evolution in Eq. (9) is qualitatively only affected by energy outflow to the environment, which determines the relaxation rate Γ_ϵ , while fuel consumption only affects the value of the steady-state temperature T_0 . In contrast, velocity evolution is not affected by fuel consumption at all. To probe more nontrivial signatures of activity, let us now generalize our hydrodynamic model to active nematics. We consider the symmetric-traceless nematic order parameter $Q_{ij} = S(n_i n_j - \frac{1}{2} \delta_{ij})$, where the unit vector $n_i = (\cos \theta, \sin \theta)$ represents the orientation of nematic order and the scalar S determines its strength. The nematic free energy density is given by

$$\mathcal{F}_{\text{nem}} = \frac{K}{2} (\partial_k Q_{ij})^2 + \frac{a}{2} (Q_{ij})^2 + \frac{b}{2} (Q_{ij})^4, \quad (12)$$

where K is the Frank distortion coefficient. In general, the Frank coefficients for bend and splay distortions may differ [2], but we focus on the case where all deformations are treated equivalently. The parameters a, b determine the state of the system. For $a > 0$, the system exists in the isotropic state, $S = 0$, without nematic order. However, for $a < 0$, the system transitions to the nematic state with $S = \sqrt{-a/b}$.

The nematic free energy (12) contributes to the constitutive relations for energy flux and stress tensor as

$$\begin{aligned}\varepsilon^i &= \varepsilon v^i - K \partial^i Q^{kl} \frac{d}{dt} Q_{kl} + \varepsilon_{\text{nhs}}^i, \\ t^{ij} &= -\pi^i v^j + (\mathcal{F}_{\text{nem}} - p) \delta^{ij} - K \partial^i Q^{kl} \partial^j Q_{kl} \\ &\quad + Q^i_k \mathcal{H}^{jk} - Q^j_k \mathcal{H}^{ik} + t_{\text{nhs}}^{ij},\end{aligned}\quad (13)$$

where $\mathcal{H}^{ij} = -\delta \mathcal{F}_{\text{nem}} / \delta Q_{ij}$. The equation of motion for Q_{ij} can be expressed as

$$\frac{d}{dt} Q_{ij} + (\Omega_i^k Q_{kj} - Q_{ik} \Omega^k_j) = \mathcal{V}_{ij}^{\text{nhs}}, \quad (14)$$

where $\Omega_{ij} = \frac{1}{2}(\partial_i v_j - \partial_j v_i)$ is the fluid vorticity tensor that enters the corotational term in the parenthesis, while $\mathcal{V}_{ij}^{\text{nhs}}$ denotes the dissipative nematic dynamics.

In the presence of active nematicity, together with the fuel source and energy sink, the total dissipation rate modifies from Eq. (7) to (see the Supplemental Material [42])

$$\begin{aligned}T \Theta_{\text{tot}} &= r_F \Delta \mu + r_E k_B \Delta T \\ &\quad - \frac{1}{T} \varepsilon_{\text{nhs}}^i \partial_i T + \tau_{\text{nhs}}^{ij} u_{ij} + \mathcal{V}_{ij}^{\text{nhs}} \mathcal{H}^{ij}.\end{aligned}\quad (15)$$

This leads to the dissipative constitutive relations [28]

$$\begin{aligned}\varepsilon_{\text{nhs}}^i &= -\kappa \partial^i T + \xi_\epsilon^i, \\ t_{\text{nhs}}^{ij} &= 2\eta u^{ij} - S \lambda' \mathcal{H}^{ij} - \zeta Q^{ij} + \xi_\pi^{ij}, \\ \mathcal{V}_{\text{nhs}}^{ij} &= \frac{1}{\sigma_Q} \mathcal{H}^{ij} + S \lambda u^{ij} + \xi_Q^{ij}, \\ r_F &= \gamma_F \Delta \mu + \alpha_F Q^{ij} u_{ij} + \xi_F,\end{aligned}\quad (16)$$

where σ_Q is the rotational viscosity, while λ and λ' correspond to the flow-alignment parameter [46,47]. In particular, the stress tensor contains an active term proportional to Q^{ij} , controlled by the coefficient ζ , which is absent for passive nematics. We have also included a mechanosensitive coefficient α_F in the fuel rate, whose relevance will be clear momentarily. The variances of respective stochastic fluxes are provided in the Supplemental Material [42].

Assuming that the microscopic system underlying the hydrodynamic model, including the fuel and environment components, is time-reversal invariant, Onsager's reciprocity relations require that $\lambda' = \lambda$, together with the mechanosensitivity constraint [48]

$$\zeta = \alpha_F \Delta \mu. \quad (17)$$

In other words, the fuel burning rate r_F becomes mechanosensitive in the presence of activity [28]. Further imposing $\Theta_{\text{tot}} \geq 0$ leads to the constraint $\sigma_Q \geq 0$.

Active temperature dynamics. Due to the mechanosensitivity of fuel consumption, temperature dynamics of an active nematic is not directly sensitive to activity. To wit, the energy balance equation leads to

$$c_v \frac{d}{dt} T - \partial_i (\kappa \partial^i T) + c_v \Gamma_\epsilon \delta T = 2\eta (u_{ij})^2 + \frac{1}{\sigma_Q} (\mathcal{H}_{ij})^2, \quad (18)$$

which is not affected by the active coefficient ζ . Had we not imposed the Onsager mechanosensitivity constraint (17), the right-hand side would contain an additional term $(\alpha_F \Delta \mu - \zeta) Q^{ij} u_{ij}$, which would indeed be sensitive to ζ . Because of this, temperature correlations of an active nematic linearized around a homogeneous steady state do not signal activity.

To see this, let us consider the steady state given by fixed values of $S = S_0 \equiv \sqrt{-a/b}$ and $T = T_0$ given in Eq. (10), and arbitrary constant values of $\theta = \theta_0$ and $v^i = v_0^i$. Small wave vector perturbations of this state, with $k < k_c(\Delta\theta)$, are dynamically unstable in the presence of activity and drive the system into a state of nematic turbulence [22]. Here,

$$k_c(\Delta\theta)^2 = \frac{\zeta S_0}{D_Q} \frac{(1 + \lambda \cos(2\Delta\theta)) \cos(2\Delta\theta)}{2\eta + S_0^2 \sigma_Q (1 + \lambda^2 + 2\lambda \cos(2\Delta\theta))} \quad (19)$$

and $\Delta\theta = \theta_0 - \arctan(k_y/k_x)$ is the relative angle between the wave vector and the nematic order and $D_Q = K/\sigma_Q$ is the nematic diffusion coefficient (see the Supplemental Material [42] for a review). Nonetheless, it is possible to stabilize the homogeneous steady state, either by introducing momentum friction to a substrate [49] or by accounting for finite system size effects [47,50,51]. In these scenarios, one may compute the correlation function of temperature in the homogeneous steady state, which may be observed with small-angle light scattering experiments [45,52]. Using the distribution of noise

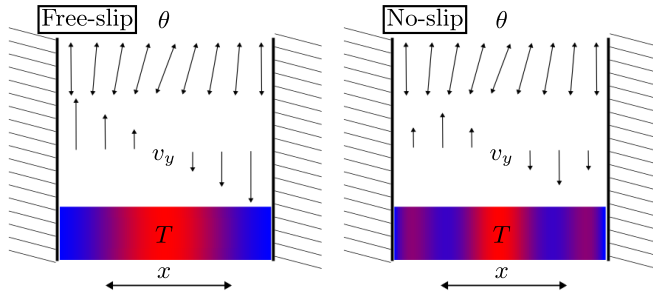


FIG. 1. Schematic diagram of slab geometry depicting the nematic angle θ , velocity v_y , and temperature T along the x axis. θ and T are subject to Dirichlet boundary conditions, whereas v_y is constrained by free-slip and no-slip boundary conditions. We have taken $L_\epsilon = 0.4L$.

fields derived in the Supplemental Material [42], we find

$$\langle T(x, t)T(x', t') \rangle = \frac{2k_B T_0^2}{c_v} \int \frac{d\omega d^2k}{(2\pi)^3} e^{-i\omega(t-t') + ik \cdot (x-x')} \times \frac{D_\epsilon k^2 + \Gamma_\epsilon}{\omega^2 + (D_\epsilon k^2 + \Gamma_\epsilon)^2}, \quad (20)$$

which, as predicted, is purely relaxational and agnostic of the active nematic coefficient ζ .

Temperature near spontaneous flow transition. Activity may indirectly heat up the fluid via shearing and twisting terms on the right-hand side of Eq. (18). This occurs at the onset of nematic turbulence, when activity destabilizes and destroys the homogeneous steady state. To demonstrate this, we consider the well-known spontaneous flow transition that arises for active nematics in a confined geometry [36]. Consider a contractile ($\zeta < 0$) active nematic confined in a two-dimensional slab geometry, $x \in (-L/2, L/2)$ and $y \in (-\infty, \infty)$, where the nematic orientation is anchored at the boundaries, $\theta(\pm L/2) = \pi/2$ (see Fig. 1). A similar setup holds for extensile active nematics ($\zeta > 0$) with $\theta(\pm L/2) = 0$ [53].

We wish to look for steady-state solutions to this problem. There is the trivial homogeneous steady-state solution $S = S_0$, $T = T_0$, $v_y = 0$, and $\theta = \pi/2$. As it turns out, with free-slip (FS) boundary conditions, $t_{xy}(\pm L/2) = 0$, the homogeneous state is dynamically stable for slabs narrower than the critical width, $L < L_c$, where $L_c = \pi/k_c(\pi/2)$ [36]. This is because finite slab width enforces a minimum wave vector in the x direction, $k_x^{\min} = \pi/L$, which is already above the stability bound in Eq. (19). As we cross to $L > L_c$, the $k_x^{\min}$ mode becomes unstable and the system undergoes a spontaneous flow transition to an inhomogeneous state [54]. Similarly, for no-slip (NS) boundary conditions, $v_y(\pm L/2) = 0$, the homogeneous state is stable for $L < 2L_c$ [36].

Sufficiently close to criticality, we can perturbatively construct the stable inhomogeneous solution [36] (see the Supplemental Material [42] for a review). In particular, the leading perturbative shear profile is given as

$$u_{xy}^{\text{FS}} \approx A_u \cos(\pi x/L), \quad u_{xy}^{\text{NS}} \approx 2A_u \cos(2\pi x/L), \quad (21)$$

where the amplitude A_u is proportional to $\sqrt{L - L_c}$ (for FS) and $\sqrt{L - 2L_c}$ (for NS), which is sensitive to the nonlinear

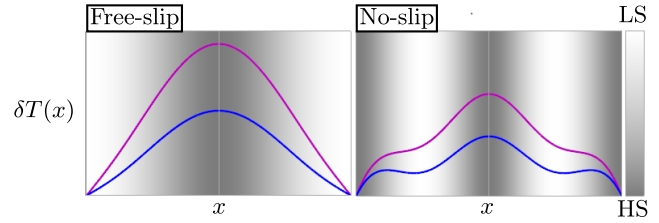


FIG. 2. Temperature profiles near the spontaneous flow transition for varying L_ϵ (decreasing top to bottom). HS and LS correspond to high shear and low shear, respectively.

structure of the theory [36]. The full nonlinear solution farther from the critical point can be constructed numerically [47,55,56].

The energy balance equation (18) implies that the temperature across the slab is sourced by the square of the shear profile; at leading perturbative order

$$(\Gamma_\epsilon - D_\epsilon \partial_x^2) \delta T \approx -\frac{4\tilde{\eta}}{c_v} u_{xy}^2, \quad (22)$$

where $\tilde{\eta} = \eta + \frac{1}{2} S_0^2 \sigma_Q (1 - \lambda)^2$ is the effective viscosity, modified due to nematic distortions. Solving Eq. (22) with Dirichlet boundary conditions, $T(\pm L/2) = T_0$, yields

$$\delta T_{\text{FS}} \approx \frac{L_\epsilon^2 A_T}{1 + L_\epsilon^2/L^2} \left(\frac{L_\epsilon^2}{2L^2} f(x) + \cos^2(\pi x/L) \right),$$

$$\delta T_{\text{NS}} \approx \frac{4L_\epsilon^2 A_T}{1 + 4L_\epsilon^2/L^2} \left(\frac{L^2 + 2L_\epsilon^2}{L^2} f(x) - \sin^2(2\pi x/L) \right), \quad (23)$$

where $f(x) = 1 - \cosh(2\pi x/L_\epsilon) \text{sech}(\pi L/L_\epsilon)$ and we have defined $A_T = A_u^2 \tilde{\eta}/(\pi^2 \kappa)$. See the Supplemental Material [42] for a derivation as well as for the computation of the temperature profile with Neumann boundary conditions, $\partial_x T(\pm L/2) = 0$. We additionally provide a heuristic estimate of the magnitude of temperature modulations for the experimental setup of Ref. [57].

The temperature profile depends qualitatively on the energy relaxation length L_ϵ . First, larger L_ϵ means that the energy gained from inhomogeneous shearing and twisting effects is transported over longer distances before relaxing to the environment, thereby heating the fluid more across the slab (see Fig. 2). In the free-slip case, heating happens near the middle of the slab, so T peaks in the middle and monotonically decreases to T_0 at the edges, with the overall amplitude controlled by L_ϵ . However, in the no-slip case, heating happens near both the middle and edges of the slab. For $L_\epsilon > 0.875L$, we find that the energy relaxes sufficiently slowly that the spatial heating structure is coarse grained and, again, T only peaks in the middle. However, for $L_\epsilon < 0.875L$, the spatial heating structure dominates, resulting in two additional peaks near the edges. In contrast, we show in the Supplemental Material [42] that when we subject the temperature to Neumann boundary conditions, changing L_ϵ does not induce any qualitative change on the temperature profile.

Discussion and perspectives. In this work, we used a hydrodynamic framework for active matter coupled to an

environment to study the local temperature dynamics of a two-dimensional active nematic. This framework is based on the usual assumptions underlying hydrodynamics, namely, local thermal equilibrium and microscopic reversibility [27,28], but includes the coupling to an external environment [30]. The interplay between energy inflow caused by microscopic self-driven agents and the outflow of energy due to exchanges with the environment allows for the existence of nonequilibrium steady states. The approach we followed is inherently two dimensional, as a three-dimensional active system is only in contact with the environment at its boundaries, which dramatically complicates the nonequilibrium steady state.

We found that the mechanosensitive nature of the fuel consumption makes it so that the activity of active nematodes does not linearly affect energy balance. However, when studying the well-known spontaneous flow transition for a confined active nematic, we find that this does leave an imprint on the temperature profile. The nature of the temperature profile depends on the ratio between the diffusion along the confined geometry and the relaxation to the environment. It would be interesting to explore whether such temperature profiles could be observed in an experimental realization of

a confined active nematic [57,58]. In the Supplemental Material [42], we study the spontaneous flow transition that is experimentally realized in Ref. [57] for free-slip boundary conditions and perform a quantitative assessment of how large the contribution from the spontaneous flow transition to the active nematic temperature would be. Our estimates indicate that in this specific experimental setup the effect on thermal gradients would not be significant enough to be observed. If the spontaneous flow transition of the active nematic could be realized in a different experimental setup where the steady state would exhibit higher level of activity and less loss of heat to the environment, it is conceivable that thermal gradients could be experimentally observed.

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Data availability. No data were created or analyzed in this study.

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