Chiral flows can induce neck formation in viscoelastic surfaces

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Abstract

The cell cortex is an active viscoelastic self-deforming sheet at the periphery of animal cells. It constricts animal cells during cell division. For some egg cells, the actomyosin cortex was shown to exhibit counter-rotating chiral flows along the axis of division. Such chiral surface flows were shown to contribute to spatial rearrangements and left-right symmetry breaking in developing organisms. In spite of this prospective biological importance, the effect of chiral forces on the flows and emergent shape dynamics of a deformable surface are completely unknown. To shed a first light on that matter, we present here a numerical study of an axisymmetric viscoelastic surface embedded in a viscous fluid. We impose a generic counter-rotating force field on this surface and study the resulting chiral flow field and shape dynamics for various surface mechanical parameters. Notably, we find that the building of a neck, as is observed during cell division, occurs if the surface contains a strong shear elastic component. Furthermore, we find that a large areal relaxation time results in flows towards the equator of the surface. These flows assist the transport of a surface concentration during the formation of a contractile ring. Accordingly, we show that chiral forces by themselves can drive pattern formation and stabilise contractile rings at the equator. These results provide first mechanistic evidence that chiral flows can play a significant role to orchestrate cell division.

1. Introduction

Most organisms are chiral, i.e. they exhibit left-right asymmetries and are not superimposable on their mirror images [1–6]. In particular, chiral flows at the level of the fertilised egg were shown to be linked to symmetry breaking and the establishment of the left-right body axis in several invertebrate species [7–9]. At the level of the cell, shape is mainly regulated by the actomyosin cortex, a thin biopolymer network at the surface of the cell underneath the plasma membrane [10]. Notably, chiral asymmetries in the flow field of the cortex were apparent during cell division of some egg cells [3, 7, 9, 11]. However, at the current state, the influence of chiral cortical flows on cellular morphogenesis remains elusive.

From a molecular biology point of view, the source of chiral cortical flows in the cell are most likely forces generated by the cytoskeleton. Local microscopic torques caused by the helix structure of the actin filaments could result in large scale chiral flows [8, 12–15]. These chiral flows, in turn, could influence shape dynamics during cell division. This is illustrated by the analogy of a balloon animal; to make a balloon animal, an elongated balloon is twisted in opposite directions which creates a neck in the centre of the balloon. Correspondingly, a chiral (i.e. counter-rotating) force field can induce a neck in an elastic surface.

As cells are not simple elastic surfaces, it is yet unclear if chiral forces can also drive neck formation in cells. Experimental measurements indicate that the cell cortex is viscoelastic with timescale-dependent mechanical properties [16–20]. In particular, it has been shown that the cortex is stiff and dominantly elastic.
at short time scales and has fluid-like properties at long time scales [16–18], a behaviour which can be described in the simplest form by a Maxwell model. This type of viscoelasticity can be best illustrated by considering the 1D Maxwell element in figure 1 left. Here, a viscous dashpot with viscosity $\eta$ is in series with an elastic spring with elastic modulus $G$. When the Maxwell element is dilated, first, elastic stresses are stored in the spring but then dissipated by viscous dissipation through the sliding of the dashpot. The ratio $\eta/G$ defines a time scale $\tau$ of stress relaxation.

Previous theoretical studies have formulated and investigated the generalised hydrodynamics of active and passive viscoelastic films with and without active chiral torques [3, 21–26]. Pattern formation and dynamics of active viscoelastic materials in the absence of chiral flows was e.g. described in [21, 22]. Other theoretical studies were dedicated to active chiral fluids in which active torques are assumed to be present modelling the influence of chiral motors. Specifically, in [3, 23, 24], the authors argue that active torques can result in large scale chiral flows in active viscous fluids. In addition, active and passive chiral viscoelastic materials were shown to exhibit counter-intuitive elastic responses perpendicular to applied stresses, referred to as odd elasticity [25–27].

The previously mentioned theoretical studies of chiral forces are limited to stationary geometries. Consequently, the effect of such forces on the flows and shape dynamics of a deformable surface (e.g. the cortical cell surface) is completely unknown. The goal of this work is to fill this gap and study the influence of a chiral force field on the emergent shape of a viscoelastic surface and the concomitant time dynamics of a surface concentration field. Therefore, we present a numerical model of an axisymmetric viscoelastic surface which is subject to a generic counter-rotating force field. We study the resulting chiral flow field and shape dynamics for various surface mechanical parameters and give first evidence that the chiral flows can lead to neck formation as is observed during cell division. Combining the model with a surface concentration of active contractile molecules, we find that chiral forces by themselves can drive pattern formation and stabilise contractile ring patterns at the equator. These results provide first mechanistic evidence that chiral flows can play a significant role to orchestrate cell division, motivating future numerical and experimental studies.

In section 2, we introduce the mathematical model of an active viscoelastic surface subject to an induced chiral azimuthal flow field. To model surface viscoelasticity, we use the upper-convected-surface Maxwell model as described in [28]. We then present results of numerical simulations starting from an initially spherical reference shape in section 3. In particular, we systematically study the influence of the viscoelastic parameters of the surface in sections 3.1–3.3. Then, we show the potential of the chiral force field to stabilise a contractile ring in an active surface during cell division in section 3.4. These results are summarised and put into a biological perspective in section 4. Finally we draw conclusions and address the future scope in section 5.

2. Governing equations

We model a viscoelastic cell surface embedded in viscous fluids. A sketch of the domain is given in figure 1 left. The domains are labelled $\Omega_0$ for the external fluid and $\Omega_1$ for the internal fluid. The cell surface $\Gamma$ separates the fluids and is assumed to have zero thickness as we anticipate that the actin cortex is thin as
compared to the cell radius [29]. Although we use an axisymmetric implementation (figure 1 right), the governing equations are given in three dimensions in the following.

Given the small length scale of biological cells, we anticipate low Reynolds numbers and model the surrounding and cytoplasmic fluid as incompressible Stokes fluids,

\[ \nabla \cdot \mathbf{v} = 0 \quad \text{in } \Omega_0 \cup \Omega_1, \]  
\[ 0 = -\nabla p + \eta_1 \nabla \cdot (\nabla \mathbf{v} + (\nabla \mathbf{v})^T) \quad \text{in } \Omega_0 \cup \Omega_1. \]  
Here \( \mathbf{v} \) represents the velocity, \( p \) the pressure and \( \eta_1 \) the fluid viscosity in \( \Omega_1 \).

The enclosing surface \( \Gamma \) is viscoelastic and the corresponding viscoelastic stress \( \mathbf{S} \) is decomposed into its areal part \( \text{tr} \mathbf{S} \) and shear part \( \mathbf{S} \), such that \( \mathbf{S} = \mathbf{S} + \frac{1}{2} (\text{tr} \mathbf{S}) \mathbf{P} \). The matrix \( \mathbf{P} = \mathbf{I} - \mathbf{n} \otimes \mathbf{n} \) is the projection matrix, it projects a vector on the surface with surface normal vector \( \mathbf{n} \). In a 2D surface, mechanical resistance with regard to shear deformation and area dilation needs to be described by a set of two elastic moduli and corresponding viscosities in the case of a Maxwell-type viscoelasticity. Equivalently, these parameters can be expressed by two viscosities and two relaxation time scales. Therefore, we will use shear and areal viscosities \( \eta_\alpha \) and \( \eta_0 \) and the shear and areal relaxation times \( \tau_\alpha \) and \( \tau_0 \) as mechanical parameters of the surface. The evolution of the stress is determined by changes in surface morphology and surface flows. Consistent evolution equations for the stress components were derived in [28] as

\[ \mathbf{S} = 2\eta_0 \mathbf{D} - \tau_0 \delta \mathbf{S} \quad \text{on } \Gamma, \]  
\[ \text{tr} \mathbf{S} = 2\eta_\alpha \text{tr} \mathbf{D} + \tau_\alpha (2(\mathbf{S} : \nabla \mathbf{v}) + \text{tr} \mathbf{S} \text{tr} \mathbf{D}) - \partial_\mathbf{v} \text{tr} \mathbf{S} \quad \text{on } \Gamma. \]

Here, the surface rate of deformation tensor is defined as \( \mathbf{D} = \frac{1}{2} \mathbf{P} \left( \nabla \mathbf{v} + (\nabla \mathbf{v})^T \right) \mathbf{P} \). Its traceless part is \( \mathbf{D} = \mathbf{D} - \frac{1}{2} (\text{tr} \mathbf{D}) \mathbf{P} \). The operators are the material derivative \( \partial_\mathbf{v} \), and the traceless upper convected surface derivative, which is defined as

\[ \delta \mathbf{S} = \partial_\mathbf{v} \mathbf{S} - \nabla \mathbf{v} \mathbf{S} - \mathbf{S} (\nabla \mathbf{v})^T + \mathbf{P} (\nabla \mathbf{v})^T - \text{tr} \mathbf{S} \mathbf{D}. \]  

for a traceless tensor \( \mathbf{S} \).

We also track the evolution of a surface quantity (e.g. surface-bound protein like myosin). The dynamics of such a surface concentration \( c \) is given by the advection diffusion equation

\[ \partial_\mathbf{v} c + c (\nabla \cdot \mathbf{v}) = D_i \Delta_{\Gamma} c, \]  
where \( D_i \) is the diffusion coefficient [30]. If the surface quantity represents molecular motor proteins, the corresponding force field can be included as an isotropic active surface tension stress given by

\[ S_a = \xi f(c) P, \]  
where the parameter \( \xi \) regulates the strength of the active contribution. The function \( f(c) \) is expressed consistently with previous literature [30–32] by a monotonically increasing Hill function \( f = \frac{c^2}{c^2 + c_0^2} \), where \( c_0 \) is the constant equilibrium concentration on the surface \( \Gamma \) [30, 31, 33]. Note, that for most of this article, the parameter \( \xi \) will be set to zero such that there is no feedback from \( c \) on the mechanics of the system. This is to remove the interplay between deformation of the surface caused by the chiral forces and the deformation caused by the active surface tension.

Finally, to systematically analyse the effect of chiral forces we prescribe a well-defined generic counter rotating force field

\[ f_\circ = \alpha \hat{e}_\circ r_0 z_0. \]  
Here, \( \hat{e}_\circ \) is the base vector in the rotational direction, \( r \) is the distance from the axis of rotation and \( z \) is the location along the axis of rotation, see figure 1 right. The surface is centred at the origin \( r = z = 0 \). The values \( r_0 \) and \( z_0 \) are the initial \( r \) and \( z \) coordinates of the material points on the surface. The strength of the chiral force field is scaled by the factor \( \alpha \). In figure 1 left, a schematic representation of the chiral force field is given. Note, that the space-dependent force field in equation (8) is defined in terms of the initial coordinates of each surface (material) point. This ensures that the overall strength of the force field (e.g. its peak magnitude) remains constant during evolution of the surface shape, which permits to analyse the effect of
chiral forces on flows and shape dynamics more systematically. Putting together the viscoelastic, active, chiral and fluid forces on the surface results in the boundary condition

$$\nabla \Gamma \cdot S + \nabla \Gamma \cdot S_\alpha + f_c = \left[-pI + \eta (\nabla v + (\nabla v)^T)\right] \mathbf{n} \quad \text{on } \Gamma,$$

where the square brackets denote the discontinuous jump of the enclosed tensor across the surface.

### 2.1. Non-dimensional equations and parameters

The equations are non-dimensionalised using the initial cell radius $R$ as characteristic length scale and setting the characteristic timescale $\tau_c = \frac{\eta v_0}{\eta R}$. This can be interpreted as the resistance of the fluid divided by the strength of the chiral force field. The system of equations in dimensionless form is

$$\tilde{S} = 2\tilde{D} - \tilde{\tau}_s \left( \partial^* S - \nabla \Gamma \tilde{v} \tilde{S} - \tilde{S}(\nabla \Gamma v)^T + P(\tilde{S} : \nabla \Gamma v) - \frac{\tilde{\eta}_A}{\tilde{\eta}_s} \text{tr}(S) \tilde{D} \right) \quad \text{on } \Gamma,$$

$$\text{tr}(S) = 2 \text{tr}(D) + \tilde{\tau}_s \left( \frac{2\tilde{\eta}_s}{\tilde{\eta}_A} (\tilde{S} : \nabla \Gamma v) + \text{tr}(S) \text{tr}(D) - \partial^* \text{tr} \tilde{S} \right) \quad \text{on } \Gamma,$$

$$0 = \nabla \cdot \tilde{v} \quad \text{in } \Omega_0 \cup \Omega_1,$$

$$0 = -\nabla \tilde{p} + 2 \frac{\tilde{\eta}_s}{\tilde{\eta}_A} \nabla \cdot (\nabla \Gamma v + (\nabla \Gamma v)^T) \quad \text{in } \Omega_0 \cup \Omega_1,$$

$$0 = \left[-pI + 2 \frac{\tilde{\eta}_s}{\tilde{\eta}_A} (\nabla \Gamma v + (\nabla \Gamma v)^T)\right] \mathbf{n} - \nabla \Gamma \cdot (S + S_\alpha) - \tilde{c}_f \mathbf{n} \quad \text{on } \Gamma,$$

$$S = \frac{\tilde{\eta}_A}{2} \text{tr} \tilde{S} P + \tilde{\eta}_s \tilde{S} \quad \text{on } \Gamma,$$

$$\tilde{D}_c \Delta \Gamma \tilde{c} = \partial^* \tilde{c} + c(\nabla \Gamma \cdot \tilde{v}) \quad \text{on } \Gamma,$$

$$S_\alpha = \tilde{c} \tilde{f}(c) P \quad \text{on } \Gamma.$$

We use the dimensionless parameters given in Table 1.

### 3. Results

To study the influence of the parameters on the mechanics, we simulated the model using the discretization described in Appendix A. We varied the viscoelastic non-dimensional parameters $\tilde{\tau}_s$, $\tilde{\tau}_r$, $\tilde{\eta}_A$, $\tilde{\eta}_s$, $\tilde{G}_A$, and $\tilde{G}_s$ to observe their influence on the surface shape dynamics. Unless stated otherwise, simulations start with a spherical surface $\Gamma$ with dimensionless radius 1. The initial stress $S$ and velocity $\mathbf{v}$ are set to zero, the dimensionless concentration $c$ is initially equal to one.

In the analysis of our simulations, we mainly study two quantities:

1. The dimensionless radius $r$ of the surface at the equator, i.e. at $z = 0$, which measures the ability of the chiral force field to induce a constricted neck region (indicated by $r < 1$).

### Table 1. Definitions and values of the non-dimensional parameters.

| Quantity                        | Symbol | Range            |
|---------------------------------|--------|-----------------|
| Scaled relaxation time          | $\tilde{\tau}_s$ | $[10^{-2}, 10^3]$ |
| Scaled surface viscosity        | $\tilde{\eta}_s$ | $[10^{-1}, 10^0]$ |
| Scaled elastic modulus          | $\tilde{G}_A$ | $[10^{-4}, 10^0]$ |
| Fluid viscosity ratio           | $\frac{\eta}{\eta_0}, i \in \{0, 1\}$ | 1 |
| Scaled diffusion coefficient    | $\tilde{D}_f$ | $10^{-6}$ |
| Activity to chiral force field  | $\tilde{\xi}$ | 0 |
2. The surface concentration \( c \), which models the coarse-grained density of a passive surface bound molecular species. We are especially interested in the deviation of the equatorial concentration from the concentration on the rest of the surface. Therefore, we calculated \( c(z = 0) - \frac{\int_{\Gamma} c d\Gamma}{|\Gamma|} \) for each simulation.

An example of a simulation of a viscoelastic surface deforming under the influence of a chiral force field is given in figure 2. There, the chiral force field induces a chiral flow pattern, so the azimuthal velocity \( v_\phi \) switches sign at the equator. The mechanical properties of the surface transforms this chiral flow into orthogonal flows shown in figure 2. These flows cause the formation of a neck at the equator.

In our simulation, we discovered that the solutions for the fluid velocity could be divided into three categories, which we refer to as flow profiles A to C. These solutions were not only different in appearance, but also resulted in different deformations of the surface and different distributions of the surface concentration \( c \), see figure 3. Flow profiles are characterised as follows in the different categories:

A This flow profile has no vortices within the surface and its highest value is along the symmetry axis. The dynamics leads to only mild changes in surface concentration at the centre (figure 3(a)).

B The velocity profile has two vortices (vortex rings in 3D, respectively) inside and two vortices outside of the surface. Due to the parallel flows towards the equator this profile resulted in the strongest growth of the ring of high concentration \( c \). It is therefore the most beneficial profile in increasing the surface concentration at the equator. This profile was only observed in simulations where \( \hat{\tau}_A > \hat{\tau}_S \) (figure 3(b)).

C This flow profile lacks vortices inside of the surface and its highest velocity is between the poles and the equator of the surface. The corresponding dynamics increases the concentration between the poles and the equator of the surface. As a result, this pattern is fundamentally different from a concentration-enriched contractile ring pattern as observed during cell division \([33–35]\). This profile was only observed in simulations where \( \hat{\tau}_A < \hat{\tau}_S \) (figure 3(c)).

For the simulations, we choose the diffusion coefficient in equation (16) to be negligibly small (\( \hat{D}_c = 10^{-4} \)). So the dynamics for \( c \) is almost exclusively defined by the advective flux, i.e. by the term \( \nabla \Gamma \cdot \nabla_c \). If the surface contracts locally (i.e. \( \nabla \Gamma \cdot \nabla_c < 0 \)) then \( c \) will increase and vice versa. For profiles B and C, the sign of \( \nabla \Gamma \cdot \nabla_c \) is mainly decided by the flows parallel to the surface \( \Gamma \). In the case of profile B, the surface is compressed at the
A chiral force field (inset top left) induces three different categories of orthogonal flow profiles in dependence of the relaxation times $\hat{\tau}_A$, $\hat{\tau}_S$. Categories are labelled as profiles A to C. The streamlines represent the fluid flow, yellow for fast, dark blue for slow. The colour of the surface represents the concentration $c$ of a transported surface quantity, yellow for high, black for low. (a) Profile A, defined by the fact that there are no vortices in the cell and that the maximal velocity is at $r = 0$. At later times it can result in the formation of a neck and a ring of high concentration. Parameters: $\hat{\tau}_A = 100$, $\hat{\tau}_S = 100$. (b) Profile B, defined by the presence of two vortices both inside and outside the cell. At later times, a ring of high concentration forms. Parameters: $\hat{\tau}_A = 100$, $\hat{\tau}_S = 1$. (c) Profile C, defined by having no vortices in the cell and its maximal velocity along the surface. At later times a neck can be formed, but it will not give a ring of high concentration in the centre. Parameters: $\hat{\tau}_A = 1$, $\hat{\tau}_S = 10$. The elastic moduli in all simulations are $\hat{G}_A = \hat{G}_S = 0.1$.

Figure 3. A chiral force field (inset top left) induces three different categories of orthogonal flow profiles in dependence of the relaxation times $\hat{\tau}_A$, $\hat{\tau}_S$. Categories are labelled as profiles A to C. The streamlines represent the fluid flow, yellow for fast, dark blue for slow. The colour of the surface represents the concentration $c$ of a transported surface quantity, yellow for high, black for low. (a) Profile A, defined by the fact that there are no vortices in the cell and that the maximal velocity is at $r = 0$. At later times it can result in the formation of a neck and a ring of high concentration. Parameters: $\hat{\tau}_A = 100$, $\hat{\tau}_S = 100$. (b) Profile B, defined by the presence of two vortices both inside and outside the cell. At later times, a ring of high concentration forms. Parameters: $\hat{\tau}_A = 100$, $\hat{\tau}_S = 1$. (c) Profile C, defined by having no vortices in the cell and its maximal velocity along the surface. At later times a neck can be formed, but it will not give a ring of high concentration in the centre. Parameters: $\hat{\tau}_A = 1$, $\hat{\tau}_S = 10$. The elastic moduli in all simulations are $\hat{G}_A = \hat{G}_S = 0.1$.

3.1. Neck formation for equal shear and areal relaxation times

To study the influence of the viscoelasticity on the dynamics, we first assume the areal and shear components to be equal, so $\hat{\tau}_A = \hat{\tau}_S = \hat{\tau}$ and $\hat{\eta}_A = \hat{\eta}_S = \hat{\eta}$. It is noteworthy that for small $\hat{\tau}$ the surface dynamics approaches the viscous limit and for $\hat{\tau}, \hat{\eta} \gg 1$ the surface dynamics approaches the elastic limit of the viscoelastic spectrum. Choosing parameters $\hat{\tau}$ in the interval $[10^{-2}, 10^{-1}]$ and $\hat{\eta}$ in the interval $[10^{-1}, 10^3]$, we exclusively obtain simulation results with flow profile A.

In figure 4 left, the radius of the equator is shown for various $\hat{\tau}$ and $\hat{G} = \hat{\eta}/\hat{\tau}$ at $t = 30$. For either time, we barely see any change in $r$ for small values of $\hat{\tau}$, i.e. for a dominantly viscous surface. We conclude that the viscous component of the surface by itself does not induce any change in shape under chiral forces. Intuitively, this makes sense as the viscosity only acts as friction. But it can also be shown analytically, as is
done in appendix B.2. Here, we find that the resulting viscous force will be in the opposite direction of the chiral forces and contains no normal components.

Furthermore, the smallest radii at the equator, $r$, are found along a line of constant elastic modulus $\hat{G}$. So there is an optimal elastic modulus which leads to the highest deformation. The highest deformations along this line are observed for large relaxation times $\hat{\tau}$. We can conclude that a purely elastic surface (i.e. large $\hat{\tau}$) gives the strongest deformation. The optimal elastic modulus $\hat{G}$ for deformation is higher for earlier simulation times and converges to $\hat{G} = 0.1$, i.e. $\hat{\tau} = 10\hat{\eta}$ for later simulation times, which is the optimum shown in figure 4 left. Our conjecture is, that this phenomenon emerges because two antagonistic effects are counteracting each other; while a high elasticity causes the surface to deform faster initially, it stops the deformation earlier as the higher shear stresses counteract the chiral forces and reduce the chiral velocity $\psi_\phi$. This behaviour can be seen in figure 7, right, where the radius at the equator and the average absolute azimuthal velocity are shown w.r.t. time for different elastic moduli. Therefore, an intermediate elastic modulus $\hat{G}$ presents the optimal choice for strong deformations.

3.2. Elasticity-dominated surface dynamics in dependence of shear and areal elastic moduli $\hat{G}_A$, $\hat{G}_S$

In section 3.1, we concluded that the deformation is caused by the elastic component. So to study the influence of the shear and areal elasticity, we ran simulations with a dominant elastic element, i.e. for large elastic relaxation times fixed at $\hat{\tau}_A/S = 10^7$ and independently varying elastic moduli $\hat{G}_A, \hat{G}_S \in [10^{-4}, 10]$. Correspondingly, the surface viscosities $\hat{\eta}_A$ and $\hat{\eta}_S$ are in the interval [0.1, 10].

The radius $r$ at the equator of the numerical solutions at time $t = 30$ is given in figure 4 right. We find that there is an optimal value for the shear elastic modulus for which the radius $r$ decreases the most. The optimum is $\hat{G}_S = \hat{\eta}_S/\hat{\tau}_S = 0.1$, which is the same optimum found for the elastic modulus $\hat{G}$ in section 3.1. We infer that the found optimum in section 3.1 was not an optimum for both elastic moduli, but only for the shear elastic modulus. We also observe that increasing the areal elastic modulus $\hat{G}_A$ actually slightly increases the radius $r$, implying that the areal elasticity counteracts the formation of a neck. To explain this, consider that the initial shape is a sphere. Therefore any deformation at constant volume will increase the surface area, which is resisted by the areal elasticity.

3.3. Surface dynamics for distinct shear and areal relaxation times

In the following, we vary the relaxation times $\hat{\tau}_A$ and $\hat{\tau}_S$ independently of each other with fixed elastic modulus $\hat{G}$. We choose the elastic moduli to be equal to the found optimum in section 3.1, i.e. $\hat{G}_A = \hat{G}_S = \hat{G} = 0.1$. With these parameter choices, we observe all three flow profiles (figure 5 top). When the relaxation times do not differ too much, the flows display profile A. However when the relaxation times are different, we find diverse profiles. For a large $\hat{\tau}_A$ and small $\hat{\tau}_S$ the flows display profile B (figure 3(b)). Characteristically, the tangential flows transport the surface bound species $c$ towards the equator resulting in a higher concentration at the equator over time, see figure 5 left. This behaviour is qualitatively similar to the enrichment of actin at the cell equator during cell division [34].
Figure 5. Study of various relaxation times $\hat{\tau}_A, \hat{\tau}_S$ with constant elastic moduli $\hat{G}_A = \hat{G}_S = 0.1$. Each dot represents a numerical solution. Top: flow profiles A (dark blue), B (green) and C (yellow) at $t = 10$. For each profile the example from the left column of figure 3 is included. Bottom left: the equatorial concentration minus the average concentration $\bar{c}$ at $t = 10$. The dots with a black outline indicate when $c - \bar{c} > 0$, which only occurs if $\hat{\tau}_A > \hat{\tau}_S$. The strongest increase in equatorial concentration is found for simulations that displayed flow profile B. Bottom right: equatorial radius at $t = 20$. Larger $\hat{\tau}_S$ result in a smaller radius $r$.

For a large $\hat{\tau}_S$ and small $\hat{\tau}_A$, the flows display profile C (figure 3(c)). This flow profile transports the surface quantity away from the equator and forms two high concentration spots between the equator and the poles. Correspondingly, the flow pattern counteracts the formation of a high concentration equatorial ring. However the flows induced by the chiral forces do result in the largest decrease in $r$ at the equator, as is shown in figure 5 right. This confirms the insight of the previous section that the surface is mainly deformed by the shear elastic component of the stress. Moreover, increasing the areal relaxation time increases $r$ which confirms the result in section 3.2 that the areal elasticity counteracts the formation of a neck.

To study the influence of the geometry, we ran the same simulations as before, but now taking an oblate and a prolate spheroid as initial surface $\Gamma$. The oblate and prolate spheroids have dimensionless radii 1.25, 1.25, 1 and 0.75, 0.75, 1 respectively. The simulations with the oblate and prolate spheroids as initial shape showed the exact same phase diagram of the flow profiles at simulation time $t = 10$ as the simulations with a sphere as initial shape (figure 5 top). For each profile, the corresponding dynamics is similar to those observed for the simulations with the sphere as initial condition. We conclude that a small change in geometry does not affect the dynamics of the system.
3.4. Chiral forces may stabilise ring structures in active pattern-forming viscoelastic surfaces

In previous work, active viscous surfaces were studied as a minimal model of the self-organisation of the cellular actin cortex [30–33]. There, active surface tension was assumed to be determined by a surface concentration \( \zeta \) of molecular regulators, see equation (7). It was shown that the interplay of surface concentration, tension and flows can lead to pattern formation [31, 36–42]. From a biological point of view, the most notable patterning is the formation of a region of high concentration around the equator of the cell, i.e. a ring mode, which might turn in turn lead to the formation of a neck. This pattern resembles the formation of a contractile actin-cytoskeletal ring in a dividing animal cell [34, 35]. However, for models of the active cortical surface, it was reported that for high activity (i.e. high \( \xi \) in equation (17)) such a contractile ring will be unstable. It does not remain at the equator, but slips towards one of the poles over time, resulting in a polar mode [30, 31, 33] (see appendix B.1 for the definitions of the polar and ring modes and our method to compare these).

Here, we test the influence of chiral forces on the formation and stability of a concentration-rich ring of cortical regulators and explore the possibility that the ring slipping is prevented by flows similar to flow profile category B. As seen earlier, this flow profile exhibits strong flows towards the equator (figure 3). These can stimulate the build-up of a surface bound species at the equator, which could prevent the slipping of a contractile ring. To study this phenomenon, we choose a more physically motivated chiral force field. The earlier definition in equation (8) depends on the shape of the initial surface to have a switch in sign at the equator. However, current literature suggests that chiral flows are caused by local torques [8, 12, 14, 15]. These local torques come from the actin filaments, which rotate due to their helix structure when myosin motors exert forces on them [3, 8, 43]. Therefore, a more physical model would assume that the chiral force field is dependent on the concentration of molecular tension regulators (myosin). Furthermore, if the concentration of actin filaments and tension regulators were uniformly distributed, then the torques caused by the actin filaments would balance each other. In turn, as a first model for a concentration dependent chiral force field, we propose a force that depends on the gradient of \( \zeta \) along the surface,

\[
f_{\zeta} = \alpha \frac{R^3}{c_0} \nabla \zeta \cdot \mathbf{n}.
\]  

(18)

The fraction \( \frac{c_0}{\zeta} \) is needed to keep the unit of \( \alpha \) the same as in the previous definition of the chiral force in equation (8). If there is a ring of high concentration around the cell, then we obtain a similar chiral counter-rotating field as before (see equation (8)). Even though we use a different definition for the chiral force than in sections 3.1 and 3.2, we will still use those results as guidance.

In our simulations, we choose \( \tilde{\tau}_A = 5 \) and \( \tilde{\tau}_A = 5 \cdot 10^3 \). For the chiral force defined in (8), these parameters resulted in numerical solutions with profile B, as is shown in section 3.3. Consistent with estimated parameters ranges found in biological cells (see appendix B.3), we anticipate the viscosity of the cell cortex to dominate the cytoplasmic viscosity, which in turn dominates the viscosity of the surrounding fluid. Correspondingly, we choose \( \tilde{\eta}_A = \tilde{\eta}_A = 10 \) and \( \frac{D_2}{\tilde{\eta}_A} = 0.1 \). Using [31] as a guidance, we choose the scaled activity \( \bar{\xi} = 0.02 \) and scaled diffusion coefficient \( D_2 = 2 \cdot 10^{-4} \) such that the steady state is unstable and we expect a polar mode for the concentration when there is no chiral force field. As we want to study ring slipping, we choose a ring mode as initial condition. To make the solution less biased towards the ring mode, we add a perturbation to it, such that the initial concentration is

\[
c_i(t = 0) = 1 + 10^{-4} \left( \frac{1}{2} \left( 3 \cos^2(\theta_i) - 1 \right) + \delta_i \right),
\]

where the index \( i \) indicates the \( i \)th grid point, \( \theta_i \) is the angle w.r.t. z-axis of the \( i \)th grid point and \( \delta_i \) is a uniform random variable between \(-1\) and 1.

We run three simulations, one with only active surface tension, one with only the chiral force field and one with both. In the case of only active tension (figure 6(a), movie 1 in SI) an equatorial ring builds up, but is unstable and slips to one of the poles over time. In the second simulation, we use a concentration-dependent chiral force without tension (figure 6(b), movie 2 in SI). As was reported in section 3.3, the chiral force results in flows towards the equator. These flows transport the surface bound species, increasing the concentration at the equator even further. This process, in combination with the concentration-dependent chiral force (see equation (18)) comprises a positive feedback loop. Accordingly, we observe the self-organisation of the chiral forces and surface concentration leading to a stable ring pattern and a neck formation at late times. The results illustrate that chiral force-feedback provides a new mode of mechano-chemical pattern formation which does not require active surface tension.

In the last simulation, we combine active tension and chiral forces (figure 6(c), movie 3 in SI). Again, a ring pattern is formed. But this time, it is even enhanced by the concentration-dependent surface tension, leading to a faster built-up of concentration and earlier neck formation. In general, for simulations with both...
Figure 6. Active pattern formation on viscoelastic surfaces in three different conditions. (a) Having only active surface tension leads to formation of a volatile high-concentration ring which slips to the left pole. (b) Having only chiral force field leads to a stable high-concentration ring and neck formation. (c) The combination of active surface tension and chiral force field strengthens the ring formation and leads to stronger and earlier neck formation. The colour on the surface represents the concentration $c$. The streamlines represent the velocity with respect to the average velocity of the cell, yellow for high, blue for low.

Bottom left: the absolute value of the correlation coefficients (appendix B.1) of the polar mode $\rho_1$ and ring mode $\rho_2$. The time domains are chosen such that the surface has not deformed too much from a sphere (appendix B.1). Bottom right: equatorial radius for all three simulations. The time domains are chosen the same as those in figures (a)–(c). If there is no chiral force field then the high concentration ring slips ($|\rho_1| \rightarrow 1, |\rho_2| \rightarrow 0$). Otherwise the ring is stabilised and a neck forms ($r(z = 0)$ decreases). Parameters: $\hat{\tau}_A = 5000, \hat{\tau}_S = 5, \hat{\eta}_A = \hat{\eta}_S = 10, \hat{D}_c = 2 \cdot 10^{-4}, \hat{\Xi} = 0.1$.

active tension and chiral flows, we find that the formation of a ring of high concentration is faster for larger $\hat{\xi}$. However, if $\hat{\xi}$ becomes too large, then the ring is not stabilised anymore but slips towards one of the poles resulting in a polar mode. We conclude that the chiral force field can not only stabilise the contractile ring, but, in addition, the chiral forces and active surface tension ‘cooperate’ in the sense that they amplify their mutual influence on surface concentration aggregation and constriction.

All simulations results are shown until the time where the pattern and shape dynamics become too strong, i.e. if the concentration peak becomes too concentrated in space or the surface develops deformations with very high local curvature. In these cases, the dynamics cannot be reliably resolved by the numerical grid.
4. Discussion

Here, we present the first numerical model of a viscoelastic surface deforming under the influence of a counter-rotating force field. Using a frame-invariant Maxwell model for the material properties of the surface, we implement a type of viscoelasticity where elastic in-plane stresses in the surface are dissipated over characteristic time scales. In this model, areal and shear deformations are characterised by two independent sets of viscoelastic parameters.

Performing simulations at different parameters, we find that the surface barely deforms if both viscoelastic relaxation times are small (sections 3.1 and 3.3). We conclude that a purely viscous surface does not change shape under a chiral force field. This result is also consistent with an analytical derivation showing that purely viscous surface stresses give rise to only tangential flows on the surface, see appendix B.2.

It is notable to point out the counter-intuitive nature of this fact, as viscous behaviour is typically associated with large deformations. In addition, we find that increasing the shear relaxation time $\hat{\tau}_S$ is optimal for the formation of a neck, indicating that the formation of a neck is caused by the shear elastic component (sections 3.1 and 3.3). In contrast, increasing the areal relaxation time $\hat{\tau}_A$, or increasing the areal elastic modulus $G_A$, decreases the formation of a neck (figures 4 right and 5). This observation can be explained as areal elasticity (which scales with $G_A$ and $\hat{\tau}_A$) resists any changes in surface area which are required for neck formation. Furthermore, we found an optimal value of the shear stress $\hat{G}_S = 0.1$ for neck formation. This can be understood by taking into account that shear elastic stress is on the one hand needed to induce a neck, on the other hand, large shear elastic moduli will resist deformation strongly and thereby reduce the rotational flows caused by the chiral force fields resulting in less deformation. Aside from the building of a neck, we also found that a ring of high concentration at the surface equator requires a high areal relaxation time $\hat{\tau}_A$ and a low shear relaxation time $\hat{\tau}_S$. In this parameter regime, we illustrate that concentration-dependent chiral forces can lead to self organisation and induce a ring pattern. This is to our knowledge the first evidence that chiral force-feedback provides a mode of mechano-chemical pattern formation which does not require active surface tension.

Finally, we added an active surface tension to the model, which has been shown to lead to ring pattern formation on viscous and viscoelastic surfaces which was, however, reported to be transient in the experimentally relevant parameter regime of low cytoplasmic viscosity [22, 32]. In animal cells, by contrast, persistent ring patterns are observed during cell division [10]. In our study, we show that for large areal viscoelastic relaxation time scales $\hat{\tau}_A$, a ring of high concentration at the surface equator can be stabilised by the flows induced by a chiral force field. Accordingly, the slipping of a pre-formed contractile ring as observed in [30, 33] is prevented, and a robust neck is formed. Moreover, we report that chiral forces and active tension collaborate on pattern and neck formation in the sense that they amplify their mutual influence on surface concentration aggregation and constriction. Our results are supported by the experimental study in [11], in which the authors found a correlation between the emergence of chiral flows and the centring of the myosin ring. That is, a symmetric distribution of myosin was shown to lead to the emergence of chiral flows, or vice versa. Our study not only confirms this behaviour, but also suggests the causality: rings are centred by chiral flows.

Our results in sections 3.1–3.3 were gained from simulations which were mirrored in the $z = 0$ plane. To test whether this symmetry emerges naturally from the dynamics, we ran similar simulations including a slight asymmetric perturbation. We found that the perturbation quickly levelled out, such that the solution went back to being mirror symmetric (data not shown). Another mechanism we tested is the influence of the initial shape of the surface. We found the same categories of flow profiles as in figure 5 which displayed qualitatively the same dynamics as described in section 3. So we conclude that the dynamics of the surface mainly depends on the material properties of the surface and not on small changes in shape.

5. Conclusion

All in all, our results give a qualitative overview over the effects of counter-rotating flows on viscoelastic surfaces. Thereby, we provide a new perspective on how viscoelastic traits may influence pattern formation and deformation of viscoelastic cell cortices in the presence of chiral flows which have been reported by experimental studies on dividing cells [7–9]. Most importantly, we give evidence that in the presence of a sufficiently strong shear elasticity, chiral cortical forces can induce neck formation by two distinct mechanisms: (i) the direct shape dynamics induced by orthogonal flows and (ii) tangential flows which lead to a high concentration ring of motor proteins. Further, pronounced neck formation is resisted by area

$\hat{G}_S = \frac{1}{\hat{\tau}_S}$ 

$\hat{\tau}_A$ 

$\hat{\tau}_S$
elasticity of the surface. We note that the ranges of parameters used in our simulations overlap with estimated parameters ranges found in biological cells (appendix B.3).

For active surfaces, our simulations put forward, that the self-organised formation of a neck in combination with a concentration-rich equatorial ring can be stabilised and promoted by the presence of chiral forces. Our simulations suggest that this phenomenon requires short shear relaxation time scales but long areal relaxation time scales. While this parameter setting has so far not been experimentally verified in the cell, we speculate that active cell surface area regulation, e.g. through exocytosis and endocytosis, may provide an effective areal elasticity that prevails over long time scales.

Throughout our study, we have focused on either a prescribed force field or a simple first-order dependence on a surface bound concentration. In the cell cortex, the chiral forces are generated by a non-trivial tension-torque coupling \[ \gamma \in (0, \infty) \], and possibly modifications in the actin helix \[ \delta \in [0, \infty) \]. In the future, it will be interesting to include a more detailed molecularly motivated description of the chiral force field in the model that enables self-organised ring formation and constriction at the equator. Finally, we note that chiral flows may also emerge in biological processes which are not axisymmetric. Our proposed numerical model can be directly extended to explore the resulting fully three dimensional shape dynamics.

Data availability statement

The data cannot be made publicly available upon publication because they are not available in a format that is sufficiently accessible or reusable by other researchers. The data that support the findings of this study are available upon reasonable request from the authors.

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Appendix A. Numerical implementation

To solve the system of partial differential equations (PDEs) in equations (10)–(17) we use an IMEX method for the time derivatives and finite elements for the spatial derivatives. We have two 2-dimensional grids for the Stokes equations (12) and (13) and one 1-dimensional curved grid for the surface equations (10), (11) and (16). To couple the surface and bulk equations we use the Arbitrary Lagrangian-Eulerian approach, as is described in [28, 48].

A.1. Time integration

The complete system of equations is split into several sub-problems that are solved subsequently in each time step: Stokes equations (equations (12) and (13)), the concentration equation (16) and the evolution of the viscoelastic stress (equations (10) and (11)). The time discretization of the concentration equation is done implicitly. The discretization of the surface stress equations is realised by an IMEX method, their exact scheme is given by equations (29) and (30) below.

If the surface is viscous, the surface force \( \nabla_S \cdot \vec{S} \) involves a second order derivative of the velocity \( \vec{v} \). The explicit coupling of surface stress evolution to the Stokes system by equation (14) results in a harsh time step restriction. To circumvent this we use forward relaxation. Assume that \( \vec{f} := \nabla_T \cdot (\vec{S} + \vec{S}_f) + \vec{f}_c \) is the sum of the surface forces at time step \( n \). Then we compute a relaxed surface force \( \vec{F}^n \) by

\[
\vec{F}^n = \omega \vec{f}^n + (1 - \omega) \vec{F}^{n-1}. \tag{19}
\]

Here \( \omega \in (0, 1] \) and \( \vec{F}^0 = 0 \). The computed force \( \vec{F}^n \) is then used to replace the surface force \( \vec{f} \) in equation (14). This forward relaxation is only needed for more viscous cases, so we chose \( \omega = 0.01 \) if \( \max \left( \frac{\eta}{n \tau}, \frac{n \tau}{\eta} \right) > 100 \). In other cases, \( \omega = 1 \), and there is no forward relaxation. Even though only the viscoelastic force component causes instabilities and requires the relaxation, it is also applied to the other surface forces to ensure they are of similar magnitudes.
To sum up, each time step \( n \) is constructed as follows:

1. Compute the velocity \( \mathbf{v}^n \) from the Stokes equation using the active and viscoelastic surface forces \( \mathbf{F}^n \) computed in the previous time step in the boundary condition (using the weak forms defined below in equations (22) and (23)).
2. Use the computed velocity at \( \Gamma \), to solve the equations for the surface concentration \( c^n \) and the viscoelastic surface stress components \( S^n \) and \( \text{tr}(S^n) \) (using the weak forms defined below in equations (29), (30) and (34)).
3. Subtract a possibly small numerical error \( \mathbf{E}^n = P^n - S^n \) to make it traceless again. Then calculate \( S^n = S^n + \frac{\text{tr}(S^n)}{\text{tr}(P^n)} P^n \), \( \nabla \cdot S^n \) and the active surface tension force. Use the forward relaxation defined in equation (19) to get the force \( \mathbf{F}^n \) that will be imposed on the surface.
4. Calculate the grid velocity \( \mathbf{w}^n \) as a harmonic extension of the surface velocity grid velocity \( \mathbf{w}^n_{tr} \), and move the meshes of \( \Gamma \) and \( \Omega \) accordingly. The surface grid velocity is the component of the velocity that is normal to the surface, \( \mathbf{w}^n_{tr} = (\mathbf{n} \cdot \mathbf{v}^n_{tr}) \mathbf{n} + \mathbf{Pv}_{avg} \). Here, \( \mathbf{v}_{avg} \) is the average velocity of the cell.

### A.2. Spatial discretization

Because of the rotational symmetry of the problem we use an axisymmetric model as is illustrated in figure 1 right. Instead of Cartesian coordinates we use the coordinates \( z, r \) and \( \phi \) for the location along the symmetry axis, \( r \) for the distance from the symmetry axis and \( \phi \) for the azimuthal position. Because of the rotational symmetry the variables do not change when changing \( \phi \). Note that this does not imply that \( v_\phi = 0 \), merely that \( \partial_\phi f = 0 \) for any function \( f \) on \( \Gamma \).

For the spatial discretization we use the C++ finite element library AMDiS [49, 50]. The grid contains three meshes, two 2-dimensional meshes for the fluid and one 1-dimensional mesh for the surface \( \Gamma \). The discretization for the fluid domains \( \Omega_0 \) and \( \Omega_1 \) will be referred to as \( T_0 \) and \( T_1 \). The mesh of the surface is named \( T_\Gamma \). For the definitions of the differential operators in cylindrical coordinates in this section we used appendix D in [51]. To make the weak forms of the equations more readable we introduce the following notation. We define \( \nabla' \) as the 2-dimensional gradient \( (\partial_r, \partial_\phi)' \). Similarly we define the velocity \( \mathbf{v}' := (v_z, v_r) := (\hat{e}_z \cdot \mathbf{v}, \hat{e}_r \cdot \mathbf{v}) \), where \( \hat{e}_z \), \( \hat{e}_r \) are the base vectors of the cylindrical coordinate system (see figure 1). The grid velocity of the surface \( w \) is only defined in the \( z, r \)-plane.

For the Stokes equations (equations (12) and (13)) we use the second order polynomial space for the velocity and an extended first order polynomial space for the pressure. The extension is required to allow for discontinuities of the pressure across the surface \( \Gamma \) [48]. The finite elements spaces are then

\[
P_i = \left\{ q \in C^0(\Omega) \cap L^2(\Omega) \mid q_k \in P_i(k), k \in T_i \right\}
\]

for the pressure and

\[
V = \left\{ u \in C^0(\Omega) \cap H^1(\Omega) \mid u_k \in P_2(k), k \in T_0 \cup T_1 \right\}
\]

for the components of velocity. Here, \( P_i(k) \) is the set polynomials of order \( i \) on a domain \( k \). The above defined spaces are an extension of the Taylor–Hood finite element space, which we choose for its optimal convergence for these low order elements. The weak formulation for the axisymmetric version of equations (12) and (13) then reads:

Find \( (\mathbf{v}, p) \in V \times P_0 \cup P_1 \) such that for all \( (\mathbf{u}, q) \in V \times P_0 \cup P_1 \) the following holds

\[
\int_{\Omega_1} \left( \nabla' \cdot \mathbf{v}' + \frac{\nu}{r} \mathbf{v}' \right) q \, d\Omega = V_{\text{restore}},
\]

\[
\int_{\Gamma} \mathbf{F} \cdot \mathbf{d}\Gamma = \sum_{i=0}^{1} \int_{\Omega_i} -p(\nabla' \cdot \mathbf{u}') + \frac{\eta}{\eta_i} \left( (\nabla' \mathbf{v}') + (\nabla' \mathbf{v}')' \right) : \nabla' \mathbf{u}'
\]

\[
+ \frac{\eta_i}{\eta} \left( \nabla' v_{\phi} \cdot \nabla' u_{\phi} + 2 \nu u_{\phi} + 2 \nu_{\phi} u_{\phi} \right)
\]

\[
- \frac{\eta_i}{\eta} \left( \frac{1}{r} (u_z \partial_r v_r + \partial_r u_z) + 2 u_z \partial_r v_r + 2 u_{\phi} \partial_r v_{\phi} + v_{\phi} \partial_r u_{\phi} \right) \right) \, d\Omega.
\]
Again, \( F \) is the relaxed sum of the surface forces (equation (19)). Additionally, \( V_{\text{restore}} \) is a scalar that helps conserve the volume of the inner domain, which due to numerical errors is not perfectly conserved. It is defined as 
\[
V_{\text{restore}} = C_{\text{restore}} \frac{V(t=0) - V(t)}{V(t)}.
\]
Here, \( V(t) \) is the volume of the inner domain \( \Omega \) at time \( t \) and \( C_{\text{restore}} \) is a constant which we choose to be \( \frac{0.125}{\Delta t^2} \).

For the discretisation of the viscoelastic equations in cylindrical coordinates we first redefine the rows and columns of the tensors. For a tensor \( S \) instead of \( x, y \) and \( z \) we now use
\[
S = \begin{pmatrix}
S_{zz} & S_{zr} & S_{z\phi} \\
S_{rz} & S_{rr} & S_{r\phi} \\
S_{\phi z} & S_{\phi r} & S_{\phi\phi}
\end{pmatrix},
\]
where \( S_{ij} = \hat{e}_i \cdot S \cdot \hat{e}_j \) for \( i, j \in \{ z, r, \phi \} \). The gradient of the velocity in cylindrical coordinates is defined as \[51\]
\[
\nabla \mathbf{v} = \begin{pmatrix}
\langle \nabla' \mathbf{v}' \rangle \\
\partial_\phi \mathbf{v} \\
\partial_r \mathbf{v}
\end{pmatrix}
\]

The normal \( \mathbf{n} \) in cylindrical coordinates at \( \phi = 0 \) is defined by
\[
\mathbf{n} = \begin{pmatrix}
n_z \\
n_r \\
0
\end{pmatrix},
\]

hence the projection matrix \( P \) is defined by
\[
P = \begin{pmatrix}
P' & 0 \\
0 & 0 & 1
\end{pmatrix},
\]
where \( P' = \hat{e}_i \cdot P \cdot \hat{e}_i \) with \( i, j \in \{ z, r \} \). To compute the viscoelastic stress we use the definitions in equations (25) and (27) and substitute them in equations (10) and (11). The finite element space for the surface stress, \( \mathcal{S}_\Gamma \), is defined by first order polynomials,
\[
\mathcal{S}_\Gamma = \{ \psi \in C(\Gamma) \cap L^2(\Gamma) \mid \psi|_k \in P_1(k), k \in \mathcal{T}_\Gamma \}.
\]

The weak form is then: Find \( \text{tr} S^{n+1} \in \mathcal{S}_\Gamma^{n+1} \) and \( \bar{S}_{ij} \in \mathcal{S}_\Gamma \) such that for all \( \psi, \psi_{ij} \in \mathcal{S}_\Gamma \) and \( i, j \in \{ z, r, \phi \} \) the following equations hold,
\[
\int_\Gamma \text{tr} S^{n+1} \left( 1 + \frac{\bar{t}_d}{\Delta t} \right) \psi \, d\Gamma
= \int_\Gamma \left( 2\text{tr} D + \bar{t}_s \left( \frac{2\bar{t}_s}{\eta_s} S^n : \nabla \Gamma \mathbf{v} \right) + \text{tr}(S^n) \text{tr}(D) - \left( (\mathbf{v}' - \mathbf{w}) \cdot \nabla \Gamma \mathbf{v} \right) \text{tr} S^n + \frac{\text{tr} S^n}{\Delta t} \right) \psi \, d\Gamma,
\]
\[
\int_\Gamma \bar{S}_{ij}^{n+1} \left( 1 + \frac{\bar{t}_s}{\Delta t} \right) \psi_{ij} \, d\Gamma
= \int_\Gamma \left( P \left( 2D - \bar{t}_d \left( (\mathbf{v}' - \mathbf{w}) \cdot \nabla \Gamma \mathbf{v} \right) S^n - \frac{S^n}{\Delta t} \right) - \nabla \Gamma \mathbf{v} S^n - \left( \nabla \Gamma \mathbf{v} \right)' S^n \right) P \psi_{ij} \, d\Gamma
- \int_\Gamma \bar{t}_s \left( P(S : \nabla \mathbf{v}') - \frac{\bar{t}_d}{\eta_s} \text{tr}(S^n) D \right) \psi_{ij} \, d\Gamma.
\]

Here \( \Gamma_n \) is the surface at time \( t = t_n \) and \( \Delta t \) is the time step size. The vectors and tensors are in cylindrical coordinates. The surface gradient and surface rate of deformation are defined as \( \nabla \Gamma \mathbf{v} = \nabla \mathbf{v} P \) and \( P_1^2 (\nabla \mathbf{v} + (\nabla \mathbf{v})') P \) respectively, with \( \nabla \mathbf{v} \) and \( P \) as defined in equations (25) and (27).

To calculate the surface divergence of the stress tensor (equation (14)) in cylindrical coordinates, let us first consider a continuous extension of the surface tensor \( S \) to the fluid. We name this extension \( T \). The
surface divergence $\nabla T \cdot S$ is then defined as $\nabla T \cdot P$. The gradient of the tensor in cylindrical coordinates is

$$
\nabla T = \frac{\partial T_{tr}}{\partial r} \hat{r} \otimes \hat{r} + \frac{1}{r} \left( \frac{\partial T_{tr}}{\partial \phi} - T_{\theta \phi} \right) \hat{r} \otimes \hat{\phi} + \frac{\partial T_{tr}}{\partial z} \hat{r} \otimes \hat{z} + \frac{\partial T_{zt}}{\partial r} \hat{z} \otimes \hat{r} + \frac{\partial T_{zt}}{\partial \phi} \hat{z} \otimes \hat{\phi} + \frac{\partial T_{zt}}{\partial z} \hat{z} \otimes \hat{z}.
$$

(31)

All derivatives w.r.t. $\phi$ are zero because of axisymmetry. If we then take the product with the projection matrix $P$ as defined in equation (27) we get the surface divergence,

$$
\nabla T \cdot P = \begin{pmatrix}
P_{rr} \frac{\partial T_{rr}}{\partial r} + P_{\theta r} \frac{\partial T_{\theta r}}{\partial r} + P_{z r} \frac{\partial T_{z r}}{\partial r} + \frac{1}{r} T_{z r} & 0 & 0 \\
P_{r \theta} \frac{\partial T_{r \theta}}{\partial r} + P_{\theta \theta} \frac{\partial T_{\theta \theta}}{\partial r} + P_{z \theta} \frac{\partial T_{z \theta}}{\partial r} + \frac{1}{r} (T_{r \theta} - S_{\theta \phi}) \\
P_{r z} \frac{\partial T_{r z}}{\partial r} + P_{\theta z} \frac{\partial T_{\theta z}}{\partial r} + P_{z z} \frac{\partial T_{z z}}{\partial r} + \frac{1}{r} (T_{r \theta} + T_{\theta \phi})
\end{pmatrix}.
$$

(32)

Finally, for the finite element space of the surface concentration we use second order polynomials,

$$
C_T = \left\{ \psi \in C(\Gamma) \cap L^2(\Gamma) \mid \psi \big|_k \in P_2(k), k \in T_T \right\}.
$$

(33)

We adopt the weak form for the surface concentration from [30]: find $c^{n+1} \in C_T$ such that for all $\psi \in C_T$ the following holds

$$
0 = \int_\Gamma \left( \frac{c^{n+1} - c^n}{\Delta t} - c^{n+1} (\nu' - w) \cdot \nabla T \psi + c^{n+1} \psi \nabla T \cdot w + D \nabla c^{n+1} \cdot \nabla (\nabla T \psi) \right) \mathrm{d}\Gamma.
$$

(34)

A.3. Verification of the numerical scheme

To test the convergence of the spatial and time discretization, we choose the parameters $\tilde{r}_A = \tilde{r}_B = 100$ and $\tilde{\eta}_A = \tilde{r}_B = 10$ as a test case. This case is chosen because it displays significant deformations in $\Gamma$. To test the convergence we compare the equatorial radius $r$ for various grid and time step sizes.

For the time steps we use $\Delta t \in \{10^{-4}, 0.5 \cdot 10^{-4}, 0.25 \cdot 10^{-4}, 0.125 \cdot 10^{-4}\}$. Using Richardson extrapolation we determine the order of convergence to be 1, as would be expected from the backward and forward Euler schemes that are used. The difference between the solutions is of the order $10^{-6}$.

To check the spatial discretization error, we use different grid distances ($0.08, 0.04, 0.02, 0.01$) on the surface and its vicinity. Using Richardson extrapolation we determine the order of convergence to be 1, which is expected for the first order polynomials used in equations (29) and (30). The difference between the solutions is of the order $10^{-3}$ between the solutions with a grid density of 0.02 and 0.01. We conclude that a grid density of 0.02 and a time step size $\Delta t = 10^{-4}$ are fine enough for sufficiently accurate solutions and used these values throughout this paper.
Figure 7. Left: radius \( r \) and concentration \( c \) at the equator w.r.t. time for three different flow profiles, corresponding to those in figure 3. The parameter values are \( \tau_A = 100 \) and \( \tau_S = 100 \) for profile A, \( \tau_A = 100 \) and \( \tau_S = 1 \) for profile B and \( \tau_A = 1 \) and \( \tau_S = 10 \) for profile C. The elastic moduli are \( G_A = G_S = 0 \). Right: radius \( r \) and the norm for the azimuthal velocity \( \|v_\phi\| = \int \Gamma \|v_\phi\| \, d\Gamma \) for different elastic moduli \( G_A = G_B = G_C \). The relaxation times are \( \tau_A = \tau_S = 10^3 \). The azimuthal velocity decreases faster for increasing elastic modulus, which initially results in deformation. This, however, is also resisted by the stronger elasticity at later times.

Appendix B. Results

B.1. Comparison of the polar and ring modes

The polar and ring mode are the first and second mode in spherical harmonics if only rotationally symmetric modes are considered. The first and second mode are defined by

\[
\begin{align*}
g_1(\theta) &= \cos(\theta) \\
g_2(\theta) &= \frac{1}{2} (3\cos^2(\theta) - 1)
\end{align*}
\]

respectively. \( \theta \in [0, \pi] \) is the angle w.r.t. z-axis. The comparison of these modes in the simulations is done by calculating the correlation coefficient of the solution \( c \) and the ring and polar modes, given by

\[
\rho_l = \frac{\int \Gamma (c - \bar{c}) g_l \, d\Gamma}{\sqrt{\int \Gamma g_l^2 \, d\Gamma \int \Gamma (c - \bar{c})^2 \, d\Gamma}}.
\]

We compare \( \rho_1 \) and \( \rho_2 \) to study the ring slipping in section 3.4. If a ring slipped \( \rho_1 \) would go to 1 or \(-1\) and \( \rho_2 \) would go from a value close to \(-1\) to 0.

Equation (35) only holds if the surface is a sphere. For this we define a measure \( \mu(\Gamma) \) to calculate the deformation from a sphere. The correlation coefficient is then only used if \( \mu(\Gamma) < 0.01 \). The measure is defined as

\[
\mu(\Gamma) = \int \Gamma \left( \frac{1}{2} \kappa - \frac{1}{R_s} \right)^2 \, d\Gamma,
\]

where \( R_s \) is the radius of a sphere with the same area as surface \( \Gamma \), and \( \kappa \) is the mean curvature.

B.2. Viscous force

Here, we show that a purely viscous spherical surface does not exhibit any shape changes if exposed to a counter-rotating force field.

If we assume the initial surface to be a sphere and that the viscous force of the surrounding fluids is negligible, then we can use spherical coordinates to express the dynamics. The generic chiral force from equation (8) in spherical coordinates is

\[
f = \begin{pmatrix} 0 \\ 0 \\ \sin(\phi) \cos(\phi) \end{pmatrix} + \begin{pmatrix} 0 \\ 0 \\ \sin(2\phi) \end{pmatrix}
\]

and the force balance from equation (14) becomes \( f + \nabla \cdot S = 0 \). Let us assume that the velocity \( v \) is proportional to \( f \), i.e. \( v = \alpha f \) for some \( \alpha \in \mathbb{R} \). Clearly this velocity field does not lead to any changes in surface area, since \( \nabla \cdot v = 0 \). Now we can calculate the rate of deformation \( D = \frac{1}{2} (\nabla \cdot v + (\nabla v) \cdot v) \). For the viscous case, the stress \( S \) reduces to \( S = 2\eta \partial \cdot D \). We can calculate the viscous force \( f_{\text{viscous}} = \nabla \cdot S \) and obtain...
\[ f_{\text{viscous}} = \alpha \begin{pmatrix} 0 \\ 0 \\ -3\eta_S \sin(2\phi) \end{pmatrix}, \]

Now we see that for \( \alpha = \frac{1}{6\eta_S} \) the force balance \( f + \nabla \cdot S = 0 \) holds. So the solution for the velocity is \( v = \frac{1}{6\eta_S} f \) which is parallel to the surface and hence does not change its shape.

**B.3. Parameters relevant for biological cells**

The following parameters have been estimated for biological cells:

- The radius of the cell, \( R = 10 \mu m \).
- The interior of the cell, i.e. the cytoplasm, was measured to have viscosities with values between 1 and 10 Pa s [52].
- The areal viscosity of the surface was previously estimated as \( \eta_A \in [0.01, 0.1] \) Ns m\(^{-1}\) [16, 17].
- The shear viscosity of the surface, \( \eta_S \), can be approximated as \( \frac{1}{3} \eta_A \) corresponding to a Poisson ratio of 0.5 [20].
- The relaxation times \( \tau_S \) and \( \tau_A \) are approximately 60 s according to measured times of molecular turnover [10].
- Naganathan et al [8] found a chiral velocity \( v_{\text{bio}} \in [10^{-8}, 10^{-7}] \) m s\(^{-1}\).

Using the above estimates, we associate the following ranges of scaled parameters:

- The areal surface viscosity \( \hat{\eta}_A \in [10^6, 10^4] \) using as surface reference viscosity \( R \eta_I \) with \( \eta_I \) between 1 and 10 Pa s.
- The surface shear viscosity \( \hat{\eta}_S \in [\frac{1}{3} \cdot 10^2, \frac{1}{3} \cdot 10^4] \).
- In our simulations, we observe maximal chiral dimensionless velocities \( v_{\text{num}} \) between \( 10^{-3} \) and \( 10^{-1} \). We calculate the range for the velocity scale \( v_{\text{sc}} \in [10^{-7}, 10^{-4}] \) m s\(^{-1}\) using \( v_{\text{bio}} = v_{\text{sc}} v_{\text{num}} \). Dividing the length scale \( R \) by the velocity scale gives us the timescale which we use to derive the range for the dimensionless relaxation times \( \hat{\tau}_A, \hat{\tau}_S \in [0.6, 600] \).

The parameters used in the parameter screens are \( \hat{\eta}_A, \hat{\eta}_S \in [0.1, 10^4], \hat{\tau}_S, \hat{\tau}_A \in [0.01, 1000] \) and \( \hat{\eta}_I = \hat{\eta}_0 \) except for simulations corresponding to figure 6 where \( \hat{\eta}_I = 10 \hat{\eta}_0 \). The ranges of scaled parameters inferred from measurements in biological cells are very broad, but they are contained in the parameter ranges chosen in our simulations.

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**References**

[1] Lebreton G, Geminard C, Lapraz F, Pyrpassopoulos S, Cerezo D, Speder P, Ostap E M and Noselli S 2018 Molecular to organismal chirality is induced by the conserved myosin 1D Scientists 362 949–52
[2] Wood W B 1997 Left-right asymmetry in animal development Annu. Rev. Cell Dev. Biol. 13 53–82
[3] Naganathan S R, Middelkoop T C, Fürthauer S and Grill S W 2016 Actomyosin-driven left-right asymmetry: from molecular torques to chiral self organization Curr. Opin. Cell Biol. 38 24–30
[4] Chen T-H et al 2012 Cellular biology left-right symmetry breaking in tissue morphogenesis via cytoskeletal mechanics Circ. Res. 110 S51–9
[5] Tee Y H et al 2015 Cellular chirality arising from the self-organization of the actin cytoskeleton Nat. Cell Biol. 17 445–57
[6] Vandenberg L N, Lemire J M and Levin M 2013 It’s never too early to get it right: a conserved role for the cytoskeleton in left-right asymmetry Commun. Integr. Biol. 6 e27155
[7] Danilchik M V, Brown E E and Riegert K 2006 Intrinsic chiral properties of the Xenopus egg cortex: an early indicator of left-right asymmetry? Development 133 4517–26
[8] Naganathan S R, Fürthauer S, Nishikawa M, Jülicher F and Grill S W 2014 Active torque generation by the actomyosin cell cortex drives left–right symmetry breaking eLife 3 e04165
[9] Blum M and Ott T 2018 Animal left-right asymmetry Curr. Biol. 28 R301–4
[10] Salbreux G, Charras G and Paluch E 2012 Actin cortex mechanics and cellular morphogenesis Trends Cell Biol. 22 536–45
[11] Pimpale I G, Middelkoop T C, Mietke A and Grill S W 2020 Cell lineage-dependent chiral actomyosin flows drive cellular rearrangements in early Caenorhabditis elegans development eLife 9 e54930
[12] Sase I, Miyata H, Ishiwata S and Kinosita K 1997 Axial rotation of sliding actin filaments revealed by single-fluorophore imaging Proc. Natl Acad. Sci. 94 5646–50
