

Supplementary Information

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1 Solution of the optimization problem

Here we show how the infinite dimensional optimization problem formulated in the main text can be reduced to an algebraic minimization problem in two dimensions.

If we substitute the function $\sigma(y)$ from (2) into the dimensionless expression of efficiency, we obtain:

$$\Lambda = \frac{\mathcal{L}V^2}{\mathcal{L} \int_{-1/2}^{1/2} \tau(y)^2 dy - 2\sigma_0^2 \tanh(\frac{\mathcal{L}}{2}) - \mathcal{L}^2 \int_{-1/2}^{1/2} \int_{-1/2}^{1/2} \Psi(y, v) \tau(y) \tau(v) dy dv + \mathcal{H}^{**}}. \quad (\text{I})$$

The constants V and σ_0 are defined in terms of the unknown function $\tau(y)$ in Eq.(3) of the main text (see also Eq.(III) below). Our strategy is to first fix V and σ_0 , optimize (I) with respect to $\tau(y)$ and then to optimize the result with respect to V and σ_0 .

The first problem is equivalent to minimizing the denominator in (I)

$$\min_{\tau} \left[Q(\tau) = \int_{-1/2}^{1/2} \tau(y)^2 dy - \mathcal{L} \int_{-1/2}^{1/2} \int_{-1/2}^{1/2} \Psi(y, v) \tau(y) \tau(v) dy dv \right], \quad (\text{II})$$

under the constraints

$$\begin{cases} 2V \sinh(\frac{\mathcal{L}}{2}) = -\mathcal{L} \int_{-1/2}^{1/2} \sinh(\mathcal{L}y) \tau(y) dy \\ 2\sigma_0 \sinh(\frac{\mathcal{L}}{2}) = \mathcal{L} \int_{-1/2}^{1/2} \cosh(\mathcal{L}y) \tau(y) dy \\ \int_{-1/2}^{1/2} \tau(y) dy = 1. \end{cases} \quad (\text{III})$$

An additional constraint $\tau(y) \geq 0$ states the active forces in our system are contractile.

In order to take the constraints into account, we introduce three scalar Lagrange multipliers ($\kappa_0, \kappa_1, \kappa_2$) and a non negative function $\kappa(y)$. Then the condition that the efficiency is maximal takes the form

$$(I - Q)\tau(y) = \Gamma(y) \quad (\text{IV})$$

where

$$Q\tau = \mathcal{L} \int_{-1/2}^{1/2} \Psi(y, v) \tau(v) dv$$

and

$$\Gamma(y) = \kappa_0 - \kappa_1 \sinh(\mathcal{L}y) + \kappa_2 \cosh(\mathcal{L}y) + \kappa(y).$$

We invert the kernel of equation (IV) using an expansion in eigenfunctions [6] to obtain

$$\tau(y) = (I - Q)^{-1}\Gamma(y) = \int_{-1/2}^{1/2} \phi(y, v)\Gamma(v)dv. \quad (\text{V})$$

Here

$$\phi = \delta(y - v) + \mathcal{L}^2 \left[\left(\frac{1}{2} + y\right)\left(\frac{1}{2} - v\right)\theta(v - y) + \left(\frac{1}{2} + v\right)\left(\frac{1}{2} - y\right)\theta(y - v) \right], \quad (\text{VI})$$

θ is the Heaviside function and δ is the Dirac distribution. Using the expression for Γ we obtain

$$\tau(y) = P(y) + \int_{-1/2}^{1/2} \phi(y, v)\kappa(v)dv. \quad (\text{VII})$$

The function

$$P(y) = \kappa_0\psi_0(y) + \kappa_1\psi_1(y) + \kappa_2\psi_2(y) \quad (\text{VIII})$$

is a parabola since

$$\psi_0(y) = 1 - \frac{\mathcal{L}^2}{2}\left(y + \frac{1}{2}\right)\left(y - \frac{1}{2}\right), \quad \psi_1(y) = -2y \sinh\left(\frac{\mathcal{L}}{2}\right) \quad \text{and} \quad \psi_2(y) = \cosh\left(\frac{\mathcal{L}}{2}\right). \quad (\text{IX})$$

The Lagrange multipliers can be found from Karush-Kuhn-Tucker conditions [1]

$$\begin{aligned} 1 &= \kappa_0 A_0 + \kappa_2 A_2 + \int_{-1/2}^{1/2} \kappa(y)\psi_0(y)dy \\ 2V \frac{\sinh(\frac{\mathcal{L}}{2})}{\mathcal{L}} &= \kappa_1 S_1 + \int_{-1/2}^{1/2} \kappa(y)\psi_1(y)dy \\ 2\sigma_0 \frac{\sinh(\frac{\mathcal{L}}{2})}{\mathcal{L}} &= \kappa_0 C_0 + \kappa_2 C_2 + \int_{-1/2}^{1/2} \kappa(y)\psi_2(y)dy \\ \tau(y) &\geq 0, \quad \kappa(y) \geq 0 \quad \text{and} \quad \kappa(y)\tau(y) = 0, \end{aligned} \quad (\text{X})$$

where

$$\begin{aligned} A_0 &= 1 + \frac{\mathcal{L}^2}{12}, \quad A_2 = \cosh\left(\frac{\mathcal{L}}{2}\right), \\ S_1 &= \frac{2(1 - \cosh(\mathcal{L})) + \mathcal{L} \sinh(\mathcal{L})}{\mathcal{L}^2}, \\ C_0 &= \cosh\left(\frac{\mathcal{L}}{2}\right) \quad \text{and} \quad C_2 = \frac{\sinh(\mathcal{L})}{\mathcal{L}}. \end{aligned}$$

If the function $\kappa(y)$ is known, the Lagrange multipliers $(\kappa_0, \kappa_1, \kappa_2)$ are readily found from the system of linear equations (X). To find $\kappa(y)$ we first notice that the function

$$\tau(y) = P^+(y), \quad (\text{XI})$$

where $P^+(y) = \max(0, P(y))$ satisfies the constraint $\tau(y) \geq 0$. The associated $\kappa(y)$ can be obtained by inverting (VII)

$$\kappa(y) = (I - Q)P^-(y). \quad (\text{XII})$$

where $P^-(y) = \max(0, -P(y))$.

Next we show that such $\kappa(y)$ satisfies the last set of conditions in (X). Define the function $\sigma_-(y) = QP^-(y)$ which solves the boundary value problem,

$$-\mathcal{L}^{-2}\sigma_-'' + \sigma_- = P^- \geq 0, \quad \sigma_-(\pm 1/2) = 0. \quad (\text{XIII})$$

Maximum principle [4] ensures that $\sigma_-(y) \leq P^-(y)$ and thus $\kappa(y) \geq 0$. We can also see that $\tau(y)\kappa(y) = -P^+(y)\sigma_-(y) = 0$, since whenever $P^+(y) > 0$, the

function σ_- satisfies (XIII) with zero Dirichlet boundary conditions. Thus (XI) satisfies all the required conditions.

The resulting optimal distribution of active stresses is

$$\tau(y) = (Ay^2 + By + C)\theta(Ay^2 + By + C). \quad (\text{XIV})$$

Notice that this function has a singularity at a point where $Ay^2 + By + C = 0$. Instead of expressing the constants A, B, C in terms of V and σ_0 and then optimizing the efficiency with respect to these two variables, in our numerical code we directly minimize efficiency with respect to A, B . The third constant C is determined by the constraint $\int_{-1/2}^{1/2} \tau(y) dy = 1$.

As an example, consider the limiting problem with $\mathcal{H}^{**} = 0$. Suppose first that there is no sign constraint on $\tau(y)$ and denote the corresponding optimal distribution $\tilde{\tau}(y)$. Then $\kappa \equiv 0$ and the system (X) is linear which allows one to find $(\kappa_0, \kappa_1, \kappa_2)$ explicitly as functions of σ_0 and V . We obtain

$$\tilde{\Lambda}(V, \sigma_0) = \frac{V^2}{\frac{V^2}{\mu(\mathcal{L})} + \frac{(1-\sigma_0)^2}{\frac{\mathcal{L}^2}{12} + 1 - \frac{\mathcal{L}}{2} \tanh(\frac{\mathcal{L}}{2})}}. \quad (\text{XV})$$

As all terms in (XV) are positive it is clear that,

$$\tilde{\Lambda}(V, \sigma_0) \leq \mu(\mathcal{L}) = \frac{\mathcal{L}}{2} \coth\left(\frac{\mathcal{L}}{2}\right) - 1.$$

We now get back to the initial problem with the sign constraint. Since by definition $\Lambda \leq \tilde{\Lambda}$, we can write $\Lambda \leq \mu(\mathcal{L})$. It is easy to find a non negative function τ from the family (XIV) which saturates the bound. A simple substitution shows that for $\tau(y) = 1 + \alpha y$ with $\alpha \in [-2, 2]$ one obtains $\Lambda = \mu(\mathcal{L})$. This means that the whole one parametric family is optimal. Negative (positive) values of α correspond to positive (negative) velocities. Therefore, the optimal velocities range is between $\pm 2\mu(\mathcal{L})/\mathcal{L}$. From this set only configurations with $\alpha = \pm 2$ can be recovered in the limit $\mathcal{H}^{**} \rightarrow 0$ from the sequence of optimal configurations with $\mathcal{H}^{**} > 0$.

2 Energetic cost of maintaining a steady state

We first specialize some standard relations of continuum thermodynamics of nonequilibrium process for our problem [2, 5]. Then we introduce the crucial definition for the 'rate of free energy consumption' and compute its value for our traveling wave solution.

Our finite 1D layer of reacting viscous fluid is exposed to: (i) distributed (bulk) forces $-\xi v$ due to friction and (ii) surface tractions σ_0 on the boundaries $x = -L/2, L/2$ due to the cortex. The power of these *external* forces can be written as

$$\begin{aligned} W &= - \int_{-L/2}^{L/2} \xi v^2 dx + \sigma_0(v(L/2) - v(-L/2)) \\ &= \int_{-L/2}^{L/2} (-\xi v^2 + \partial_x(\sigma v)) dx = \int_{-L/2}^{L/2} (-\xi v^2 + v \partial_x \sigma + \sigma \partial_x v) dx. \end{aligned}$$

By taking into account the force balance

$$\partial_x \sigma = \xi v,$$

we can further rewrite W as the power of the *internal* forces

$$W = \int_{-L/2}^{L/2} \sigma \partial_x v dx.$$

The next step is to compute the rate of change of the free energy

$$F = \int_{-L/2}^{L/2} \hat{\rho} f dx,$$

where $\hat{\rho}$ is the total density of the mixture which is a conserved quantity

$$\partial_t \hat{\rho} + \partial_x(\hat{\rho} v) = 0.$$

In addition to temperature, the free energy density may depend on $\hat{\rho}$, on the mass fraction of the motor component of the mixture $\phi = \rho/\hat{\rho}$ and on the advancement of the hydrolysis reaction per unit of mass ζ . Due to the assumption of infinite compressibility and the presence of a thermostat, we are left with only two essential variables, so

$$f = f(\phi, \zeta).$$

To compute the time derivative of F we use standard manipulations. First we write,

$$\dot{F} = \int_{-L/2}^{L/2} \partial_t(\hat{\rho} f) dx = \int_{-L/2}^{L/2} (\partial_t \hat{\rho} f + \hat{\rho} \partial_t f) dx.$$

We then use the mass balance for $\hat{\rho}$ to obtain

$$\int_{-L/2}^{L/2} \partial_t \hat{\rho} f = - \int_{-L/2}^{L/2} \partial_x(\hat{\rho} v) f dx = -[\hat{\rho} v f]_{-L/2}^{L/2} + \int_{-L/2}^{L/2} \hat{\rho} v \partial_x f dx,$$

where the expression in brackets vanishes because there is no external mass flux. As a result, we have

$$\dot{F} = \int_{-L/2}^{L/2} \hat{\rho} (\partial_t f + v \partial_x f) dx = \int_{-L/2}^{L/2} \hat{\rho} \dot{f} dx = \int_{-L/2}^{L/2} \hat{\rho} (-A\dot{\zeta} + \mu\dot{\phi}) dx,$$

where

$$A(\phi, \zeta) = -\partial_\xi f$$

is the affinity of the reaction and

$$\mu(\phi, \zeta) = \partial_\phi f$$

is the chemical potential of the motors.

Finally, we make an assumption that motors are not created in the bulk by writing

$$\hat{\rho} \dot{\phi} = \partial_x J, \tag{XVI}$$

where J is the flux of motors.

For our isothermal system the rate of irreversible entropy production can be written as

$$R = T\dot{S}_i = W - \dot{F} \geq 0.$$

Since there is no fluxes on the boundaries, we obtain

$$R = \int_{-L/2}^{L/2} (\sigma \partial_x v + \hat{\rho} \dot{\zeta} A + J \partial_x \mu) dx \geq 0.$$

The three terms in the right hand side can be interpreted as products of the thermodynamic fluxes $\sigma, \hat{\rho} \dot{\zeta}, J$ and the conjugate thermodynamic forces $\partial_x v, A, \partial_x \mu$. We make a simplifying assumption that fluxes and forces are related through Onsager type relations

$$\begin{aligned} \sigma &= l_{11} \partial_x v + l_{12} A + l_{13} \partial_x \mu \\ \hat{\rho} \dot{\zeta} &= l_{21} \partial_x v + l_{22} A + l_{23} \partial_x \mu \\ J &= l_{31} \partial_x v + l_{32} A + l_{33} \partial_x \mu \end{aligned} \quad (\text{XVII})$$

Here the different tensorial nature of the fluxes/forces is not an issue because anisotropy is proscribed by our 1D ansatz.

Finally, we make another simplifying assumption that the diffusion flux J depends only on $\partial_x \mu$ which implies that $l_{31} = l_{32} = l_{13} = l_{23} = 0$. Since time inversion symmetry requires that $l_{12} = -l_{21}$ we are left with four coefficients $l_{11}, l_{22}, l_{33}, l_{12}$.

We assume that two of these coefficients describe genuinely linear dissipative mechanisms and are therefore standard: $l_{11} = \eta \geq 0$ is the viscosity and $l_{33} \geq 0$ is a mobility per unit volume. To specify the diffusion coefficient fully as,

$$\hat{\rho} \dot{\phi} = \dot{\rho} - \frac{\rho}{\hat{\rho}} \dot{\hat{\rho}} = \partial_t \rho + v \partial_x \rho + \rho \partial_x v = \partial_t \rho + \partial_x(\rho v),$$

we can rewrite (XVI) in the form

$$\partial_t \rho + \partial_x(\rho v) = \partial_x(l_{33} \partial_x \mu).$$

Assuming that the acto-myosin gel is a dilute mixture we can write

$$f = f_0(\zeta) + k_B T \phi \log \phi$$

where k_B is the Boltzmann constant. Therefore

$$\mu = \mu_0 + k_B T \log \phi$$

and

$$\partial_x \mu = k_B T \left(\frac{\partial_x \rho}{\rho} - \frac{\partial_x \hat{\rho}}{\hat{\rho}} \right).$$

To recover a standard diffusion equation we need to make an additional assumption that the variation of the total density is small compared to the variation of the density of motors

$$\frac{\partial_x \rho}{\rho} \gg \frac{\partial_x \hat{\rho}}{\hat{\rho}}.$$

Then we obtain the Einstein-Smoluchowski relation

$$D = \nu k_B T,$$

where $\nu = l_{33}/\rho$ is the mobility per motor. To remain in the framework of Onsager theory we need to assume that $\rho \sim \bar{\rho}$ and $l_{33} = l_{33}(\bar{\rho})$; this approximation clearly fails near the singularities of ρ where the model needs to be appropriately modified.

To finalize the model we need to specify the two remaining coefficients: l_{12} , which describes chemo-mechanical coupling [3] and does not contribute to entropy production and l_{22} , which describes reaction kinetics and must be non-negative to ensure positive definiteness of the dissipation. Notice that in this model we deal with an enzymatic reaction. This is a nonlinear phenomenon because the kinetics is accelerated in the presence of motors. Therefore the straightforward linear Onsager relations do not apply and we need to replace them with quasi-linear relations by making Onsager coefficients dependent on the fields. The simplest way to take the enzymatic activity of the motors into account is to assume that

$$l_{12} = a\rho, l_{22} = b\rho,$$

where a, b are now constants. One consequence of these assumptions is the constitutive relation for stress

$$\sigma = \eta \partial_x v + aA\rho,$$

where the first term describes classical viscosity while the second term represents the active stress due to mechano-chemical coupling. We assume that $a \geq 0$ which ensures that the reaction induced stresses are contractile whenever $A > 0$. Another consequence of our quasi-linearity assumption is the specific form of the kinetic equation for the hydrolysis reaction

$$\partial_t(\hat{\rho}\zeta) + \partial_x(\hat{\rho}\zeta v) = \rho(bA - a\partial_x v).$$

Observe that in this model the reaction stops completely in the absence of motors ($\rho = 0$).

If the passive system described above is left isolated, it reaches equilibrium (all fluxes vanish and the entropy production stops). To maintain the non-equilibrium state, the dissipated energy must be continuously re-injected into the system. Since the temperature reservoir is in equilibrium, the system is not exchanging mass with the environment, and no directional forces conduct external work, the only way to prevent the equilibration of the system, is to keep the driving force of the reaction A away from zero.

More specifically, this means that the corresponding ratio of the concentrations of ATP, ADP and P is kept at a fixed 'distance' from its equilibrium value through incessant breaking or assembling of the associated molecular complexes. The exact microscopic mechanism of such a continuous 'fine tuning' performed by an *external* 'chemostat' is not fully clear, however, in our formalism such assumption of perpetual disequilibrium is tantamount to the assumption that

$$f_0(\zeta) = -A\zeta,$$

where $A > 0$ is a prescribed constant. This bottomless decrease of the energy landscape mimics the continuous rebuilding of the non-equilibrium state despite

the tendency of the system to reach equilibrium (where $A = 0$). The crucial assumption that $A = \text{const}$ allows one to decouple the reaction equation from the system and compute the energetic cost of maintaining disequilibrium from the knowledge of the free energy losses per unit time that must be compensated externally.

We now make the important assumption that the cost of maintaining the non-equilibrium steady state is equal to the rate of consumptions by the system of its free energy 'reserves' (that are being continuously replenished)

$$H = H^* + H^{**} = -\dot{F}.$$

Then, using the constitutive relations we can write

$$\begin{aligned} -\dot{F} &= \int_{-L/2}^{L/2} (\hat{\rho}\dot{\zeta}A + J\partial_x\mu)dx \\ &= \int_{-L/2}^{L/2} (-\chi\rho\partial_x v + bA^2\rho + D\frac{k_B T}{\bar{\rho}}(\partial_x\rho)^2)dx. \end{aligned} \quad (\text{XVIII})$$

If we multiply the force balance equation by v and use the boundary conditions, we obtain

$$-\chi \int_{-L/2}^{L/2} \rho\partial_x v dx = \xi \int_{-L/2}^{L/2} v^2 dx + \eta \int_{-L/2}^{L/2} (\partial_x v)^2 dx.$$

By substituting this relation into (XVIII) we finally obtain

$$-\dot{F} = \int_{-L/2}^{L/2} (\xi v^2 + \eta(\partial_x v)^2 + bA^2\rho + D\frac{k_B T}{\bar{\rho}}(\partial_x\rho)^2)dx \geq 0. \quad (\text{XIX})$$

We can now identify the terms H^* and H^{**} . The mechanical cost function

$$H^* = \xi \int_{-L/2}^{L/2} v^2 dx + \eta \int_{-L/2}^{L/2} (\partial_x v)^2 dx \geq 0$$

is a sum of contributions due to frictional and viscous dissipation. The non-mechanical part

$$H^{**} = bA^2 \int_{-L/2}^{L/2} \rho dx + D\frac{k_B T}{\bar{\rho}} \int_{-L/2}^{L/2} (\partial_x\rho)^2 dx.$$

represents the energetic cost of maintaining the finite rate of chemical reaction and the cost of keeping a nonzero concentration gradient.

To summarize, the steady state self-propulsion in the proposed model requires: (i) work against friction which is necessary for acquiring momentum, (ii) work against viscosity which is a mechanism of long range interactions in the cell providing mechanical coordination at distant points, (iii) work against diffusion to ensure optimal distribution of motors and finally, (iv) work to keep the reaction 'burning' which ensures mechano-chemical generation of active forces. All these processes are dissipative and the consumed free energy needs to be compensated.

As we have seen, the steady state is maintained due to the exterior chemostat which ensures that $A \neq 0$. If $A = 0$, the active stress is equal to zero and the velocity vanishes so the first two terms in (XIX) contributing to the cost vanish as well. The third term obviously vanishes because it is proportional to A^2 . In the absence of flow, the density of motors becomes homogeneous because the destabilizing advection disappears. Therefore the fourth term is also equal to zero.

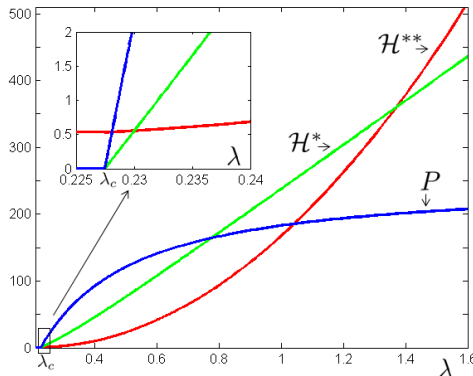


Figure I: Dimensionless Stokes power $P = \mathcal{L}V^2$ and metabolic costs \mathcal{H}^* and \mathcal{H}^{**} as functions of λ . Parameters are $\mathcal{L} = 10$, $\mathcal{M} = 0.053$ and $\mathcal{E} = 0.05$.

To illustrate this argument, we present in Fig. I different terms entering the expression for efficiency

$$\Lambda = \frac{P}{\mathcal{H}^* + \mathcal{H}^{**}}$$

as functions of the parameter λ which can be viewed as a dimensionless version of A . One can see that at $A = 0$ all three terms are equal to zero. It is also easy to show by asymptotic expansion that right above the motility initiation threshold $A = A_c$ the mechanical energy rates (\mathcal{H}^* and P) depend linearly on $A - A_c$ while the non-mechanical cost function $\mathcal{H}^{**} \sim A_c^2$, see the inset in Fig. I.

3 Comparison of experimental and computed distributions of actin and myosin

In Fig. II, taken from the seminal paper of A. Verkhovskiy and his colleagues [7], we show the distributions of actin filaments and of myosin II motors before and after the motility initiation in a keratocyte fragment. The goal is to compare these distributions with the ones predicted by the model.

From Fig. II we see that before motility initiation ($V = 0$), both actin and myosin concentration are almost homogeneous inside the fragment. The near surface boundary layers present more complex behavior due to cortex-membrane effects. If we neglect these boundary layers, the motile regime is characterized by the the myosin concentration localized at the trailing edge and decaying

sharply (linearly) to almost zero at a particular point inside the cell. Instead, the dynamic actin concentration shows bi-modality with a tendency to localize at the front.

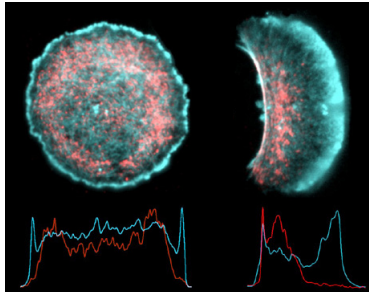


Figure II: The experimental distributions of actin (cyan) and myosin (red) from [7]. Picture is taken from <http://lcb.epfl.ch/cms/lang/en/pid/71379>, courtesy A. Verkhovsky.

We interpret the function $\rho(y)$ as the distribution of myosin (density of motors) and the function $\hat{\rho}(y)$ as the distribution of actin (cytoskeletal density). The method of computing the function $\rho(y)$ is presented in the main part of the paper. As we show below, the function $\hat{\rho}$ can be reconstructed from the actin mass balance equation.

It is natural to non-dimensionalize $\hat{\rho}$ differently than $\rho(y)$ by using the scale $M/(\sqrt{\eta/\xi})$ where M is the total mass of actin. In dimensionless variables we can write the equation for $\hat{\rho}$ in the form

$$\partial_t \hat{\rho} + \mathcal{L}^{-1} \partial_y (\hat{\rho}(v - V)) = 0.$$

The characteristic curves, describing the trajectories of actin particles [8, 9] can be found from

$$\frac{d\phi}{dt} = \mathcal{L}^{-1}(v(\phi) - V),$$

where ϕ is the spatial coordinate along the trajectory. One can see that points where the function $v(\phi) - V$ vanishes and $v' > 0$ are sources of particles while similar points where $v' < 0$ are sinks of particles. For the motile regimes, the function v has been found in the main part of the paper and the corresponding function $v(\phi) - V$ is shown in Fig.III. It displays a source at the leading edge and a sink at the trailing edge. In Fig.III we introduced small zones of size $\epsilon > 0$ around the source and the sink where our 1D model is no longer adequate.

Notice that in the traveling wave regime the (non-dimensional) turnover time for the flow from the source to the sink is

$$\mathcal{T} = \int_{-1/2+\epsilon}^{1/2-\epsilon} (V - v(y))^{-1} dy. \quad (\text{XX})$$

We recall that the turnover of actin in our model is passive and is induced by contraction. Since the model is one dimensional, the closure of the turnover cycle requires that the disappearance of actin in the trailing edge (in a sink domain) is exactly compensated by its reappearance near the front of the cell

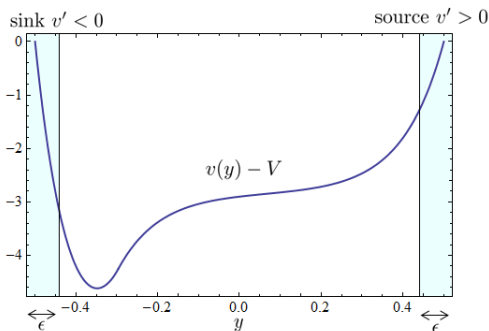


Figure III: Velocity profile of actin in the moving coordinate system with source and sink domains shown in color. Parameters: $\mathcal{L} = 10$, $\mathcal{M} = 0.053$, $\mathcal{E} = 0.04$ and $\lambda = 0.5$. Characteristic scale of velocity is $\bar{\tau}/\sqrt{\eta\xi} \sim 0.02\mu\text{m} \cdot \text{s}^{-1}$

(in a source domain). If the parameter \mathcal{T} , characterizing the mass flux of actin is known, the density distribution of actin can be written as

$$\hat{\rho}(y) = (\mathcal{T}(V - v(y)))^{-1}.$$

From [10], the dimensional turnover time can be estimated as $T \sim 30\text{s}$. Then, using parameters from the main part of the paper, we obtain $\mathcal{T} = \chi T/\eta \sim 0.33$. Now we can obtain from (XX) that $\epsilon = 0.07$. We reiterate that in the boundary layers of this size additional physical effects may have to be taken into consideration including active polymerization and de-polymerization, bundle formation at the rear creating an obstacle for the motors and cortex activity in the vicinity of the membrane.

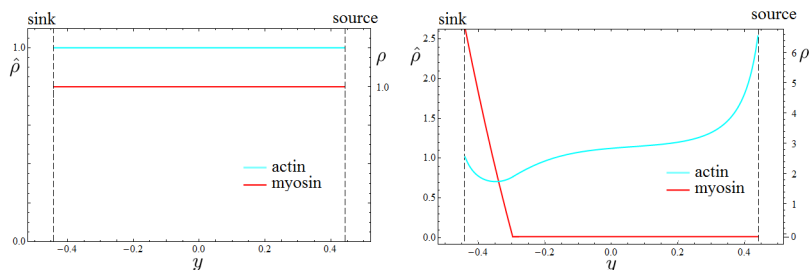


Figure IV: Distribution of myosin (red) and actin (cyan) in the static (left) and motile (right) regimes. Parameters: $\mathcal{L} = 10$, $\mathcal{M} = 0.053$, $\mathcal{E} = 0.04$, $\lambda = 0.5$ and $\mathcal{T} = 0.33$. Density ρ is normalized by $\bar{\tau}/\chi$ and density $\hat{\rho}$ by $M/(\sqrt{\eta/\xi})$.

In the static regimes $V = 0$, the stress is homogeneous $\sigma = \sigma_0$ and the flow of actin vanishes $v = 0$. In such regimes the model predicts constant densities of actin and myosin, see Fig.IV (left). This result is fully compatible with the experimental observations given that we disregard fluctuations and neglect near-membrane effects. For the motile regimes the distributions $\rho(y)$ and $\hat{\rho}(y)$ are presented in Fig.IV (right). Outside boundary layers the qualitative agreement

between the theory and the experiment is rather striking and it is clear that our prototypical model captures the main effect: the sweeping of actin to the de-polymerization zone at the back of the cell by the retrograde flow and its regeneration on the polymerization zone at the front of the cell.

4 Sensitivity to the variation of \mathcal{M} and \mathcal{E}

In Fig. V we show how the variation of \mathcal{M} and \mathcal{E} over two orders of magnitude affects the efficiency-velocity relation presented in the main text (Fig.4). One can see that the increase of \mathcal{M} shifts the optimal plateau region towards larger velocities while decreasing its size and slightly increasing the efficiency level. Similar variations of \mathcal{E} affect only mildly the values of efficiency at small and large velocities however it introduces more substantial variations in the middle range. While the biological relevance of the parameter variations at this scale remains an open question, it is clear that the optimality claim made in the paper is rather robust. A quantitative study of the parameter sensitivity in the 4D space $(\lambda, \mathcal{L}, \mathcal{M}, \mathcal{E})$, requiring an introduction of a specific measure of the closeness to optimality, will be presented elsewhere.

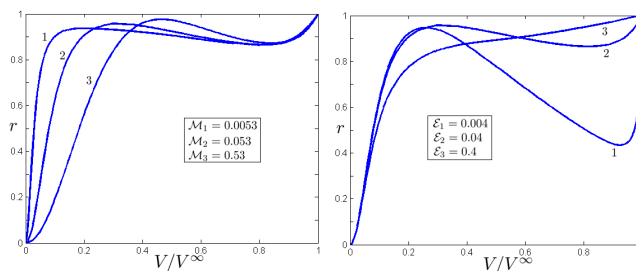


Figure V: Sensitivity of the normalized efficiency r to the variation of parameters \mathcal{M} and \mathcal{E} . The parameter $\mathcal{L} = 10$.

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