Active fluid theory for Tribolium tissue flow

Here, we introduce our minimal physical model to quantitatively describe the velocity of blastoderm tissue movement during the onset of Tribolium gastrulation. For the theoretical description, we focus on the one-dimensional tissue flows that have been experimentally quantified in the sagittal cross-section of the embryo imaged in toto with multi-view light sheet microscopy. This cross section captures the myosin distribution with the highest intensities occurring in the embryo at the posterior pole and along the ventral mid-line. Importantly, blastoderm flows along this circumference of the embryo are virtually exclusively parallel to the sagittal cross section.

1 Model

For the description of the blastoderm tissue, we consider a one-dimensional periodic domain of length L, representing the circumference of the embryo in the sagittal cut. We describe the tissue as a thin-film, active fluid, for which the stress σ is given by [1, 2]

$$\sigma = \eta \partial_x v + C(x). \tag{1}$$

Here, η is an effective viscosity that describes the internal resistance of the tissue against compression and shear. The local flow velocity v is measured with respect to the stationary reference frame provided by the egg shell and $C(x) \geq 0$ is a contractile active stress that is described in more detail in Section 1.3. The force balance for the material is given by

$$\partial_x \sigma + f_{\text{ext}} = 0, \tag{2}$$

where we neglect inertial effects, which is a valid assumption on the small length scales of a Tribolium embryo. The term f_{ext} denotes external forces. From Eqs. (1) and (2), we then find the force balance for the tissue

$$\eta \partial_x^2 v + \partial_x C(x) = -f_{\text{ext}}. \tag{3}$$

Before using this model to describe the experimental data, we discuss the external forces f_{ext} in more detail.

1.1 Homogeneous friction: Absence of net tissue movement

The blastoderm tissue is in contact with surrounding material, such as the yolk on the basal side as well as the vitelline envelope on the apical side. Therefore, frictional forces can occur that work against the tissue motion. We can consider such an external friction force as

$$f_{\text{ext}} = -\gamma v, \tag{4}$$

where γ denotes the friction coefficient, which we first assume to be homogeneous. From integrating the force balance in Eq. (2), we find

$$\int_0^L \partial_x \sigma \, dx = -\int_0^L f_{\text{ext}} \, dx \tag{5}$$

$$\Rightarrow \sigma|_0^L = \gamma \int_0^L v \, dx. \tag{6}$$

Here, we take into account that γ is constant along the entire circumference of the embryo. Given periodic boundary conditions on a closed circumference, we have $\sigma(0) = \sigma(L)$ and therefore find $\sigma|_0^L = 0$. Assuming that γ is finite, we therefore find from Eq. (6) in the case of homogeneous friction a constraint on the flow v in the form

$$\int_0^L v \; dx = 0. \tag{7}$$

We define the integral on the right-hand side as the *net movement of the tissue*, which vanishes in the case of homogeneous friction according to Eq. (7). In particular, Eq. (7) can only be fulfilled if (*i*) the flow is vanishing everywhere $v = 0$, or (*ii*) the flow velocity along the domain changes its sign at least twice (assuming that the flow field is continuous). The flow profile observed in the wild-type embryo is unidirectional, i.e. it has the same sign across the whole domain (see Fig. 1e in the main text and movie S2,3) and can, therefore, not fulfill the constraint of a vanishing net movement (Eq. (7)). This provides a hint for potentially inhomogeneous external forces that break the symmetry and lead to a net movement of the tissue in the wild-type embryo. Finally, we note that for the *Tc.inflated* RNAi phenotype (Fig. 3e in the main text), the flow profile of the tissue changes its sign twice and the integral over the flow speeds (i.e. *net movement*) is indeed close to zero for all time points (see movie S13). This qualitative argument shows that the removal of the attachment zone by knock-down of *Tc.inflated* leads to tissue flows that are consistent with the assumption of homogeneous friction forces in the system.

1.2 Inhomogeneous friction: Occurrence of net tissue movement

In general, the friction described by γ can be inhomogeneous. Inspired by the experimental observations presented in the main text (namely the presence of unidirectional blastoderm tissue flow and the apparent lack of flow on the anterior ventral side of the embryo), we consider an inhomogeneity in the friction that represents a local attachment region of width w of the tissue. This corresponds to a region with a very large friction γ_a, in which the velocity v of the tissue essentially vanishes. In this case, $F_a \approx w\gamma_a v$ describes an attachment force that is required to hold the tissue locally in place against the contractile stresses that are generated in the surrounding tissue. If the attachment region is small compared to the overall domain, i.e. $w \ll L$, we can describe it as an effective contribution to the external force in the form $f^a_{\mathrm{ext}} = F_a\delta(x)$. Here, we have placed the attachment region for convenience at $x = 0$, which is not essential for the argument to hold. Furthermore, we assume for simplicity that the friction γ away from the attachment region is approximately constant, such that the total external force is given by

$$f_{\mathrm{ext}} = f^a_{\mathrm{ext}} - \gamma v. \tag{8}$$

By integrating the force balance Eq. (2) for external forces given in Eq. (8), we find

$$F_a = \gamma \int_0^L v\, dx, \tag{9}$$

which follows from Eq. (6) and $\sigma|_0^L = F_a$. With Eq. (9), we can now relate the net movement of the tissue, defined as $\int_0^L v\, dx$, to an attachment force F_a.

1.3 Active stress in the tissue

Following previously published theoretical models of tissue flow [2, 3], we assume that active contractile stresses are predominantly generated by myosin motor proteins. We use the local fluorescence intensity $I(x)$ of the Tc.sqh::GFP construct as proxy for the magnitude of the active stress:

$$C(x) = C_0 I(x). \tag{10}$$

Here, C_0 is an effective parameter that emerges from the microscopic details of the active stress generation in the tissue. The acquisition and preprocessing of the profiles $I(x)$ is explained in detail in the Materials & Methods section.

2 Fitting procedure

To compare the theoretical prediction of the outlined thin-film theory to the experimentally determined flow profiles, we use Eq. (3) with $f_{\mathrm{ext}} = -\gamma v + F_a\delta(x)$ and $C(x)$ given in Eq. (10) to calculate flow fields v and fit these solutions to the experimentally measured velocity profiles.

To identify the independent fitting parameters, we first nondimensionalise Eq. (3). Using the domain length L as characteristic length scale, we can write $x = \tilde{x}L$ with $\tilde{x} \in [0, 1]$. The non-dimensional form of the force balance Eq. (3) is then given by

$$\partial_{\tilde{x}}^2 \tilde{v} + \partial_{\tilde{x}} I = \alpha^2 \tilde{v} + \tilde{F}_a \delta(\tilde{x}), \tag{11}$$

where the $\tilde{v} = v/v_c$ is the non-dimensional flow velocity and the fitting parameter $v_c = C_0 L/\eta$ is a characteristic velocity that encodes the material properties of the system. The second fitting parameter $\alpha = L\,(\gamma/\eta)^{1/2}$ characterises the friction. This parameter can also be interpreted as the ratio between the tissue size L and a hydrodynamic screening length $l_h = (\eta/\gamma)^{1/2}$, i.e.

$$\alpha = \frac{L}{l_h}. \tag{12}$$

The parameter l_h describes the length scale over which flows that emerge from a local contractile stress decay [1]. The non-dimensional attachment force is given by $\tilde{F}_a = F_a/C_0$.

To find solutions of Eq. (11), we note that due to the localisation of the attachment region, it suffices to solve

$$\partial_{\tilde{x}}^2 \tilde{v} + \partial_{\tilde{x}} I = \alpha^2 \tilde{v}, \tag{13}$$

while the attachment region only affects the boundary conditions. An infinite friction in the attachment region leads to boundary conditions $\tilde{v}(0) = 0$ and $\tilde{v}(1) = 0$ (Sec. 2.1). In the absence of the attachment region, we simply use periodic boundary conditions $\tilde{v}(0) = \tilde{v}(1)$ and $\partial_{\tilde{x}}\tilde{v}|_{\tilde{x}=0} = \partial_{\tilde{x}}\tilde{v}|_{\tilde{x}=1}$ (Sec. 2.2). To determine the fitting parameters v_c and α, solutions of Eq. (13) are fitted to experimentally measured flow profiles of a single time point. This time point is always chosen right before the posterior pole invagination begins so that different experiments can be compared to one another. At this time, blastoderm flows are maximal and the geometry of the circumference is still approximately an ellipse.

To determine the fitting parameters v_c and α in practice, we use the nonlinear least-square fitting routine `lsqnonlin` implemented in Matlab [4]. Initial values for the least-square search are found as follows. First, we fit the experimentally measured velocity profile to velocity profiles determined from Eq. (13) keeping $\alpha = 0$ fixed. From this, we find an initial guess $v_c^{(0)}$. In the next step, the latter is held fixed and Eq. (13) is fitted to the experimental flow profile, yielding an initial guess for $\alpha^{(0)}$. Finally, we run `lsqnonlin` using $v_c^{(0)}$ and $\alpha^{(0)}$ as initial values to determine both fitting parameters, v_c and α.

2.1 Wild-type embryos

Using the procedure just described, we find for the wild-type case $v_c = 0.4\,\mu$m/s and $\alpha = 0.29$. The latter corresponds according to Eq. (12) to a hydrodynamic length of about three times the embryo's circumference, or about one and a half times the embryo length. This indicates that the hydrodynamic screening is not relevant for the tissue flows, and it implies that external friction forces are small compared to the viscous forces within the tissue. As a consequence, the relative attachment force $\tilde{F}_a = F_a/C_0$ given by

$$\tilde{F}_a = \alpha^2 \int_0^1 \tilde{v}\, d\tilde{x} \tag{14}$$

is also small, i.e. the required attachment force F_a is much smaller than the active forces in the tissue.

Using the fitting parameters determined for a single time-point, we can also predict flow velocities accurately for a significant time interval preceding posterior pole invagination (as seen in SI video fitting a **V1**).

2.2 Inflated RNAi phenotype

Under the assumption that there is no attachment region present in the *Tc.inflated* RNAi knock-down, we use Eq. (13) with periodic boundary conditions to calculate flow fields from the measured myosin

distribution $I(x)$. This effectively corresponds to solving Eq. (11) for $F_a = 0$ on the periodic circumference of the embryo. We fit these solutions to the experimentally measured flow profiles using the same procedure as described above. In this case, we find fitting parameters given by $v_c = 0.54\,\mu$m/s and $\alpha = 10^{-3}$. The small value of α indicates that the homogeneous friction in the textitTc.inflated RNAi knock-down is reduced even further compared to the wild-type case.

References

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