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Supporting Material

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Mihaela Enculescu, Mohsen Sabouri Ghomi, Gaudenz Danuser, and Martin Falcke

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Mihaela Enculescu
Department of Theoretical Physics,
Helmholtz Centre Berlin for Materials and Energy

Mohsen Sabouri-Ghomi, Gaudenz Danuser[2]
Department of Cell Biology,
The Scripps Research Institute, La Jolla, USA
[2]Current address: Harvard Medical School, Boston, MA

Martin Falcke[1]
Mathematical Cell Physiology,
Max-Delbrück-Centre for Molecular Medicine, Berlin, Germany

[1]Corresponding author. Address: Mathematical Cell Physiology, Max-Delbrück-Centre for Molecular Medicine, Robert-Rössle-Str. 10, Berlin, D-13125, Germany, Tel.: +49-30-94062753

Filament orientation

We have chosen the value $\pm 35°$ of the angle of filaments to the grafting direction according to experimental results suggesting it to be prevalent in lamellipodia (1, 2). Other studies found a broad distribution of angles (3). The variety of dynamic regimes reported in the main paper does not depend on the specific choice of the value for the angle, but can be found with a large range of angles (see ref. (4) their Fig. 5). Therefore we conclude that the results presented here do not depend essentially on the choice of angle.

Force exerted by detached filaments

Following (5), the entropic force f_d exerted on the membrane by a single filament with contour length l and a fixed distance z from the membrane tangent is

$$f_d(l, z, \theta) = \frac{f_c}{\cos\theta} \tilde{f}(\eta_{||}, \mu).$$

Here, θ denotes the angle between the filament and the normal to the membrane; f_c is the Euler buckling force and $\tilde{f}$ is a scaling function

$$\tilde{f}(\eta_{||}, \mu) = -\frac{\partial}{\partial \eta_{||}} \ln \tilde{Z}(\eta_{||}, \mu),$$

expressed in terms of the dimensionless variables

$$\eta_{||} = \frac{(l\cos\theta - z) l_p}{l^2 \cos\theta}, \quad \mu = \sqrt{\frac{l_p}{3l}} \tan\theta.$$

Thereby, $\tilde{Z}(\eta_{||}, \mu)$ denotes the restricted partition sum:

$$\tilde{Z}(\eta_{||}, \mu) = \frac{1}{2}\mathrm{erfc}\frac{\eta_{||}}{\sqrt{2}\mu} - \int_0^\infty \frac{dq}{\pi q} \,\mathrm{Im}\left[e^{iq\eta_{||}} \left(a(iq) e^{-\frac{3}{2}(\mu q)^2 b(iq)} - e^{-\frac{1}{2}(\mu q)^2}\right)\right],$$

with the complex functions

$$a(z) = \frac{1}{\cosh\sqrt{z}} \quad \text{and} \quad b(z) = \frac{\sqrt{z} - \tanh\sqrt{z}}{z^{3/2}}.$$

Linear response coefficient of attached filaments

Following (6), we used in the computations for the linear response coefficient of a single attached filament with contour length l

$$k_{||}(l,\theta)^{-1} = \frac{l_p^2}{k_B T}\left[\frac{2l}{3l_p} - \frac{5}{9} + \frac{1}{18}e^{-3l/l_p} + \cos(2\theta)\left(\frac{1}{3} + \frac{e^{-3l/l_p}}{6}\right) + (\sin\theta)^2 e^{-l/l_p} - (\cos\theta)^2\left(e^{-l/l_p} - 1\right)^2\right],$$

where θ is the angle between the direction of the applied force and the grafting direction.

Dependence of filament density and monomer concentration on Arp2/3 and cofilin concentrations

The model parameters most likely to depend on Rac1 activity are the total filament density $n = n_a^+ + n_a^- + n_d^+ + n_d^-$ and the polymerization velocity $v_p^{\max}$. How they vary with the Arp2/3 and cofilin levels can be estimated in a simple way. Since the total amount of actin G^0 stays constant, the amount of monomeric actin G is related to the amount of filamentous actin by

$$G + c_1 n L = G^0. \tag{1}$$

Here, L denotes the mean value of the total length of the filaments, including the cross-linked part, and c_1 is a proportionality constant. Since only a very short part of the filaments is fluctuating freely, we have $l \ll L$, therefore we neglect the variations of L when the dynamics of the membrane is oscillatory. A similar conservation argument holds for the total amount A^0 of active Arp2/3-complex

$$A + c_2 n = A^0, \tag{2}$$

where A and $c_2 n$ denote the free Arp2/3 and Arp2/3 bound to filaments, respectively.

We assume that the actin network grows until it reaches a steady state, where the number of branching filaments balances the number of capped filaments. The analysis includes capping of barbed ends at a constant rate and neglects capping of pointed ends as well as uncapping. For the Arp2/3 induced branching we follow the kinetic analysis in (7), predicting a condition for stationarity that follows from the balance of nucleation and capping events

$$A(G - G_C^B)^2 n = c_3 n. \tag{3}$$

Here, G_C^B denotes the critical concentration for addition of actin monomers at the barbed end, and c_3 is a further proportionality constant.
The equilibrium length L is reached when polymerization at the front balances depolymerization at the back, therefore

$$G - G_C^B = c_4 L C, \tag{4}$$

where we assume that polymerization is proportional to the amount of available monomers and depolymerization increases with filament age and amount of cofilin C available. Thereby c_{1-4} are positive proportionality constants. Eqs. 1-4 can be solved to find total filament density n and equilibrium monomer concentration G and how they respond to changes of the concentrations A^0 and C of the regulating proteins. We set $\tilde{G} := \tilde{G} - G_C^B$ and $\tilde{G}^0 := G^0 - G_C^B$. Conservation of the filament density (Eq. 3) relates the free Arp2/3 concentration A to relative actin monomer concentration $\tilde{G}$: $A = c_3/\tilde{G}^2$. Conservation of the total filament length (Eq. 4) relates the total filament length to the concentrations of actin monomers $\tilde{G}$ and cofilin C: $L = \tilde{G}/(c_4 C)$. Substitution of A and L in the remaining equations that express conservation of actin (Eq. 1) and Arp2/3 (Eq. 2) leads to two relations between relative monomer concentration $\tilde{G}$ and filament density n:

$$\tilde{G} = \frac{\tilde{G}_0}{1 + \dfrac{c_1 n}{c_4 C}} \quad \text{and} \quad n = \frac{1}{c_2}\left(A^0 - \frac{c_3}{\tilde{G}^2}\right). \tag{5}$$

Consequently, we have

$$\frac{\partial \tilde{G}}{\partial A^0} = -\frac{\tilde{G}_0}{\left(1 + \dfrac{c_1 n}{c_4 C}\right)^2} \cdot \frac{c_1}{c_4 C} \cdot \frac{\partial n}{\partial A^0} \Rightarrow \left(\frac{\partial \tilde{G}}{\partial A^0}\right) \cdot \left(\frac{\partial n}{\partial A^0}\right) < 0 \tag{6}$$

and

$$\frac{\partial n}{\partial C} = \frac{1}{c_2} \cdot \frac{2c_3}{\tilde{G}^3} \cdot \frac{\partial \tilde{G}}{\partial C} \Rightarrow \left(\frac{\partial n}{\partial C}\right) \cdot \left(\frac{\partial \tilde{G}}{\partial C}\right) > 0. \tag{7}$$

Combining Eqs. 5 leads to a quadratic equation for the filament density n:

$$\frac{c_1^2}{c_4^2 C^2} n^2 + \left(\frac{2c_1}{c_4 C} + \frac{c_2 \tilde{G}_0^2}{c_3}\right) n + 1 - \frac{A^0 (\tilde{G}^0)^2}{c_3} = 0.$$

With

$$a_n = \frac{c_1^2}{c_4^2 C^2},\ b_n = \left(\frac{2c_1}{c_4 C} + \frac{c_2 (\tilde{G}_0)^2}{c_3}\right),\ c_n = 1 - \frac{A^0 (\tilde{G}^0)^2}{c_3}$$

and $\Delta_n = b_n^2 - 4a_n c_n > 0$ we get a unique positive solution

$$n = \frac{-b_n + \sqrt{\Delta_n}}{2a_n}$$

if $c_n < 0$, i.e., when total concentrations of available Arp2/3 and actin satisfy $A^0(\tilde{G}^0)^2 > c_3$. If not enough Arp2/3 and actin are available, capping prevents the formation of a filamentous network. However, when $c_n < 0$, we have

$$\frac{\partial n}{\partial a_n} = -\frac{(b_n - \sqrt{\Delta_n})^2}{4a_n^2\sqrt{\Delta_n}} < 0,\ \frac{\partial n}{\partial b_n} = -\frac{n}{\sqrt{\Delta_n}} < 0,\ \frac{\partial n}{\partial c_n} = -\frac{1}{\sqrt{\Delta_n}} < 0.$$

It follows

$$\frac{\partial n}{\partial A^0} = -\frac{(\tilde{G}^0)^2}{c_3}\frac{\partial n}{\partial c_n} > 0 \quad \text{and}$$

$$\frac{\partial n}{\partial C} = \frac{\partial n}{\partial a_n}\cdot\left(-\frac{2c_1^2}{c_4^2 C^3}\right) + \frac{\partial n}{\partial b_n}\cdot\left(-\frac{2c_1}{c_4 C^2}\right) > 0.$$

From Eqs. 6 and 7 we get

$$\frac{\partial \tilde{G}}{\partial A^0} < 0 \quad \text{and} \quad \frac{\partial \tilde{G}}{\partial C} > 0.$$

From Eqs. 1-4, the ratio between the variations of the monomer concentration with the amount of Arp2/3 and cofilin is given by

$$\frac{(\partial G/\partial A^0)}{(\partial G/\partial C)} = \frac{C}{A^0 - A},$$

being therefore independent of the constants c_{1-4}.

Membrane fluctuations and polymerization rate

A recent study by Shaevitz et al. (8) showed that the Brownian motion of Listeria bacteria, which are also propelled by actin polymerization, may contribute to the polymerization velocity. This study prompted us to examine whether membrane fluctuations may contribute to the intercalation probability for monomers. Assessing membrane fluctuations has to take into account that the leading edge membrane is under tension and is bound to the attached filaments. Additionally, detached filaments exert a force on the membrane. In order to obtain an idea of the size of membrane fluctuations we estimate their standard deviation.

The function $h(\vec{r})$ describes the hight of the membrane over a plane surface. The Hamilton function of the membrane under tension $\tilde{S}$, with bending modulus $\tilde{B}$ and in a potential $\tilde{V}(h(\vec{r}))$ is (9)

$$H(\vec{r}) = \int d^2\vec{r}\left[\frac{1}{2}\tilde{S}\left(\nabla h(\vec{r})\right)^2 + \frac{1}{2}\tilde{B}\left(\nabla^2 h(\vec{r})\right)^2 + \tilde{V}(\vec{r})\right]. \quad (8)$$

The motion of the membrane at the leading edge is restricted by the attached filaments. Therefore we consider a quadratic piece of membrane of extension $L \times L$ attached at its four corners to stiff rods without any excluded volume restrictions. L corresponds to a typical distance of attached filaments. First, we set the potential to 0. That case was considered in reference (10). We obtain for $\Delta^2 = \left\langle \left(h(\vec{r})\right)^2 \right\rangle$ with tension $\tilde{S} = 0$

$$\Delta^2 = \frac{6.03 k_B T}{(2\pi)^4 \tilde{B}} L^2. \quad (9)$$

With the parameter range mentioned in the next paragraph we obtain Δ=0.19 - 89 nm. Extending this result to a membrane under tension yields

$$\Delta^2 = \frac{6.03 k_B T}{(2\pi)^2 \tilde{S}} \ln\left[\frac{1 + \frac{\tilde{S}}{\tilde{B}}\left(\frac{L}{2\pi}\right)^2}{1 + \frac{\tilde{S}}{\tilde{B}}\left(\frac{l}{2\pi}\right)^2}\right] \quad (10)$$

Here, l is a cut-off length corresponding to the thickness of the membrane of about 5 nm. The value of $\tilde{S} = 0.05$ pN nm^{-1} is given by the total tension along the leading edge S divided by the height of the leading edge of 200 nm (11). With $k_B T \approx 4$ pN nm, $\tilde{B} = 5 - 50\ k_B T = 20 - 200$ pN nm and a distance of attached filaments of ≈32 nm (12) or ≈22 nm (3) we arrive at a standard deviation of 0.26-0.82 nm (L_m=32 nm) or 0.17-0.54 nm (L_m=22 nm). Note, that we have neglected the vertical curvature of the leading edge with a radius R_c of approximately 100 nm (11), which will further reduce fluctuations. In summary, the gap required for monomer insertion is larger than 3Δ, if we assume the largest estimate 0.82 nm to apply. The intercalation probability is less than 1%, if we estimate it with a Gaussian distributions for the amplitude of membrane fluctuations (9). It is unlikely that membrane fluctuations of this magnitude contribute to the intercalation probability.

But if we assume we underestimated Δ by a factor 2 or 3 and membrane fluctuations do contribute, would this change the form of the dependence of the polymerization rate on the force f_d exerted by detached filaments? The

probability for large membrane fluctuations is reduced by f_d. We describe the effect of this force by a potential $\tilde{V}(h(\vec{r}))$ acting on the membrane (see Eq. 8) (9). The function $h\,(\vec{r})$ denotes the deviation of the membrane from its force free position and $h(\vec{r_t})$ is the position of the membrane at the tip of the filament pushing against the membrane. Following refs. (5, 13), we assume the probability for a membrane fluctuation of size δ_m away from $h(\vec{r_t})$ to be proportional to $\exp(-[V(h(\vec{r_t}) + \delta_m) - V(h(\vec{r_t}))]/k_BT)$, which can be approximated by $\exp(-f_d(\vec{r_t})\delta_m/k_BT)$.
A gap between membrane and filament tip larger than the size d required for monomer insertion can arise from filament and membrane fluctuations together. Its probability is proportional to $\exp(-f_d(\vec{r_t})\delta_m/k_BT)\exp(-f_d(\vec{r_t})(d-\delta_m)/k_BT) = \exp(-f_d(\vec{r_t})d/k_BT)$, where we assumed independence of membrane and filament fluctuations. The first factor on the left hand side arises from membrane fluctuations and the second one from filament fluctuations. Corrections to this expression might arise from correlations between membrane and filament tip fluctuations. Since we obtain the same force dependency as in Eq. 1 in the main paper, we assume that the current form of the polymerization velocity captures also the essential force dependence of the contribution from membrane fluctuations.
We arrive at a structure of the polymerization velocity like

$$v_p \;=\; v_p^{max} e^{-\frac{f_d(\vec{r})d}{k_BT}}. \tag{11}$$

The fact that v_p does not vanish even for a rigid membrane suggests to approximate v_p^{max} by

$$v_p^{max} \;=\; v_p^{filament} + v_p^{membrane}\,(f_d)\,. \tag{12}$$

The contribution of the membrane will depend on other parameters than f_d also, but we explicitly note the dependence of $v_p^{membrane}$ on f_d only to underline that for the model its dependence on dynamic variables is crucial. In the model, we neglect that force dependence of $v_p^{membrane}$, since we assume it would only further reduce membrane contributions.

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