Supplementary Materials for

The emergence of spontaneous coordinated epithelial rotation on cylindrical curved surfaces

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SECTION 1: PHYSICAL DESCRIPTION OF AN ACTIVE POLAR FLUID

MDCK cell monolayers are described as a 2d active polar fluid with a polarization field $p_\alpha$ and a velocity field $v_\alpha$, representing the average cell polarization and the average cell velocity, respectively. We consider that the system forms a steady-state disordered phase with $p_\alpha = 0$ and vanishing average velocity $v_\alpha = 0$ in the absence of drivings.

Previous work studied the effects of couplings between the extrinsic curvature and an orientational order on the steady-state evolution of passive liquid crystals [68–74]. This work was extended to active liquid crystals for different types of geometries like planar, cylindrical, toroidal or spherical shells, and different types of orientational order that were described by either a director vector field or a nematic tensor field [26, 75–79]. The previous studies focused on the effects of quadratic couplings between the extrinsic curvature and the orientational order parameter. Unlike to linear couplings, quadratic couplings do not differentiate between convexity/concavity of the embedding geometry. Even though linear couplings are allowed by the symmetries of some biological systems, like apico-basal polarity in cells, their effects in active liquid crystal have been only studied recently for the case of stripes with curvature in the transverse direction [80]. Here, we will study the steady-state patterns generated via the interplay between polar traction forces and linear/quadratic couplings between the extrinsic curvature and the orientational order on a cylindrical geometry.

To describe the effects of the substrate curvature, we consider that the extrinsic curvature tensor $C_{\alpha \beta}$ behaves as an external field, which is coupled to $p_\alpha$. The effective free-energy density of our system reads

$$\mathcal{F} = \int_{\mathcal{A}} f \, da = \int_{\mathcal{A}} \left( \frac{\chi_2}{2} p_\gamma p_\gamma + \frac{\chi_4}{4} (p_\gamma p_\gamma)^2 + \frac{K}{2} (\partial_\beta p_\gamma)(\partial_\beta p_\gamma) + f_C^{(1)}(C_{\alpha \beta}, p_\alpha) + f_C^{(2)}(C_{\alpha \beta}, p_\alpha) \right) \, da. \quad (S1)$$

The first three terms in Eq. (S1) correspond to the Landau-Ginzburg free-energy density in the one constant approximation [81]. The coefficients $\chi_2$ and $\chi_4$ are typical Landau-Ginzburg parameters, and $K$ is a Frank elastic modulus associated with distortions of the polarization field. Specifically, the first and second terms in Eq. (S1) penalise configurations with a finite local order (i.e. $p_\gamma p_\gamma \neq 0$), and the third term penalises configurations with spatial gradients of the polarization field. The third term in the free-energy density is computed by taking $3D$ derivatives in cylindrical coordinates of $\partial_\beta p_\gamma$ and subsequently, summing over repeated indices. Because the analysis is restricted to cylindrical geometries and the director field is enforced to remain parallel to the surface, this term takes the expression derived in Refs. [68, 69] for a cylindrical shell. For a general discussion on the thin-film limit of this term in liquid crystal surfaces with arbitrary shapes, we refer to Ref. [82]. The
fourth and fifth terms depend explicitly on the geometry of the substrate through the extrinsic curvature tensor $C_{\alpha\beta}$. The functional $f_C^{(1)}$ includes terms linear in $C_{\alpha\beta}$, whereas $f_C^{(2)}$ includes quadratic terms in $C_{\alpha\beta}$. The third term in the free-energy density can also lead to quadratic couplings between the orientational order and the extrinsic curvature, [68, 69]. Importantly, the sign of the curvature tensor depends on whether the system sits on the inner or outer face of the substrate. Therefore, the functional $f_C^{(1)}$ changes sign upon changing the face of the substrate that the system sits on, whereas $f_C^{(2)}$ does not.

Symmetry requires that $f_C^{(1)}$ in Eq. (S1) takes the form

$$f_C^{(1)} = \frac{\beta_1}{2} C_{\alpha\beta} p_\beta p_\alpha + \frac{\beta_1}{2} C_{\gamma\alpha\gamma} p_\alpha,$$

and, similarly, $f_C^{(2)}$ reads

$$f_C^{(2)} = \frac{\beta_2}{2} C_{\alpha\gamma} C_{\alpha\beta} p_\gamma p_\beta + \frac{\beta_2}{2} C_{\gamma\alpha\gamma} C_{\alpha\beta} p_\beta + \frac{\beta_2}{2} C_{\alpha\alpha} C_{\beta\beta} p_\gamma p_\gamma,$$

The coarse-grained interactions between cells and the underlying substrate are described by four terms: a linear viscous-like friction force ($\sim \xi v_\alpha$) with friction coefficient $\xi$, an active polar traction force ($\sim T_0 p_\alpha$) with amplitude $T_0$, and two active nematic traction forces with amplitudes $\lambda_s$ and $\lambda_b$ corresponding to splay and bend deformation of the polarization field. Thereby, in the overdamped limit, momentum conservation equation reduces to

$$\partial_\beta \sigma^t_{\alpha\beta} = \xi v_\alpha - T_0 p_\alpha + \lambda_s p_\alpha \partial_\beta p_\beta + \lambda_b p_\beta \partial_\beta p_\alpha,$$

where the total stress tensor $\sigma^t_{\alpha\beta}$ can be decomposed in two terms $\sigma^t_{\alpha\beta} = \sigma^e_{\alpha\beta} + \sigma_{\alpha\beta}$, the first term being the Ericksen stress tensor $\sigma^e_{\alpha\beta}$ and the second term being the deviatoric stress tensor $\sigma_{\alpha\beta}$ [81]. The Ericksen stress tensor reads

$$\sigma^e_{\alpha\beta} = -P \delta_{\alpha\beta} - \frac{\partial f}{\partial (p_{\beta\gamma})} \partial_\alpha p_{\gamma} = -P \delta_{\alpha\beta} - \mathcal{K} \partial_\beta p_{\gamma} \partial_\alpha p_{\gamma},$$

where $P$ corresponds to the pressure field, and $f$ the effective free-energy density given by Eq. (S1). Keeping a one-viscosity description, the deviatoric stress tensor $\sigma_{\alpha\beta}$ takes the form

$$\sigma_{\alpha\beta} = 2 \eta v_{\alpha\beta} - \zeta \Delta \mu p_{\alpha} p_{\beta} + \nu \left( p_{\alpha} h_{\beta} + p_{\beta} h_{\alpha} \right) + \frac{1}{2} \left( p_{\alpha} h_{\beta} - p_{\beta} h_{\alpha} \right)$$

where $v_{\alpha\beta} = (\partial_\alpha v_\beta + \partial_\beta v_\alpha)/2$ is the symmetric part of the velocity gradient tensor and $h_\alpha$ is the molecular field defined as the functional derivative of $\mathcal{F}$ with respect to $p_\alpha$, $h_\alpha = -\delta \mathcal{F}/\delta p_\alpha$. The coefficient $\Delta \mu$ is the chemical potential difference of an out-of-equilibrium reaction, such as the ATP hydrolysis in cells, which renders the system active. From left to right, the terms of $\sigma_{\alpha\beta}$ are:
viscous stresses with a shear viscosity $\eta$, anisotropic active stresses proportional to $\zeta$ ($\zeta > 0$ for extensile materials), nemato-elastic stresses with transport coefficients $\nu$, and the asymmetric part of the deviatoric stress tensor [57, 58].

We consider that our system is incompressible

$$\partial_\gamma v_\gamma = 0,$$  \hspace{1cm} (S7)

consequently the pressure $P$ in Eq. (S5) acts as a Lagrange multiplier to ensure that the density field remains constant. Finally, the dynamics of the polarization field reads

$$\partial_t p_\alpha + v_\beta \partial_\beta p_\alpha + \omega_{\alpha\beta} p_\beta = \frac{h_\alpha}{\gamma} + \lambda p_\beta \partial_\beta p_\alpha - \nu v_{\alpha\beta} p_\beta$$  \hspace{1cm} (S8)

where $\omega_{\alpha\beta} = (\partial_\alpha v_\beta - \partial_\beta v_\alpha)/2$ is the antisymmetric part of the velocity gradient tensor, $\gamma$ is a rotational viscosity, $\lambda$ is an active transport coefficient and $\nu$ is the so-called flow-aligning parameter. The term proportional to $\lambda$ exists only in polar systems. The sign of the transport coefficient $\nu$ is not fixed by thermodynamical principles, and in the context of liquid crystals this coefficient depends, for instance, on the aspect ratio of the constituting particle shape, being $\nu < -1$ for rod-like particles and $\nu > 1$ for disk-like particles. For more details about the derivation of the constitutive equations, we defer the reader to Refs. [57, 58].

**SECTION 2: ACTIVE POLAR FLUID EMBEDDED ON A CYLINDRICAL SHELL**

In this section, we apply the physical description that was presented in Section 1 to a cylindrical substrate of radius $R$, Fig. S17. We consider that the physical fields are independent of the azimuthal coordinate $\theta$ as well as independent of the longitudinal coordinate $z$, except for the pressure field $P$.

The uniform polarization field takes the form $\mathbf{p} = p_\theta \hat{\theta} + p_z \hat{z}$, where $\hat{\theta}$ and $\hat{z}$ are unit vectors along the circular cross-section of the cylinder (i.e. azimuthal direction) and along its long axis (i.e. longitudinal direction), respectively. The normal direction to the cylinder surface is the radial direction $\hat{r}$. Hence, $p_\theta$ and $p_z$ are the components of the polarization field in each of the in-plane directions. Note that since we are looking for the onset of polarity parallel to the cylindrical surface, naturally $p_r = 0$. Similarly, the uniform velocity field is expressed as $\mathbf{v} = v_\theta \hat{\theta} + v_z \hat{z}$.

Under these approximations, the free-energy density $f$ given by Eq. (S1) reduces to

$$f = \left( \frac{\chi_2}{2} + \frac{\beta_1}{2R} + \frac{\beta_{2,1} + \beta_{2,2}}{2R^2} \right) (p_\theta^2 + p_z^2) + \frac{\chi_4}{4} (p_\theta^2 + p_z^2)^2 + \left( \frac{\beta_1}{2R} + \frac{K + \beta_{2,1} + \beta_{2,2}}{2R^2} \right) p_\theta^2$$  \hspace{1cm} (S9)
FIG. S17: Schematic drawing of two cell monolayers (light green), laying on either the outer side of a cylindrical substrate (dark gray) in a or its inner side in b. The radius of the substrate is \( R \). \( z \) and \( \theta \) correspond to the longitudinal coordinate and azimuthal angle, respectively.

where the only non-vanishing component of the curvature tensor is \( C_{\alpha\beta} = (1/R)\hat{\theta} \otimes \hat{\theta} \) and of the polarization gradient tensor is \( \partial_\alpha p_\beta = (-p_\theta/R)\hat{\theta} \otimes \hat{r} \). For convenience, we redefine the parameters as follows: \( \beta_{2,1} + \beta_{2,2} \to \beta_2 \), and \( \mathcal{K} + \beta_{2,1} + \beta_{2,2} \to \beta_2 \). Note that depending on whether the cell monolayer is inside microtubes or on fibers, the curvature tensor changes from \( C_{\theta\theta} = -1/R \) for microtubes to \( C_{\theta\theta} = 1/R \) for fibers. For convenience, we allow \( R \) to change sign to account for the curvature change between microtubes and fibers, and use the convention that \( R > 0 \) for fibers and \( R < 0 \) for microtubes. This way, the linear curvature couplings \( f_C^{(1)} \) change sign upon changing the face of the substrate that the system sits on, whereas the quadratic curvature couplings \( f_C^{(2)} \) do not.

In this case, the components of the molecular field are expressed as

\[
\begin{align*}
  h_\theta &= -\delta \mathcal{F} / \delta p_\theta = -\left( \chi_2 + \frac{\beta_1 + \beta_{12}}{R} + \frac{\beta_2 + \beta_{22}}{R^2} \right) p_\theta - \chi_4 \left( p_{\theta}^2 + p_z^2 \right) p_\theta, \\
  h_z &= -\delta \mathcal{F} / \delta p_z = -\left( \chi_2 + \frac{\beta_1 + \beta_{12}}{R} + \frac{\beta_2 + \beta_{22}}{R^2} \right) p_z - \chi_4 \left( p_{\theta}^2 + p_z^2 \right) p_z
\end{align*}
\]

(S10)

(S11)

The non-vanishing components of the total stress tensor \( \sigma'_{\alpha\beta} \) given by Eqs. (S5) and (S6) read

\[
\begin{align*}
  \sigma'_{rr} &= -P, \\
  \sigma'_{r\theta} &= \sigma'_{\theta r} = -\eta_{\theta} v_{\theta} / R, \\
  \sigma'_{\theta\theta} &= -\zeta \Delta \mu p_{\theta}^2 / R^2 + \nu p_{\theta} h_{\theta} - P - \mathcal{K} \frac{p_{\theta}^2}{R^2}, \\
  \sigma'_{\theta z} &= -\zeta \Delta \mu p_z p_{\theta} + \frac{\nu}{2} \left( p_z h_{\theta} + p_\theta h_z \right) + \frac{1}{2} \left( p_{\theta} h_z - p_z h_{\theta} \right), \\
  \sigma'_{z\theta} &= -\zeta \Delta \mu p_z p_{\theta} + \frac{\nu}{2} \left( p_z h_{\theta} + p_\theta h_z \right) - \frac{1}{2} \left( p_{\theta} h_z - p_z h_{\theta} \right), \\
  \sigma'_{zz} &= -\zeta \Delta \mu p_z^2 + \nu p_z h_z - P
\end{align*}
\]

(S12a)

(S12b)

(S12c)

(S12d)

(S12e)

(S12f)
where the only non-vanishing component of the velocity gradient tensor is \( \partial_{\alpha} v_\beta = (-v_\theta / R) \hat{\theta} \otimes \hat{r} \).

The incompressibility condition (S7) is satisfied by uniform velocity fields (i.e. \( v_z = \text{cte} \)) and reads

\[
\partial_z v_z = 0. \tag{S13}
\]

The dynamic equations for the polarization field given by Eqs. (S8) reduces to

\[
\begin{align*}
\partial_t p_\theta &= h_\theta, \tag{S14a} \\
\partial_t p_z &= h_z. \tag{S14b}
\end{align*}
\]

Note that in our case, the term proportional to \( \lambda \) in Eq. (S8) gives a contribution in the radial direction (i.e. \( \lambda p_\beta \partial_\beta p_\alpha = (-\lambda p_\theta^2 / R) \hat{r} \)). Consequently, this term does not influence the dynamics of the in-plane components of the polarization field.

Finally, Eqs. (S4) reduces to force balance in the direction \( \hat{\theta} \)

\[
\partial_r \sigma^t_{\theta r} |_{r=R} + \frac{\sigma^t_{\theta z} + \sigma^t_{z \theta}}{R} = -\eta \frac{v_\theta}{R^2} = \xi v_\theta - T_0 p_\theta, \tag{S15}
\]

where the term \( \partial_r \sigma^t_{\theta r} |_{r=R} = \eta \frac{v_\theta}{R^2} \) gives a contribution due to the explicit dependence on the cylinder radius \( R \), as well as, force balance in the direction \( \hat{z} \)

\[
-\partial_z P = \xi v_z - T_0 p_z. \tag{S16}
\]

Note that in our case, the terms proportional to \( \lambda_s \) and \( \lambda_b \) in Eq. (S4) read \( \lambda_s p_\alpha \partial_\beta p_\alpha = 0 \) and \( \lambda_b p_\beta \partial_\beta p_\alpha = (-\lambda_b p_\theta^2 / R) \hat{r} \), respectively. The latter can yield forces normal to the cylinder surface, so that these terms do not influence the transition that we discuss here.

**SECTION 3: EQUILIBRIUM UNIFORM SOLUTIONS**

In the following, we study the equilibrium uniform solutions for the polarization field.

The free-energy density of our system given by Eq. (S9) for a uniform field reads

\[
f = \left( \frac{\chi^2}{2} + \frac{\beta_1}{2R} + \frac{\beta_2}{2R^2} \right) (p_\theta^2 + p_z^2) + \left( \frac{\beta_1}{2R} + \frac{\beta_2}{2R^2} \right) p_\theta^2 + \frac{\chi^4}{4} (p_\theta^2 + p_z^2)^2. \tag{S17}
\]

The equilibrium uniform solutions for the polarization field correspond to the minimum of Eq. (S17), being either an azimuthal ordered phase with both \( p_z = 0 \) and \( p_\theta \neq 0 \), or an longitudinal ordered phase with both \( p_z \neq 0 \) and \( p_\theta = 0 \), or a disordered phase with \( p_z = p_\theta = 0 \). Such solutions satisfy \( h_\theta = h_z = 0 \) in Eqs. (S10). To simplify notation, we denote \( \mathcal{A} = \chi^2 + \beta_1 / R + \beta_2 / R^2 \), and \( \mathcal{B} = \beta_1 / R + \beta_2 / R^2 \).
In the following, we study the stability of each of these solutions. Expanding Eq. (S17) within a neighbourhood of each uniform solution, one obtains for an azimuthal ordered phase

\[ f = (A + B) \left( \frac{p_\theta^0}{4} \right)^2 - (A + B) \left( p_\theta - p_\theta^0 \right)^2 - \frac{B p_z^2}{2} + O_3(p_z, (p_\theta - p_\theta^0)), \]  

where \( p_\theta^0 = \pm \sqrt{-(A + B)/\chi^4} \), and for an longitudinal ordered phase

\[ f = A \left( \frac{p_z^0}{4} \right)^2 - A \left( p_z - p_z^0 \right)^2 + B \frac{p_\theta^2}{2} + O_3(p_\theta, (p_z - p_z^0)), \]

where \( p_z^0 = \pm \sqrt{-A/\chi^4} \), and finally for a disordered phase

\[ f = (A + B) \frac{p_\theta^2}{2} + A \frac{p_z^2}{2} + O_3(p_z, p_\theta), \]

where \( O_3 \) denotes third-order corrections.

As shown in Fig. S18, each solution is stable in a different domain of the parameter space. Specifically, an azimuthal ordered phase is stable when both \( A + B < 0 \), and \( B < 0 \), according to Eq. (S18). An longitudinal ordered phase is stable when both \( A < 0 \), and \( B > 0 \), according to Eq. (S19). Finally, a disordered phase is stable when both \( A + B > 0 \), and \( A > 0 \), according to Eq. (S20). Note that in the absence of couplings between the polarization and the curvature tensor, \( B, A > 0 \) as \( \chi^2 > 0 \) and \( \mathcal{K} > 0 \), hence the disordered phase is linearly stable.

FIG. S18: Phase diagram of equilibrium uniform phases as a function of the parameters \( \mathcal{A} = \chi_2 + \beta_1/R + \beta_2/R^2 \) and \( \mathcal{B} = \beta_1/R + \beta_2/R^2 \). The solid lines delimit the boundaries between each stability region of equilibrium phases: blue \( \mathcal{A} + \mathcal{B} = 0 \), pink \( \mathcal{A} = 0 \), and green \( \mathcal{B} = 0 \). The equilibrium phases are labelled as: AzO for an azimuthal ordered phase, LO for a longitudinal ordered phase and D for a disordered phase.

The stability of equilibrium uniform solutions depend on the geometry of the substrate \( R \), as well as the side of the substrate that the system sits on. To understand how the substrate...
geometry can influence the solution’s stability, we restrict the following discussion to a parameter space wherein $\mathcal{A} > 0$ for any value of $R$. This parameter regime guarantees that only a transition between an azimuthal ordered phases and a disordered phase could occur, and it can be achieved by, for instance, assuming that $\beta_1 = \beta_2 = 0$ as $\chi_2 > 0$, which we assume hereon. Under this simplification, the transition occurs whenever $\mathcal{A} + \mathcal{B} = 0$, resulting in two different critical radii

$$R^1_{\chi_2}/\beta_1 = \frac{-1 + \sqrt{1 - 4\beta_2\chi_2/\beta_1^2}}{2},$$  \hspace{1cm} (S21)

$$R^2_{\chi_2}/\beta_1 = \frac{-1 - \sqrt{1 - 4\beta_2\chi_2/\beta_1^2}}{2}. \hspace{1cm} (S22)$$

For convenience, we define the rescaled radius $r = R\chi_2/\beta_1$, and the rescaled critical radius $r^1_c = R^1_c\chi_2$ and $r^2_c = R^2_c\chi_2$.

If $\beta_2 < 0$, there exists two real critical radius $r^1_c$ and $r^2_c$, Fig. 6 in the main text, whereat $\mathcal{A} + \mathcal{B} = 0$ in Fig. S18. For a radius $r > r^1_c$ or $r < r^2_c$, the disordered phase with $p_z = p_\theta = 0$ is favoured. For $r^2_c < r < r^1_c$, substrate curvature aligns the polarization in the azimuthal direction that is $p_z = 0$ and $p_\theta = \pm \mathcal{P}$, that reads

$$\mathcal{P} = \sqrt{-\left(\chi_2 + \frac{\beta_1}{R} + \frac{\beta_2}{R^2}\right)/\chi_4}. \hspace{1cm} (S23)$$

If $\beta_2 > 0$, one can have two different scenarios, Fig. 6 in the main text. The first scenario is obtained when both $r < 0$, and $\beta^2_1 > 4\beta_2\chi_2$. In this case, there exist two positive critical radii, $r^1_c$ and $r^2_c$, for which a transition between a disordered and an azimuthal ordered phase occurs. For $r > r^1_c$ or $r < r^2_c$, the disordered phase with $p_z = p_\theta = 0$ is dominant. For $r^2_c < r < r^1_c$, a phase with an azimuthal alignment $p_z = 0$ and $p_\theta = \pm \mathcal{P}$ is dominant, where $\mathcal{P}$ is given by Eq. (S23).

In the second scenario, when $r < 0$, and $\beta^2_1 < 4\beta_2\chi_2$ or $r > 0$, the dominant phase is disordered.

To gain further insights into the influence of the linear curvature-polarization couplings in the free-energy density (S1) on the solution’s stability, let us consider the limiting case whereby $f^{(1)}_c$ given by Eq. (S2) vanishes. Following the same reasoning as above, if $\beta_2 < 0$, both critical radius have the same absolute value $|R^1_c| = |R^2_c|$. This means that the transition between a disordered and an azimuthal ordered phase occurs for the same radius $|R|$ on both sides of the substrate. If $\beta_2 > 0$, no real critical radii exists and the system forms a disordered phase regardless of the substrate radius $R$. Therefore, linear curvature-polarization couplings (S2) are crucial to establish an asymmetry between the critical radii for the transition on both sides of the substrate.

Similarly, to gain further insights into the influence of the quadratic curvature-polarization couplings in the free-energy density (S1) on the solution’s stability, let us consider the limiting case whereby $f^{(2)}_c$ given by Eq. (S2) vanishes. As $\beta_2 = \mathcal{K} > 0$ can only be positive, the disordered
phase is dominant regardless of $R$ on, at least, one of the two sides of the substrate. Therefore, quadratic curvature-polarization couplings (S3) are crucial to sustain an azimuthal ordered phase over a range of radii $R$ on both sides of the substrate.

In conclusion, depending on the sign of $\beta_2$, we predict two distinct scenarios: first, an active polar fluid that on one side of the substrate, could either form an azimuthal ordered phase at intermediate substrate radii $R$ or a disordered phase regardless of the values of $R$, while on the other side of the substrate it forms a disordered phase regardless of $R$. Second, an active polar fluid forming an azimuthal ordered phase for $R$ smaller than a critical radius that depends on the side of the substrate on which the system sits.

SECTION 4: STEADY-STATE DYNAMICS OF UNIFORM SOLUTIONS

In the following, we study the stress and velocity patterns of the uniform solutions for the polarization field from Section 3.

The equilibrium uniform solutions for the polarization field can be stable to fluctuations in the absence of activity or specific boundaries, see Section 3. In the geometry we consider, our active polar fluid includes, however, two active contributions controlled by the parameters: $\zeta \Delta \mu$ corresponding to the amplitude of the anisotropic active stresses, and $T_0$ corresponding to the amplitude of the traction forces. It is expected that for sufficiently large values of $\zeta \Delta \mu$, the uniform ordered solutions of the polarization field become unstable to linear fluctuations, as reported in other contexts by many authors [83]. A detailed analysis of the influence of $\zeta \Delta \mu$ on the stability of our uniform solutions falls beyond the scope of this manuscript. However, it is important to note that due to the substrate geometry and the coupling terms $f_C^{(1)}$ and $f_C^{(2)}$ given by Eqs. (S2)-(S3), the rotational symmetry of the system is broken. In this case, global rotations of the polarization field are linearly stable for small enough activity. Here, we assume that the uniform solutions for the polarization field that were found in the previous section are stable over the range of radii $R$ under study.

The longitudinal component of the velocity field $v_z$ is obtained by solving Eq. (S13) and reads

$$v_z = V,$$

(S24)

where $V$ is an integration constant that is set by boundary conditions. For a uniform azimuthal ordered phase, according to Eq. (S16), we predict that the pressure field $P$ is a linear function of
the longitudinal coordinate

\[ P - P_0 = -\xi V_z, \quad (S25) \]

where \( P_0 \) is an integration constant. Note that a non-vanishing \( v_z \) requires different boundary conditions on each end of the cylindrical surface, such as in the presence of a leading edge. Otherwise, \( v_z = 0 \) and \( P = P_0 \), and only azimuthal motion could be observed.

In this case, from Eq. (S15), one obtains for the azimuthal component of the velocity field

\[ v_\theta = \frac{T_0}{\xi + \eta/R^2} \mathcal{P}, \quad (S26) \]

where \( \mathcal{P} \) is given by Eq. (S23).

For a uniform disordered phase, the velocity field \( v_\theta \) vanishes, see Eq. (S15).

As shown in Fig. 6 in the main text, the azimuthal velocity \( v_\theta \) exhibits a non-monotonic dependence on the substrate radius \( R \). Normalising the velocity amplitude by the factor \( T_0 \sqrt{\chi_2/\chi_4}/\xi \) and the substrate radii by \( x = -R\chi_2/\beta_1 \), one obtains that the azimuthal velocity given by Eq. (S26) depends on two dimensionless parameters: \( \alpha_1 = -\chi_2/\beta_1 \), and \( \alpha_2 = \eta\chi_2^2/\xi\beta_1^2 \). The dimensionless azimuthal velocity takes the form

\[ v_\theta = \pm \frac{1}{1 + \alpha_2/x^2} \sqrt{\frac{\alpha_1}{x^2} + \frac{1}{x} - 1}. \quad (S27) \]

The existence of this velocity is linked to the region of stability of the azimuthal ordered phase, which is discussed in the above section.

Thus we find that for an infinite cylindrical surface, we expect pure azimuthal rotation, whereas in the presence of boundaries, such as a leading edge, we expect helical migration. The latter results from the combination of the longitudinal velocity induced by the leading edge, and the azimuthal velocity resulting from curvature-induced symmetry breaking.

**SECTION 5: FITTING PROCEDURE ON THE VELOCITY PATTERNS**

In the following, we detail the procedure for computing the fitting parameters from the experimental curves of the azimuthal component of the velocity field as a function of the substrate radius \( R \) for MDCK cell monolayers.

As MDCK cells, in both microtubes and fibers, exhibit collective rotation along the azimuthal direction for radii smaller than a critical value, we consider that \( \beta_2 < 0 \) (see Section 3). As shown in Section 4, the theoretical curve for the azimuthal velocity reads

\[ v_\theta = \frac{T_0 \sqrt{\chi_2/\chi_4}}{\xi + \eta/R^2} \sqrt{-\left(1 + \frac{\beta_1}{\chi_2 R} - \frac{\beta_2}{\chi_2 R^2}\right)}, \quad (S28) \]
FIG. S19: Region of the parameter space whereby the error function $\varepsilon$ given by Eq. (S29) is at most 10% larger than the absolute minimum error $\varepsilon_{\text{min}}$. panel a shows a cross-section of the parameter space on the plane $|\beta_1|/\chi_2|\sqrt{\eta/\xi}$, panel b on $|\beta_2|/\chi_2|\sqrt{\eta/\xi}$, and panel c on $T_0\sqrt{\chi_2/\chi_4/\eta}-|\beta_2|/\chi_2$. The parameters $\bar{\beta}_1 = \bar{\beta}_2 = 0$ and the unit of length was set to 100 $\mu$m, and the unit of velocity to 1 $\mu$m/h.

where we can identify four distinct parameters: a velocity scale $V = T_0\sqrt{\chi_2/\chi_4/\xi}$, a friction length $L_\eta = \sqrt{\eta/\xi}$, and two coupling parameters between the polarization field and the substrate curvature $c_1 = \beta_1/\chi_2$, and $c_2 = |\beta_2|/\chi_2$. Remember that according to our convention, we allow $R$ to change sign to account for the curvature change between microtubes and fibers, and use the convention that $R > 0$ for fibers and $R < 0$ for microtubes.

For a given set of the fitting parameters $(V, L_\eta, c_1, c_2)$, we compute the error function

$$\varepsilon = \sqrt{\sum_{#\text{exp}} |v_\theta^{\text{exp}}(R) - v_\theta|^2},$$

where $v_\theta$ is given by Eq. (S28), and $v_\theta^{\text{exp}}(R)$ corresponds to the experimental value of the azimuthal velocity for a given radii $R$ in either microtubes or fibers. The sum in Eq. (S29) runs over all experimental values, namely MDCK monolayers on microtubes and fibers in a range of substrate diameters $2|R|$ from 25 $\mu$m to 250 $\mu$m (see Methods). For substrate diameter $2|R| > 150$ $\mu$m in microtubes and $2|R| > 100$ $\mu$m in fibers, collective rotation is not found to be the dominant phase, and we consider that the $v_\theta^{\text{exp}}(R) = 0$ for these values of $R$.

We compute the error function $\varepsilon$ in the parameter space $(V, L_\eta, c_1, c_2) = (10^{-1}, 10^8) \times (10^{-2}, 10^2) \times (10^{-3}, 10) \times (10^{-2}, 10^2)$, where the units of length were set to 100 $\mu$m, and the units of velocity to 1 $\mu$m/h. We search for the absolute minimum $\varepsilon_{\text{min}}$ of the error function over the parameter space $(V, L_\eta, c_1, c_2)$. Fig. S19 shows the subset of the previous parameter space whereby the error function $\varepsilon < 1.1*\varepsilon_{\text{min}}$. Our analysis disclosed a single region of the parameter space that is compatible with the experimental measurements. Fig. 6 in the main text shows the comparison in both microtubes and fibers between the experimental profiles of the azimuthal velocity $v_\theta^{\text{exp}}(R)$.
Parameter | Definition | Mean±SD  
--- | --- | ---  
$V/L_n^2 = T_0 \sqrt{\chi_2/\chi_4/\eta}$ | Ratio between velocity scale and friction length squared | $0.0064 \pm 0.0007 \ 1/(\mu m \ h)$  
$L_n = \sqrt{\eta/\xi}$ | Friction Length | $> 40 \ \mu m$  
$|\beta_1/\chi_2|$ | Linear coupling between the polarization field and the substrate curvature | $21 \pm 8 \ \mu m$  
$\beta_2/\chi_2$ | Quadratic coupling between the polarization field and the substrate curvature | $-6000 \pm 1000 \ \mu m^2$  

TABLE S1: Estimation of material parameters for an active polar fluid. $\beta_1/\chi_2 R$ is positive for fibers. The error bars correspond to the SD in the region of the parameter space that satisfies $E < 1.1 \cdot E_{min}$.

as a function of the radii $R$, and the theoretical fits of $v_\theta$ for the optimal parameter region.

Table S1 contains the average and standard deviation of the fitting parameters in the region of parameters from Fig. S19. We find that the lower bound of the friction length $L_n$ is compatible to that found in MDCK monolayers spreading on flat surfaces [56]. Both coupling parameters $(\beta_1, \beta_2)$ between the polarization field and the substrate curvature are finite. $\beta_2/\chi_2 < 0$ showing that the effect of substrate curvature are dominant compared to the elastic deformations of the polarization field associated with the Frank constant $K$. We found that the ratio $|\beta_2/\beta_1| > 200 \ \mu m$ is larger than the typical threshold of collective rotation in microtubes and fibers, $2|R| > 150 \ \mu m$ and $2|R| > 100 \ \mu m$ respectively, showing that quadratic couplings are predominant for collective rotation in cylindrical MDCK monolayers.

**SECTION 6: GENERALISATION WITH TWO ORIENTATIONAL ORDERED FIELDS**

In experiments, the orientation of actin fibrils was found on average in the longitudinal direction for microtubes, and in the azimuthal direction for fibers, see Fig. 4 in the main text. Such organisation contrasts with the average direction of collective rotation, which is in the azimuthal direction for both microtubes and fibers, see Fig. 2 and 3 in the main text. In the following, we discuss steady-state patterns made of two coupled orientational ordered fields in a liquid crystal on a cylindrical surface and show that one can understand these experimental observations.

Actin fibrils exhibit a clear nematic order, which contrasts with the polar order corresponding to the azimuthal motion of cell monolayers. Hence, we consider a liquid crystal with two coupled orientational ordered fields: a polarization field $p$ corresponding to the spontaneous motion and a director field $n$ corresponding to the actin fibrils. This means that the physical description
is invariant to \( n \rightarrow -n \) but is not invariant to \( p \rightarrow -p \). A convenient way for discussing the orientation patterns for an azimuthally moving system consists in writing an effective free-energy density:

\[
\mathcal{F} = \int_\mathcal{A} f \, da = \int_\mathcal{A} \left( \frac{\chi_2}{2} \overline{n}_\beta p_\gamma + \frac{\chi_4}{4} (p_\gamma \overline{n}_\gamma)^2 + \frac{K}{2} (\partial_\beta \overline{n}_\gamma)(\partial_\beta p_\gamma) + f_C^{(1)}(C_{\alpha\beta}, p_\alpha) + f_C^{(2)}(C_{\alpha\beta}, p_\alpha) \right) \, da,
\]

where we assumed a one-constant approximation for both fields [81]. In view of the fact that in experiments, the orientational order of actin fibrils is well developed, we consider that \( |n| = 1 \). In this case, the parameter \( \chi_2 \) acts as a Lagrange multiplier. Additionally, we consider that both orientational fields \( p \) and \( n \) are uniform. In the previous free-energy density, the term \( \mathcal{F}/2(\partial_\beta p_\gamma)(\partial_\beta n_\gamma) \) is computed in a similar way to the term \( \mathcal{K}/2(\partial_\beta n_\gamma)(\partial_\beta n_\gamma) \) as it was explained in Section 1.

The first two coupling functions \( f_C^{(1)} \) and \( f_C^{(2)} \) are given by Eqs. (S2)-(S3). The other coupling functions read

\[
h_C^{(1)} = \frac{\beta_3}{2} C_{\alpha\beta\gamma\beta\gamma} n_\alpha n_\gamma, \quad (S31)
\]

\[
h_C^{(2)} = \frac{\beta_{4,1}}{2} C_{\alpha\gamma} C_{\alpha\beta\gamma\beta\gamma} n_\gamma + \frac{\beta_{4,2}}{2} C_{\gamma\gamma} C_{\alpha\beta\gamma\beta\gamma} n_\gamma n_\alpha \quad (S32)
\]

\[
g_{pm}^{(0)} = \frac{\lambda_{0,1}}{2} p_\alpha p_\beta n_\gamma n_\alpha \quad (S33)
\]

\[
g_{pm}^{(1)} = \frac{\lambda_{1,2}}{2} C_{\alpha\beta\gamma\beta\gamma} p_\gamma n_\beta n_\alpha + \frac{\lambda_{1,3}}{2} C_{\alpha\beta\gamma\beta\gamma} p_\gamma n_\alpha n_\beta + \frac{\lambda_{1,4}}{2} C_{\gamma\gamma} p_\alpha p_\beta n_\alpha n_\beta \quad (S34)
\]

\[
g_{pm}^{(2)} = \frac{\lambda_{2,1}}{2} C_{\gamma\gamma} C_{\alpha\beta\gamma\beta\gamma} p_\gamma n_\beta n_\alpha + \frac{\lambda_{2,2}}{2} C_{\gamma\gamma} C_{\alpha\delta\gamma\beta\gamma} p_\gamma n_\alpha n_\beta + \frac{\lambda_{2,3}}{2} C_{\gamma\gamma} C_{\delta\delta\gamma\beta\gamma} p_\gamma n_\alpha n_\beta + \frac{\lambda_{2,4}}{2} C_{\gamma\gamma} C_{\delta\delta\gamma\beta\gamma} p_\gamma n_\alpha n_\beta \quad (S35)
\]

We restrict ourselves to couplings that are compatible with the symmetries of the system and at most of second order in either \( p, n \), or the extrinsic curvature tensor \( C \).

To simplify the discussion, we consider directly the experimental case, where \( p = \theta \hat{\theta} \) as discussed in Section 3. Then, the effective free energy density \( f \) given by Eq. (S30) reduces to

\[
f = \frac{\chi_2}{2} \theta \hat{\theta}^2 + \frac{\chi_4}{4} \theta \hat{\theta}^4 + \frac{\chi_2}{2} |n|^2 + \frac{\beta_1}{R} \theta \hat{\theta}^2 + \frac{\beta_2}{2R^2} \theta \hat{\theta}^2 + \frac{\beta_3}{2R^2} n_\theta^2 + \frac{K + \beta_{2,1} + \beta_{2,1} + \beta_{2,2} + \beta_{2,2}}{2R^2} \theta \hat{\theta}^2 + \frac{\beta_{0}}{2R^2} n_\theta^2 + \frac{\lambda_{0,1}}{2} \theta \hat{\theta}^2 n_\theta^2 + \frac{\lambda_{1,2}}{2} \theta \hat{\theta}^2 n_\theta^2 + \frac{\lambda_{1,4}}{2} \theta \hat{\theta}^2 n_\theta^2 + \frac{\lambda_{2,1}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,2}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,3}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,4}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,5}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,6}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,7}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,8}}{2} \theta \hat{\theta}^2 + \frac{\lambda_{2,9}}{2} \theta \hat{\theta}^2 + cte \quad (S36)
\]

which can be recast as

\[
f = \frac{A}{2} \theta \hat{\theta}^2 + \frac{B}{4} \theta \hat{\theta}^4 + \frac{C + D \theta \hat{\theta}^2}{2} n_\theta^2 + cte, \quad (S37)
\]
where the effective parameters $\mathcal{A}$, $\mathcal{B}$, $\mathcal{C}$, and $\mathcal{D}$ depend on the material parameters of Eqs. (S36) and the substrate radius $R$. The third term is the only one that influences the orientation field $\mathbf{n}$. The steady-state solution for $\mathbf{n}$ can be obtained by minimising the effective free-energy density (S37).

Recall, that according to our convention, we allow $R$ to change sign to account for the curvature change between microtubes and fibers, and use the convention that $R > 0$ for fibers and $R < 0$ for microtubes. This effect can change both the amplitude of the polarization field $\mathbf{p}$ given by $\mathbf{p}$ and the linear couplings with the extrinsic curvature tensor $C_{\alpha\beta}$ in a microtube and in a fiber. To denote the values of the effective parameters on microtubes and fibers, we use from now on, the superscript, $t$ and $f$, respectively.

As actin-fibril networks orient in the longitudinal direction for microtubes, Fig. 4 in the main text, this implies that $0 < C^t + D^t(\bar{p}^t)^2$. Whereas as actin-fibril networks orient in the azimuthal direction for fibers, Fig. 4 in the main text, this implies that $0 > C^f + D^f(\bar{p}^f)^2$. Rearranging these conditions leads us to

$$0 < C^t + D^t(\bar{p}^t)^2 - D^f(\bar{p}^f)^2.$$  \hspace{1cm} (S38)

The inequality (S38) can only be satisfied in the regime where the dominant coupling terms are those linearly proportional to the extrinsic curvature tensor $C_{\alpha\beta}$ in Eq. (S37). Indeed, let us neglect such terms in Eq. (S37). In this case, the effective parameters are independent on the side of the substrate that the system sits on, meaning that $C^t = C^f$ and $D^t(\bar{p}^t)^2 = D^f(\bar{p}^f)^2$, and the inequality (S38) is unfulfilled. Therefore, the experimental actin-fibril organisation for microtubes and fibers shows that the steady-state orientation patterns of such actin organisations are dominated by couplings that are linearly proportional to the extrinsic curvature tensor.

Note that the theoretical analysis suggests that such linear couplings could arise from two different microscopical mechanisms. For instance, they could result from direct interactions between the curvature and actin fibrils through the effective couplings included in $C$; or they could result from indirect interactions between the curvature and actin fibrils mediated by cell polarization markers like cryptic lamellipodia through the effective couplings included in $D$. 

---
Fig. S1 to S16

(A) and (B) Images at different z-positions of a histone 1-GFP (H1-GFP) MDCK spherical cyst (A) and two tubular MDCK ducts (B) of different diameters (Øs) grown inside Matrigel, stained for actin filaments (red). H1-GFP nuclei are colored in blue. From left to right, the bottom, middle and top views of the 3D tissues are shown. Scale bars, 50 µm. (C) Time-lapsed images of a rotating spherical H1-GFP MDCK acinus. Single cell trajectories are portrayed with varying color lines for
each cell. Scale bar, 50 µm. (D) Graph showing the duration of collective epithelial rotation (CeR) in MDCK ducts ($n = 10$) and acini ($n = 14$), from 3 independent experiments. (E) Graph showing angular variation of rotational axes over time relative to x-axis in a representative MDCK duct (orange line) and acinus (blue line). (F) Snapshot image of a time-lapse movie showing the distal pronephric tubule of a transgenic Tg(cldnb:lynEGFP) embryo. Cells of the pronephric tubule express a membrane-bound GFP and H2B-mcherry in nuclei. Zoom-in region highlighted by magenta dash box is shown in (G). Scale bar, 20µm. (G) Cropped region (magenta dash box in (F)) from (F) highlighting part of the tubule in which cells rotate in azimuthal direction (indicated by red arrow) during tubule elongation at approximately 35 hours post-fertilization (hpf). Single cell trajectories are portrayed with varying color lines. Cells outside the tubule are indicated by white and yellow lines while cells inside the tubule are indicated by other colors. Cells outside have longitudinal-aligned trajectories. In contrast, the trajectories for cells of the tubule show features of a helical movement, resulting from the superposition of azimuthal rotation and longitudinal displacement. Scale bar, 10 µm. (H) Absolute values of average single cell azimuthal velocities ($V_\theta$) in rotating zebrafish pronephric tubules (red, $n = 11$), MDCK ducts in Matrigel (blue, $n = 13$) and MDCK tubular cylindrical tissues ($t$-CTs) inside PDMS microtubes (green, $n = 19$) of similar size ($\varnothing = 20 – 25$ µm). Data are presented as individual values with mean ± s.d.
Fig. S2.

(A) Schematic representation of the experimental set up to form in vitro MDCK t-CTs. Cells were loaded in the reservoir areas and let grow inside various PDMS tubes until confluence to form t-CTs of varying diameters. Yellow dash box indicates a typical observation region for CeR. (B) 3D fluorescent representations of MDCK t-CTs of different diameters. Nuclei in green (H1-GFP) and actin in red. Scale bars, 50 µm. (C) Representative fluorescent image of a confluent MDCK t-CTs with Ø = 75 µm, stained for apical marker – Gp135 (green), actin (red) and DAPI (blue). The white dashed lines mark inner borders of PDMS tube. Zoom-in image highlighted by the magenta dashed-box is shown at the lower part of the image. Scale bar, 20µm.
Fig. S3.

Representative graphs (A) and kymographs (B) showing average velocities ($V$) of a MDCK H1-GFP t-CT in azimuthal and longitudinal directions as a function of time. The t-CT grows in a PLL-coated PDMS microtube of $\Omega = 75 \, \mu m$. $V$ is calculated using particle imaging velocimetry (PIV) analysis. The graphs then plot the average azimuthal and longitudinal component of $V$ for each time point (A), reflecting the average movement of the whole t-CT. The kymographs (B) demonstrate spatial average azimuthal, $\bar{V}_\theta$ and longitudinal, $\bar{V}_z$ velocities along the $l$-axis for every time point for entire observation period, thus showing spatiotemporal distribution of local velocities.
**Fig. S4.**

(A) Representative cropped snapshots of particle imaging velocimetry (PIV) analysis performed on 2D projections of H1-GFP MDCK t-CTs of various diameters. Green arrows show local velocity direction. Scale bars, 20µm. (B) Representative examples of kymographs showing PIV-calculated spatial average $\overline{V_\theta}$ along l-axis as a function of time for different t-CTs. The color code indicates overall average $\overline{V_\theta}$ peaks at $\Theta = 100$ µm.
Fig. S5.

(A) Schematic representation of collective helical migration inside a non-confluent PDMS microtube with an advancing MDCK t-CT. (B) Representative snapshot of PIV analysis on a 2D projection of a H1-GFP MDCK t-CT of Ø = 50 µm showing features of helical movement. Green arrows map the velocity field. (C) Graph (top) and kymograph (bottom) showing spatiotemporal average azimuthal velocity ($V_\theta$) of the advancing t-CT in (B) evolving with time. Black dash line indicates the start time point of the collective helical movement. (D) Representative single cell trajectories in the advancing t-CT in (B) showing cell displacement in both $a$- and $l$-axes, a feature of collective helical migration. Cell trajectories were determined by tracking displacement of H1-GFP nuclei.
Fig. S6.

(A) Representative cropped snapshot of PIV analysis on a 2D projection of a Ø = 75µm H1-GFP MDCK t-CT where two neighboring cell groups engage in opposite azimuthal movements. Red dash box indicates the cell group rotating towards the right and blue dash box indicates the cell group rotating towards the left. Scale bar, 50µm. (B) Graphs (top panel) and kymographs (bottom panel) showing spatiotemporal average azimuthal and longitudinal velocities of the t-CT in (A). The azimuthal velocity kymograph shows that as time passes, the cohort rotating towards the left prevails and the whole t-CT rotates uniformly in one direction.
**Fig. S7.**

(A) Schematic representation of the experimental set up to form *in vitro* MDCK CTs on PDMS microfibers (*f*-CTs). Cells were loaded in the reservoir areas and let grow on various PDMS fibers until confluence to form convexly curved *f*-CTs of varying diameters. (B) 3D fluorescent representations of H1-GFP MDCK *f*-CTs of different diameters. Actin, red and nuclei, green. Scale bars, 50µm. (C) A cross-sectional fluorescent image of a confluent MDCK *f*-CT of Ø = 75 µm, stained for apical marker – Gp135 (green), actin (red) and DAPI (blue). The white dashed lines denote the borders of PDMS microfiber (marked as teal area). Zoom-in image highlighted by magenta dashed-box is shown at the lower part of the image. Scale bar, 20µm. (D) Time-lapse 2D projections of a H1-GFP MDCK *f*-CT rotating on a Ø = 100 µm PDMS microfiber. Tracking individual cell nuclei shows cell trajectories as parallel colored lines. Scale bar, 20 µm. (E) Graph showing counts of clockwise and counter-clockwise rotating *f*-CTs of varying Øs. (F) Graph presenting percentage of CeR events observed in *f*-CTs of different diameters (*n* = 4–9 for each condition).
Fig. S8.

(A) and (B) Representative graphs (A) and kymographs (B) (like fig. S3) showing average velocity of a H1-GFP MDCK f-CT in azimuthal and longitudinal directions and spatial distribution along \( l \)-axis as a function of time. The f-CT grows on a PLL-coated PDMS microfiber of \( \varnothing = 75 \, \mu m \).
Fig. S9.

(A) 2D time-lapse projections of a MDCK t-CT (Ø = 50µm) expressing Myosin IIA-RFP showing alignment of actomyosin network is perpendicular to its CeR direction. Cell periphery is marked by red line. (B) 2D projection of a MDCK t-CT (Ø = 100µm) expressing LifeAct-GFP presenting longitudinally aligned actin filaments in a Matrigel-coated PDMS microtube. (C) and (D) Rose diagrams showing actin filament alignment in t-CTs (Ø = 75 and 100µm, n = 18) inside Matrigel-coated PDMS microtubes (C) and in Matrigel-grown MDCK ducts (D), Ø = 20 – 75µm, n = 183). The angle between actin filaments and the azimuthal axis was calculated. (E) Rose diagrams presenting cell orientation in different CTs. An ellipsoidal fit to cell shape was performed and cell orientation is the relative angle between the major ellipsoid axis and the azimuthal axis (n = 19 – 211 for each condition).
Fig. S10.
Fluorescent images showing paxillin (green) and actin (red) in rotating MDCK t-CT and f-CT. White arrowheads mark paxillin staining. Scale bars, 10 µm.
Fig. S11.
Normalized E-cadherin fluorescent intensity in CCJs of different orientations (relative to the CeR direction, i.e., α-axis) in t-CTs and f-CTs. The relative angles between CCJs and $\vec{V_0}$ were presented in x-axis (left panel, $n = 66$ and right panel, $n = 65$). Data are shown as individual values overlapped with box charts showing mean ± s.d. (coef = 1 for the box and coef = 1.5 for the whiskers). Student’s t-test, NS non-significant.
Fig. S12.

(A) Immunofluorescence staining of β-catenin, along with (B) representative western blot for cadherin-6 (cat-6) in MDCK E-cad KO and MDCK E-cad&cadherin-6 double KO cells.
Fig. S13.

(A) Column graph presenting percentage of CeR events observed in E-cad KO t-CTs and f-CTs of different diameters. \( n = 19 – 24 \) for each diameter. (B) Graph showing \( |\bar{V}_\theta| \) of different E-cad KO t-CTs and f-CTs. \( n = 3 – 5 \) for each diameter. In (A) and (B), values are mean ± s.d. (C) and (D) Representative graphs (C) and kymographs (D) (like fig. S3) showing average velocity of a MDCK E-cad KO t-CT with \( \Theta = 75 \, \mu \text{m} \) in azimuthal and longitudinal direction, as well as spatial distribution along \( l \)-axis as a function of time. (E) and (F) Similar representative graphs and kymographs for a MDCK E-cad KO f-CT with \( \Theta = 50 \, \mu \text{m} \) as (C) and (D).
Fig. S14.

(A) and (B) Representative graphs (A) and kymographs (B) (like fig. S3) showing average velocity of a MDCK cadherin double KO t-CT with Ø = 75 µm in azimuthal and longitudinal direction, as well as spatial distribution along I-axis as a function of time. (C) and (D) Similar representative graphs and kymographs for a MDCK cadherin double KO f-CT with Ø = 50 µm as (A) and (B).
Fig. S15.

(A) and (B) Representative graphs (A) and kymographs (B) (like fig. S3) showing average velocity of a MDCK α-catenin knock-down (KD) t-CT with Ø = 75 µm in azimuthal and longitudinal direction, as well as spatial distribution along l-axis as a function of time. (C) and (D) Similar representative graphs and kymographs for a MDCK α-catenin knock-down f-CT with Ø = 50 µm as (A) and (B).
Fig. S16.
2D time-lapse projections of MDCK expressing YFP-PBD in rotating t-CT (Ø = 50 µm) and f-CT (Ø = 50 µm). PBD signal intensity is displayed in fire color code. Orange arrows indicate the direction of protrusions. Scale bars, 20 µm. Red arrows indicate CeR direction.
Movies S1 to S14

Movie S1.
Persistent collective rotation in MDCK acini. Scale bar, 50 μm.

Movie S2.
Persistent collective rotation in a MDCK duct.

Movie S3.
Helical movement in an elongating pronephric tubule expressing a membrane-bound GFP and H2B-mcherry in nuclei. Cell trajectories are portrayed with varying color lines. Scale bar, 10 μm.

Movie S4.
Persisting collective rotation in a H1-GFP MDCK tubular cylindrical tissue (t-CT). Scale bar, 50 μm.

Movie S5.
Particle imaging velocimetry mapping of collective rotation in a H1-GFP MDCK t-CT (2D projection). Scale bar, 50 μm.

Movie S6.
Helical movement of an advancing H1-GFP MDCK t-CT. Scale bar, 50 μm.

Movie S7.
Particle imaging velocimetry mapping of evolution of a H1-GFP MDCK t-CT with two adjacent groups of cells rotating in opposite directions. Scale bar, 50 μm.

Movie S8.
Traction force microscopy measurement of a rotating H1-GFP MDCK t-CT in a soft silicon microtube. Scale bar, 40 μm.

Movie S9.
Synchronized collective rotation in a H1-GFP MDCK cylindrical tissue on a microfiber (f-CT). Scale bar, 50 μm.
**Movie S10.**
2D projection of a rotating MDCK t-CT expressing myosin-IIA RFP showing \( a \)-axial movement of cells with \( l \)-axial aligned actomyosin networks. Scale bar, 20 \( \mu \)m.

**Movie S11.**
Y-27 treatment on rotating H1-GFP MDCK t-CT fails to halt collective rotation. Scale bar, 100 \( \mu \)m.

**Movie S12.**
Persisting collective rotation in an Ecad-KO MDCK t-CT expressing LifeAct-GFP. Scale bar, 50 \( \mu \)m.

**Movie S13.**
Radom cell movement in a confluent MDCK cadherin double KO t-CT. Nuclei were stained with NUCLEAR-ID\textsuperscript{®} Blue DNA Dye. Scale bar, 50 \( \mu \)m.

**Movie S14.**
A rotating MDCK \( f \)-CT expressing LifeAct-GFP showing persistent \( a \)-axial actin filaments. Scale bar, 10 \( \mu \)m.
REFERENCES AND NOTES

1. S. L. Haigo, D. Bilder, Global tissue revolutions in a morphogenetic movement controlling elongation. *Science* **331**, 1071–1074 (2011).

2. M. Cetera, G. R. Ramirez-San Juan, P. W. Oakes, L. Lewellyn, M. J. Fairchild, G. Tanentzapf, M. L. Gardel, S. Horne-Badovinac, Epithelial rotation promotes the global alignment of contractile actin bundles during Drosophila egg chamber elongation. *Nat. Commun.* **5**, 5511 (2014).

3. A. Popkova, O. J. Stone, L. Chen, X. Qin, C. Liu, J. Liu, K. Belguise, D. J. Montell, K. M. Hahn, M. Rauzi, X. Wang, A Cdc42-mediated supracellular network drives polarized forces and Drosophila egg chamber extension. *Nat. Commun.* **11**, 1921 (2020).

4. K. Sato, T. Hiraiwa, E. Maekawa, A. Isomura, T. Shibata, E. Kuranaga, Left–right asymmetric cell intercalation drives directional collective cell movement in epithelial morphogenesis. *Nat. Commun.* **6**, 10074 (2015).

5. K. Tanner, H. Mori, R. Mroue, A. Bruni-Cardoso, M. J. Bissell, Coherent angular motion in the establishment of multicellular architecture of glandular tissues. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 1973–1978 (2012).

6. P. A. Fernández, B. Buchmann, A. Goychuk, L. K. Engelbrecht, M. K. Raich, C. H. Scheel, E. Frey, A. R. Bausch, Surface-tension-induced budding drives alveologenesis in human mammary gland organoids. *Nat. Phys.* **17**, 1130–1136 (2021).

7. J. Zhang, K. F. Goliwas, W. Wang, P. V. Taufalele, F. Bordeleau, C. A. Reinhart-King, Energetic regulation of coordinated leader–follower dynamics during collective invasion of breast cancer cells. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 7867–7872 (2019).

8. H. Wang, S. Lacoche, L. Huang, B. Xue, S. K. Muthuswamy, Rotational motion during three-dimensional morphogenesis of mammary epithelial acini relates to laminin matrix assembly. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 163–168 (2013).
9. P. Rørth, Fellow travellers: Emergent properties of collective cell migration. *EMBO Rep.* **13**, 984–991 (2012).

10. S. Jain, V. M. L. Cachoux, G. H. N. S. Narayana, S. de Beco, J. D’Alessandro, V. Cellerin, T. Chen, M. L. Heuzé, P. Marcq, R.-M. Mège, A. J. Kabla, C. T. Lim, B. Ladoux, The role of single-cell mechanical behaviour and polarity in driving collective cell migration. *Nat. Phys.* **16**, 802–809 (2020).

11. R. Mayor, S. Etienne-Manneville, The front and rear of collective cell migration. *Nat. Rev. Mol. Cell Biol.* **17**, 97–109 (2016).

12. B. Ladoux, R.-M. Mège, Mechanobiology of collective cell behaviours. *Nat. Rev. Mol. Cell Biol.* **18**, 743–757 (2017).

13. M. Reffay, L. Petitjean, S. Coscoy, E. Grasland-Mongrain, F. Amblard, A. Buguin, P. Silberzan, Orientation and polarity in collectively migrating cell structures: Statics and dynamics. *Biophys. J.* **100**, 2566–2575 (2011).

14. R. Farooqui, G. Fenteany, Multiple rows of cells behind an epithelial wound edge extend cryptic lamellipodia to collectively drive cell-sheet movement. *J. Cell Sci.* **118**, 51–63 (2005).

15. D. J. Montell, Morphogenetic cell movements: Diversity from modular mechanical properties. *Science* **322**, 1502–1505 (2008).

16. X. Trepat, M. R. Wasserman, T. E. Angelini, E. Millet, D. A. Weitz, J. P. Butler, J. J. Fredberg, Physical forces during collective cell migration. *Nat. Phys.* **5**, 426–430 (2009).

17. F. Peglion, F. Llense, S. Etienne-Manneville, Adherens junction treadmilling during collective migration. *Nat. Cell Biol.* **16**, 639–651 (2014).

18. K. M. Sherrard, M. Cetera, S. Horne-Badovinac, DAAM mediates the assembly of long-lived, treadmilling stress fibers in collectively migrating epithelial cells in *Drosophila*. bioRxiv 2021.2008.2007.455521 [Preprint]. 8 August 2021. https://doi.org/10.1101/2021.08.07.455521.
19. T. Chen, A. Callan-Jones, E. Fedorov, A. Ravasio, A. Brugués, H. T. Ong, Y. Toyama, B. C. Low, X. Trepas, T. Shemesh, R. Voituriez, B. Ladoux, Large-scale curvature sensing by directional actin flow drives cellular migration mode switching. *Nat. Phys.* **15**, 393–402 (2019).

20. Y. Y. Biton, S. A. Safran, The cellular response to curvature-induced stress. *Phys. Biol.* **6**, 046010 (2009).

21. W. Xi, S. Sonam, T. Beng Saw, B. Ladoux, C. Teck Lim, Emergent patterns of collective cell migration under tubular confinement. *Nat. Commun.* **8**, 1517 (2017).

22. H. G. Yevick, G. Duclos, I. Bonnet, P. Silberzan, Architecture and migration of an epithelium on a cylindrical wire. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 5944–5949 (2015).

23. Y. Maroudas-Sacks, L. Garion, L. Shani-Zerbib, A. Livshits, E. Braun, K. Keren, Topological defects in the nematic order of actin fibres as organization centres of Hydra morphogenesis. *Nat. Phys.* **17**, 251–259 (2021).

24. M. Gupta, B. R. Sarangi, J. Deschamps, Y. Nematbakhsh, A. Callan-Jones, F. Margadant, R.-M. Mège, C. T. Lim, R. Voituriez, B. Ladoux, Adaptive rheology and ordering of cell cytoskeleton govern matrix rigidity sensing. *Nat. Commun.* **6**, 7525 (2015).

25. D. J. G. Pearce, S. Gat, G. Livne, A. Bernheim-Groswasser, K. Kuruse, Defect-driven shape transitions in elastic active nematic shells. arXiv:2010.13141 [cond-mat.soft] (25 October 2020).

26. L. A. Hoffmann, L. N. Carenza, J. Eckert, L. Giomi, Theory of defect-mediated morphogenesis. *Sci. Adv.* **8**, eabk2712 (2022).

27. I. Nitschke, S. Reuther, A. Voigt, Liquid crystals on deformable surfaces. *Proc. R. Soc. A Math. Phys. Eng. Sci.* **476**, 20200313 (2020).

28. A. S. Chin, K. E. Worley, P. Ray, G. Kaur, J. Fan, L. Q. Wan, Epithelial cell chirality revealed by three-dimensional spontaneous rotation. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 12188–12193 (2018).
29. D. T. Tambe, C. Corey Hardin, T. E. Angelini, K. Rajendran, C. Y. Park, X. Serra-Picamal, E. H. Zhou, M. H. Zaman, J. P. Butler, D. A. Weitz, J. J. Fredberg, X. Trepat, Collective cell guidance by cooperative intercellular forces. *Nat. Mater.* **10**, 469–475 (2011).

30. P. Leroy, K. E. Mostov, Slug is required for cell survival during partial epithelial-mesenchymal transition of HGF-induced tubulogenesis. *Mol. Biol. Cell* **18**, 1943–1952 (2007).

31. T. Hirashima, M. Hoshuyama, T. Adachi, In vitro tubulogenesis of Madin–Darby canine kidney (MDCK) spheroids occurs depending on constituent cell number and scaffold gel concentration. *J. Theor. Biol.* **435**, 110–115 (2017).

32. S. Horne-Badovinac, D. Bilder, Mass transit: Epithelial morphogenesis in the drosophila egg chamber. *Dev. Dyn.* **232**, 559–574 (2005).

33. A. Doostmohammadi, S. P. Thampi, T. B. Saw, C. T. Lim, B. Ladoux, J. M. Yeomans, Celebrating soft matter's 10th anniversary: Cell division: A source of active stress in cellular monolayers. *Soft Matter* **11**, 7328–7336 (2015).

34. R. W. Naylor, H.-H. G. Chang, S. Qubisi, A. J. Davidson, A novel mechanism of gland formation in zebrafish involving transdifferentiation of renal epithelial cells and live cell extrusion. *eLife* **7**, e38911 (2018).

35. F. Martin-Belmonte, K. Mostov, Regulation of cell polarity during epithelial morphogenesis. *Curr. Opin. Cell Biol.* **20**, 227–234 (2008).

36. J. d’Alessandro, A. Barbier--Chebbah, V. Cellerin, O. Benichou, R. M. Mège, R. Voituriez, B. Ladoux, Cell migration guided by long-lived spatial memory. *Nat. Commun.* **12**, 4118 (2021).

37. S. R. K. Vedula, M. C. Leong, T. L. Lai, P. Hersen, A. J. Kabla, C. T. Lim, B. Ladoux, Emerging modes of collective cell migration induced by geometrical constraints. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 12974–12979 (2012).

38. L. Balasubramaniam, A. Doostmohammadi, T. B. Saw, G. H. N. S. Narayana, R. Mueller, T. Dang, M. Thomas, S. Gupta, S. Sonam, A. S. Yap, Y. Toyama, R.-M. Mège, J. M. Yeomans, B. Ladoux,
Investigating the nature of active forces in tissues reveals how contractile cells can form extensile monolayers. *Nat. Mater.* **20**, 1156–1166 (2021).

39. R. Sunyer, V. Conte, J. Escribano, A. Elosegui-Artola, A. Labernadie, L. Valon, D. Navajas, J. M. García-Aznar, J. J. Muñoz, P. Roca-Cusachs, X. Trepat, Collective cell durotaxis emerges from long-range intercellular force transmission. *Science* **353**, 1157–1161 (2016).

40. W. Xi, T. B. Saw, D. Delacour, C. T. Lim, B. Ladoux, Material approaches to active tissue mechanics. *Nat. Rev. Mater.* **4**, 23–44 (2019).

41. A. Ravasio, I. Cheddadi, T. Chen, T. Pereira, H. T. Ong, C. Bertocchi, A. Brugues, A. Jacinto, A. J. Kabla, Y. Toyama, X. Trepat, N. Gov, L. Neves de Almeida, B. Ladoux, Gap geometry dictates epithelial closure efficiency. *Nat. Commun.* **6**, 7683 (2015).

42. M. Luciano, S.-L. Xue, W. H. De Vos, L. Redondo-Morata, M. Surin, F. Lafont, E. Hannezo, S. Gabriele, Cell monolayers sense curvature by exploiting active mechanics and nuclear mechanoadaptation. *Nat. Phys.* **17**, 1382–1390 (2021).

43. L. Pieuchot, J. Marteau, A. Guignandon, T. Dos Santos, I. Brigaud, P.-F. Chauvy, T. Cloatre, A. Ponche, T. Petithory, P. Rougerie, M. Vassaux, J.-L. Milan, N. Tusamda Wakhloo, A. Spangenberg, M. Bigerelle, K. Anselme, Curvotaxis directs cell migration through cell-scale curvature landscapes. *Nat. Commun.* **9**, 3995 (2018).

44. P. Rougerie, L. Pieuchot, R. S. dos Santos, J. Marteau, M. Bigerelle, P.-F. Chauvy, M. Farina, K. Anselme, Topographical curvature is sufficient to control epithelium elongation. *Sci. Rep.* **10**, 14784 (2020).

45. S.-M. Yu, J. M. Oh, J. Lee, W. Lee-Kwon, W. Jung, F. Amblard, S. Granick, Y.-K. Cho, Substrate curvature affects the shape, orientation, and polarization of renal epithelial cells. *Acta Biomater.* **77**, 311–321 (2018).

46. I. D. Johnston, D. K. McCluskey, C. K. L. Tan, M. C. Tracey, Mechanical characterization of bulk Sylgard 184 for microfluidics and microengineering. *J. Micromech. Microeng.* **24**, 035017 (2014).
47. L. Lu, S. J. Oswald, H. Ngu, F. C. Yin, Mechanical properties of actin stress fibers in living cells. *Biophys. J.* **95**, 6060–6071 (2008).

48. C. S. Chen, J. Tan, J. Tien, Mechanotransduction at cell-matrix and cell-cell contacts. *Annu. Rev. Biomed. Eng.* **6**, 275–302 (2004).

49. M. Bienz, β-Catenin: A pivot between cell adhesion and wnt signalling. *Curr. Biol.* **15**, R64–R67 (2005).

50. K. A. Knudsen, A. P. Soler, K. R. Johnson, M. J. Wheelock, Interaction of alpha-actinin with the cadherin/catenin cell-cell adhesion complex via alpha-catenin. *J. Cell Biol.* **130**, 67–77 (1995).

51. S. Yonemura, Y. Wada, T. Watanabe, A. Nagafuchi, M. Shibata, α-Catenin as a tension transducer that induces adherens junction development. *Nat. Cell Biol.* **12**, 533–542 (2010).

52. M. Rauzi, P. Verant, T. Lecuit, P.-F. Lenne, Nature and anisotropy of cortical forces orienting Drosophila tissue morphogenesis. *Nat. Cell Biol.* **10**, 1401–1410 (2008).

53. K. Matsuzawa, T. Himoto, Y. Mochizuki, J. Ikenouchi, α-Catenin controls the anisotropy of force distribution at cell-cell junctions during collective cell migration. *Cell Rep.* **23**, 3447–3456 (2018).

54. W. Y. Wang, C. D. Davidson, D. Lin, B. M. Baker, Actomyosin contractility-dependent matrix stretch and recoil induces rapid cell migration. *Nat. Commun.* **10**, 1186 (2019).

55. S. Jain, B. Ladoux, R. M. Mège, Mechanical plasticity in collective cell migration. *Curr. Opin. Cell Biol.* **72**, 54–62 (2021).

56. C. Blanch-Mercader, R. Vincent, E. Bazellières, X. Serra-Picamal, X. Trepat, J. Casademunt, Effective viscosity and dynamics of spreading epithelia: A solvable model. *Soft Matter* **13**, 1235–1243 (2017).

57. K. Kruse, J. F. Joanny, F. Jülicher, J. Prost, K. Sekimoto, Generic theory of active polar gels: A paradigm for cytoskeletal dynamics. *Eur. Phys. J. E* **16**, 5–16 (2005).
58. F. Jülicher, K. Kruse, J. Prost, J. F. Joanny, Active behavior of the cytoskeleton. *Phys. Rep.* **449**, 3–28 (2007).

59. M. Poujade, E. Grasland-Mongrain, A. Hertzog, J. Jouanneau, P. Chavrier, B. Ladoux, A. Buguin, P. Silberzan, Collective migration of an epithelial monolayer in response to a model wound. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 15988–15993 (2007).

60. T. E. Angelini, E. Hannezo, X. Trepat, M. Marquez, J. J. Fredberg, D. A. Weitz, Glass-like dynamics of collective cell migration. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 4714–4719 (2011).

61. J. M. López-Gay, H. Nunley, M. Spencer, F. di Pietro, B. Guirao, F. Bosveld, O. Markova, I. Gaugue, S. Pelletier, D. K. Lubensky, Y. Bellaïche, Apical stress fibers enable a scaling between cell mechanical response and area in epithelial tissue. *Science* **370**, eabb2169 (2020).

62. P. Haas, D. Gilmour, Chemokine signaling mediates self-organizing tissue migration in the zebrafish lateral line. *Dev. Cell* **10**, 673–680 (2006).

63. Q. Guo, B. Xia, S. Moshiach, C. Xu, Y. Jiang, Y. Chen, Y. Sun, J. M. Lahti, X. A. Zhang, The microenvironmental determinants for kidney epithelial cyst morphogenesis. *Eur. J. Cell Biol.* **87**, 251–266 (2008).

64. W. Xi, S. Sonam, C. T. Lim, B. Ladoux, in *Methods in Cell Biology*, J. Doh, D. Fletcher, M. Piel, Eds. (Academic Press, 2018), vol. 146, pp. 3–21.

65. Q. Tseng, E. Duchemin-Pelletier, A. Deshiere, M. Balland, H. Guillou, O. Filhol, M. Théry, Spatial organization of the extracellular matrix regulates cell–cell junction positioning. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 1506–1511 (2012).

66. L. Petitjean, M. Reffay, E. Grasland-Mongrain, M. Poujade, B. Ladoux, A. Buguin, P. Silberzan, Velocity fields in a collectively migrating epithelium. *Biophys. J.* **98**, 1790–1800 (2010).

67. Z. Püspöki, M. Storath, D. Sage, M. Unser, Transforms and operators for directional bioimage analysis: A survey. *Adv. Anat. Embryol. Cell Biol.* **219**, 69–93 (2016).
68. G. Napoli, L. Vergori, Extrinsic curvature effects on nematic shells. *Phys. Rev. Lett.* **108**, 207803 (2012).

69. G. Napoli, L. Vergori, Surface free energies for nematic shells. *Phys. Rev. E* **85**, 061701 (2012).

70. A. Segatti, M. Snarski, M. Veneroni, Equilibrium configurations of nematic liquid crystals on a torus. *Phys. Rev. E* **90**, 012501 (2014).

71. D. Jesenek, S. Kralj, R. Rosso, E. G. Virga, Defect unbinding on a toroidal nematic shell. *Soft Matter* **11**, 2434–2444 (2015).

72. I. Nitschke, M. Nestler, S. Praetorius, H. Löwen, A. Voigt, Nematic liquid crystals on curved surfaces: A thin film limit. *Proc. R. Soc. A Math. Phys. Eng. Sci.* **474**, 20170686 (2018).

73. M. Nestler, I. Nitschke, S. Praetorius, A. Voigt, Orientational order on surfaces: The coupling of topology, geometry, and dynamics. *J. Nonlinear Sci.* **28**, 147–191 (2018).

74. M. Nestler, I. Nitschke, H. Löwen, A. Voigt, Properties of surface Landau–de Gennes Q-tensor models. *Soft Matter* **16**, 4032–4042 (2020).

75. D. J. G. Pearce, P. W. Ellis, A. Fernandez-Nieves, L. Giomi, Geometrical control of active turbulence in curved topographies. *Phys. Rev. Lett.* **122**, 168002 (2019).

76. D. J. G. Pearce, Defect order in active nematics on a curved surface. *New J. Phys.* **22**, 063051 (2020).

77. D. Khoromskaia, G. Salbreux, Active morphogenesis of patterned epithelial shells. arXiv:2111.12820 [physics.bio-ph] (24 November 2021).

78. M. Nestler, A. Voigt, Active nematodynamics on curved surfaces—The influence of geometric forces on motion patterns of topological defects. arXiv:2107.07779 [cond-mat.soft] (1 July 2021).

79. G. Salbreux, F. Jülicher, J. Prost, A. Callan-Jones, Theory of nematic and polar active fluid surfaces. arXiv:2201.09251 [cond-mat.soft] (23 January 2022).
80. S. Bell, S.-Z. Lin, J.-F. Rupprecht, J. Prost, Active nematic flows on curved surfaces. arXiv:2203.05644 [physics.bio-ph] (10 March 2022).

81. P. G. de Gennes, J. Prost, *The Physics of Liquid Crystals* (Clarendon Press, 1993).

82. M. Nestler, I. Nitschke, A. Voigt, A finite element approach for vector- and tensor-valued surface PDEs. *J. Comput. Phys.* **389**, 48–61 (2019).

83. M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, R. A. Simha, Hydrodynamics of soft active matter. *Rev. Mod. Phys.* **85**, 1143–1189 (2013).