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Dampening effects on the polymerization rate of actin gel surface growth

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ABSTRACT

This letter addresses the delicate balance between a local surface growth mechanism, driven by actin polymerization, and the resulting macroscopic stress field, with emphasis on the effect of external dampening on the growth process. In connection with available experimental studies, we consider a spherically symmetric setting in which new mass is constantly being formed on the surface of a bead. In that unique growth process the previously formed layers are constantly being pushed outwards by new mass, thus resulting in an internal stress field which, in turn, effects the growth process. It is shown that external dampening effects the growth rate as well as the steady-state thickness in the treadmilling regime.

1. Introduction

The molecular mechanism of actin polymerization drives cell movement. Fascinating examples of such phenomena have been observed in embryonic cells and several intracellular pathogens such as Listeria monocytogenes [1]. The latter example has motivated Noireaux et al. [2] to perform a series of experiments designed to obtaining further insight into the chemo-mechanical process. Therein actin gel was grown on spherical beads under varying conditions (i.e. bead radius and concentration of necessary proteins to promote the reaction). It was shown that if symmetry is maintained the growth process eventually assumes a steady-state treadmilling response. Van der Gucht et al. [3] later explained, based on experimental observations in a similar setting, that stress release due to symmetry breaking of the actin layer can drive movement. In that study it is further shown that the symmetry breaking can occur before or after arriving at the treadmilling state, is independent on the bead size, but is sensitive to the growth rate.

In the present study we suggest a simplified framework which ties the microscopic growth process to the macroscopic evolution of mass, to expose the sensitivity of the process and specifically the growth rate to external dampening effects. That sensitivity may play a key role in the limit state of symmetry breaking and thus in actin based motility.

Actin polymerization and depolymerization is widely considered in the scope of Brownian dynamics and is thus an 'overdamped' dynamic process at the limit where no average acceleration takes place. The dampening is a product of the crowding of solvent molecules which causes friction. Specifically, considering the growth of actin gel on a spherical bead, the process requires inflow of solid mass (monomers) through the out-flowing material at an identical rate, to sustain the growth. Hence the process and the resulting stress field are expected to depend on the growth rate. On the other hand, the bio-chemical process of polymerization (and depolymerization) depends on the

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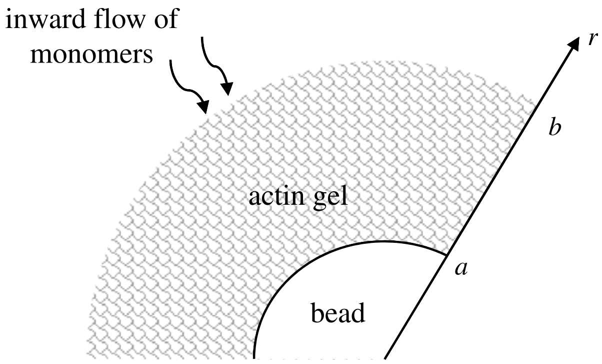

Fig. 1. Illustration of actin layer grown on a bead in a spherically symmetric setting. The spatial radial coordinate is denoted by r, the radius of the bead is a and the external radius of the grown mass is b. Actin polymerization takes place only on the bead surface at $r = a$, while inward flow of monomers is required to maintain the growth.

stress. Therefore there is a coupled relation between the growth rate and the stress.

Considering the collective behavior of the solid mass at the continuum limit, the present derivation by-passes the stochastic aspects of Brownian dynamics which is then plugged back into the model through the chemo-mechanical coupling with the rate of polymerization dictated by a simplified form of Kramers equation [4], which was previously suggested by Noireaux et al. [2] and applied therein, in comparison with experimental results. Employing an incompressible continuum model of finite strain elasticity it will be shown that external dampening influences not only the time required to achieve a steady thickness of the actin gel but also the steady thickness itself.

Recent studies [5–7] account for the growth process and induced stress fields considering several constitutive models of compressible and incompressible elasticity and hyperelasticity for both infinitesimal and finite strains in spherical and cylindrical geometries. It is shown therein that material compressibility can have a profound effect on the stress field and thus on the steady thickness in the treadmilling state. In the present study we restrict the discussion to an incompressible material response. The novel ingredient of the present study compared to the aforementioned ones is the role of the external dampening effects.

2. Problem setting and formulation

We consider the spherically symmetric growth of actin gel on a bead of radius a, as illustrated in Fig. 1, where the spatial radial coordinate is denoted by r and the external radius of the actin layer is b. New mass is formed only on the bead surface ($r = a$), hence the previously formed layers are constantly being pushed outwards by new mass, thus resulting in an internal stress field which, in turn, effects the growth process.

The formulation centers on the simplifying assumption that the actin gel is an isotropic homogeneous continuum. However, the interactions with solvent molecules and the constant inward flow of monomers is accounted for by considering an external dampening effect.

We consider the grown mass to be an incompressible Hookean elastic medium while accounting for finite strains. Therefore, by inserting Poisson's ratio $\nu = 0.5$ (for incompressibility) into the regular Hookean elastic relations in spherical symmetry, we have

$$h_r = \frac{1}{E}(\sigma_r - \sigma_\theta), \qquad h_\theta = h_\varphi = -\frac{1}{2E}(\sigma_r - \sigma_\theta) \tag{1}$$

where E is the elastic modulus, $(\sigma_r, \sigma_\theta = \sigma_\varphi)$ are the radial and tangential stress components and $(h_r, h_\theta = h_\varphi)$ are the radial and tangential logarithmic (Hencky) strains, respectively. Note that in the present analysis compressive stress has a negative sign.

According to (1) we have the relation $h_r + 2h_\theta = 0$ which is a basic requirement for conservation of mass in an incompressible medium. In that context, it should be mentioned that, being a polymeric gel, actin can have some level of compressibility. Since the network alone (without the surrounding fluid) is compressible, outflow of fluid through the network allows for change in volume. This is a subtle time dependent effect which depends on the boundary conditions and is apparent only in the low frequency loading regime [8]. Poisson ratio measurements reported in [9] are near the incompressibility limit. Nevertheless, in previous studies [5–7] the effect of compressibility on the stress field, without consideration of dampening effects, has been thoroughly addressed, hence, the combined damped-compressible response can be accounted for in the future.

By employing kinematic considerations as in [7] we find that the tangential stretch of any material segment is the ratio between its initial length and current length, hence the logarithmic tangential strain component is

$$h_\theta = \ln\left(\frac{r}{a}\right). \tag{2}$$

Conservation of mass of the incompressible medium implies that the inward mass flow due to polymerization on the bead surface (with velocity $v(a) = v_p$) must be equal to the outward flow through the spherical surface at any radius, thus bringing us to the relation for the material velocity

$$v = v_p\left(\frac{a}{r}\right)^2. \tag{3}$$