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Continuum theory of contractile fibres

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Abstract. – The generation of contractile forces by living cells often involves linear arrangements of actively interacting polar filaments. We develop a physical description of the dynamics of active fibers based on a general expression for the tension in terms of the filament density and the bundle polarisation. We discuss the long-time behaviour of oriented and of nonpolar fibres, discuss effects of polymerization and depolymerization, and relate this continuum theory to nonlocal descriptions of filament-motor systems. We show that a nonpolar arrangement of filaments suppresses oscillatory instabilities which could be relevant for muscle fibers.

Important aspects of cellular dynamics depend on the cells' ability to generate contractile forces [1]. For example, in the late stage of cell division, eucaryotic cells are cleaved by contracting a ring between the two newly formed nuclei, and during locomotion on a substrate the cell body has to be dragged behind the advancing leading edge. Often, these contractile forces are generated by fibres composed of cytoskeletal filaments, usually actin filaments, as well as many other proteins including molecular motors [2].

Active cytoskeletal systems have recently attracted a lot of attention both experimentally [3–7] and theoretically [8–15]. Theoretical descriptions of contractile fibres have typically been based on the specific interactions between filaments and motor proteins [8–11]. By hydrolyzing adenosinetriphosphate (ATP), which is a chemical fuel, complexes of molecular motors can induce relative sliding of aligned filaments. Indeed, in an *in vitro* experiment it was found that disordered bundles of actin filaments can shorten after the mere addition of the motor protein myosin and ATP [3]. The relative sliding due to molecular motors depends crucially on the relative orientation of the filaments: filaments are polar as their ends, commonly denoted as plus- and minus-end, are structurally different. This polarity determines in particular the direction of the forces applied by molecular motors on a filament. A physical description of the interactions between filaments mediated by motors leads to nonlocal expressions, since filaments can transmit stresses over a finite distance [10, 12].

The dynamics at length scales large compared to the filament length can be appropriately described by a local theory. In the present work, we develop a continuum description of the dynamics and mechanics of contractile fibres, which allows to extract generic features without a detailed consideration of the underlying microscopic mechanisms. Since fibers are

linear objects, we use a one-dimensional description where the fiber is aligned along the x -axis. At any position, we define the local filament density $c = c^+ + c^-$ and the polarization $p = c^+ - c^-$. Here, c^+ and c^- denote the number of filaments per unit length, respectively for the two possible filament orientations along the fiber axis. We will focus our analysis on two simplified situations which provide particular insights in general properties of active fibers: fully polarized and nonpolar fibers. In the first case, all filaments are oriented in the same direction, $p = \pm c$, while in the second case, there is an equal density of filaments of both orientations everywhere along the fiber, $p = 0$.

In general, the filament dynamics can be written in the form of continuity equations:

$$\partial_t c + \partial_x j = s, \quad (1)$$

$$\partial_t p + \partial_x j_p = s_p. \quad (2)$$

In the absence of polymerization and depolymerization, the filament density c is a conserved quantity and $s = 0$. If, in addition, we assume that filaments do not change their orientation, p is conserved as well and $s_p = 0$. In the absence of external forces, the currents j and j_p result from active interactions between filaments. We assume that the filament densities and polarization locally define the state of the active material. As a consequence, the currents j and j_p depend on c and p and their derivatives only. Similarly, the mechanical tension σ which is generated in the bundle by active processes is also fully determined by c and p . Note that, in our one-dimensional description, σ has units of force.

Gradients in the tension are balanced by viscous forces that are due to filament currents relative to the surrounding fluid. In the rest frame of this fluid and ignoring filament treadmilling, the filament current can thus be expressed as

$$j = \eta^{-1} \partial_x \sigma, \quad (3)$$

where η is a friction coefficient. In the absence of external forces, or for periodic boundary conditions, the total current $I \equiv \int_0^L dx j = \eta^{-1} (\sigma(L) - \sigma(0))$ vanishes. Here L denotes the system length.

The constitutive equation of the fiber relates the fiber tension to filament density and polarization as well as their derivatives⁽¹⁾. Up to second order in c and p , and up to second-order derivatives, the most general expression for σ is given by⁽²⁾

$$\begin{aligned} \eta^{-1} \sigma = & -Dc + A_1 \partial_x p + A_2 \partial_x^2 c + \\ & + B_1 c^2 + B_2 p^2 + E_1 c \partial_x p + E_2 (\partial_x c) p + \\ & + F_1 c \partial_x^2 c + F_2 p \partial_x^2 p + F_3 (\partial_x c)^2 + F_4 (\partial_x p)^2. \end{aligned} \quad (4)$$

Here, we have written all terms which are permitted by symmetry. Indeed, under reflections $x \rightarrow -x$, c and σ are even, while p is odd, which limits the possible terms.

The current j_p is not induced by tension gradients. However, we also assume that it is determined by the state of the system, given by c and p , alone. Retaining only those terms

⁽¹⁾We obtain an expression for σ by expanding the tension in the variations $\delta c = c - \bar{c}$ and $\delta p = p - \bar{p}$ with respect to a reference state of homogeneous filament density \bar{c} and polarization \bar{p} . Finally, one can re-express the result in terms of c and p to obtain eqs. (4) and (5).

⁽²⁾Nonlinearities are required to stabilize the dynamic equations. We can ignore higher-order terms if the sign of the second-order terms is such that they are stabilizing.

that satisfy the symmetry requirements, the most general form of j_p reads

$$\begin{aligned}
j_p = & \epsilon(c^2 - p^2) - D\partial_x p + A_1\partial_x^2 c + A_2\partial_x^3 p + \\
& + \bar{B}_1 c \partial_x p + \bar{B}_2 (\partial_x c) p + \\
& + \bar{E}_1 c \partial_x^2 c + \bar{E}_2 p \partial_x^2 p + \bar{E}_1 (\partial_x c)^2 + \bar{E}_2 (\partial_x p)^2 + \\
& + \bar{F}_1 c \partial_x^3 p + \bar{F}_2 (\partial_x^3 c) p + \bar{F}_3 (\partial_x c) \partial_x^2 p + \bar{F}_4 (\partial_x^2 c) \partial_x p.
\end{aligned} \tag{5}$$

Here, we have used an additional constraint. In the case of a fully polarized fiber, polarization and density are the same $c = p$, and consequently, $j = j_p$. Comparing the expressions for j and j_p in the limit $c = p$ requires the expression (5) and furthermore implies $\bar{B}_1 + \bar{B}_2 = 2(B_1 + B_2)$, $\bar{E}_1 + \bar{E}_2 = \bar{E}_1 + \bar{E}_2 = E_1 + E_2$, $\bar{F}_1 + \bar{F}_2 = F_1 + F_2$, and $\bar{F}_3 + \bar{F}_4 = 2(F_3 + F_4) + F_1 + F_2$.

The source and sink terms s and s_p describe effects of filament polymerization and depolymerization. Using the same arguments as described above, we can write simplified expressions for s and s_p . Assuming for simplicity that polymerization and depolymerization rates only depend on local densities, they are given by

$$s = c - \mu c^2 - \nu p^2, \tag{6}$$

$$s_p = p - (\mu + \nu)pc. \tag{7}$$

Again, we have used the constraint that $s = s_p$ for $c = p$. This constraint remains valid if we neglect spontaneous changes of filament orientation and assume that filaments of one orientation are generated by polymerization only if filaments of this orientation already exist. Furthermore, we exclude situations where polymerization and depolymerization are controlled externally. In order to ensure stability of the system we choose μ and ν to be positive.

We will now discuss the properties of contractile fibers governed by the dynamic equations introduced above. First, consider the case of a fully polarized fiber in the absence of polymerization and depolymerization, *i.e.* $p = c$ and $s = s_p = 0$. In this case, we obtain a single equation for the density c . The tension simplifies and reads

$$\eta^{-1}\sigma = -Dc + A\partial_x c + \frac{B}{2}(c^2 - \lambda^2(\partial_x c)^2) + Ec\partial_x c + Fc\partial_x^2 c, \tag{8}$$

where $\lambda^2 = -(F_3 + F_4)/(B_1 + B_2)$, and λ is a length scale, $A = A_1$, $B = 2(B_1 + B_2)$, $E = E_1 + E_2$, and $F = (F_1 + F_2)$. We assume $F > 0$ in order to avoid instabilities on small length scales. Furthermore, we consider the simple case $A_2 = 0$, as this term is irrelevant in the following. Equation (1) together with the tension (8) describes the dynamic and mechanic behavior of this system. The homogeneous state $c(x) = c_0$ is a stationary solution where $c_0 = L^{-1} \int dx c$ and L is the system size. For periodic boundary conditions, this state is linearly stable for $B < B_c$ with $B_c = D/c_0 + 4\pi^2 F/L^2$. The tension in the homogeneous state is given by

$$\sigma_0 = \eta \left(\frac{B}{2} c_0^2 - Dc_0 \right), \tag{9}$$

which is positive, *i.e.*, contractile, for $B > 2D/c_0$. As long as $F > DL^2/4\pi^2 c_0$, there exist stable homogeneous states with contractile tension σ_0 . Provided $A + Ec_0 \neq 0$, the system undergoes a Hopf bifurcation towards solitary-wave solutions at $B = B_c$. These solutions have the form $c(x, t) = u(x - vt)$. Inserting this ansatz into the dynamic equation $\partial_t c = -\eta^{-1} \partial_x^2 \sigma$,

we obtain an ordinary differential equation of third order for the density profile u . With periodic boundary conditions, this equation has a discrete set of solutions with distinct values of v . Note that a unique stationary solution with $v = 0$ always exists. As the system size is increased, solitary waves maintain their shapes but cease to propagate in an infinite system.

It is interesting to consider the limit $F = 0$ where the differential equation is of second order and can be represented by the pair of first-order equations

$$\sigma' = v\eta(u - c_0), \quad (10)$$

$$u' = \frac{1}{\lambda^2 B} (Eu + A \pm \sqrt{(Eu + A)^2 + 2\lambda^2 B(Bu^2/2 - Du - \sigma)}), \quad (11)$$

where the primes denote derivatives with respect to x . Here, we have used the condition $\sigma(0) = \sigma(L)$. The corresponding solutions $u(x)$ exhibit discontinuities in the first derivative at the extrema of u where the two branches of solutions to eq. (11) are connected. For finite F , solitary-wave solutions can be obtained from numerical integrations of the dynamic equations. For small F these waves approach solutions to eq. (11). Numerical solutions to the dynamic equations reveal that the stationary solution with $v = 0$ is unstable if solitary waves exist.

A particular example is the case $A = E = 0$, where the steady state for $F = 0$ in the interval $0 < x < L$ with periodic boundary conditions is given by

$$c_s(x) = H \cosh \frac{x - L/2}{\lambda} + \frac{D}{B}, \quad (12)$$

which has a discontinuity of c' at $x = 0$ and $x = L$. The amplitude

$$H = \frac{L(c_0 - D/B)}{2\lambda \sinh L/2\lambda} \quad (13)$$

is determined by the total number of filaments $c_0 L$. This state has a constant tension

$$\sigma_s = \eta \left(\frac{B}{2} H^2 - \frac{D^2}{2B} \right), \quad (14)$$

which obeys $\sigma_s < \sigma_0$ for $B > B_c$, indicating that tension is relaxed by the instability of the homogeneous state.

Generically, the coefficients A and E are nonzero. For periodic boundary conditions such as in the case of filament rings, we therefore expect propagating solutions to occur as soon as the bundle becomes inhomogeneous.

Consider now the second important case of a nonpolar bundle with $p = 0$. Such a case occurs if small groups of filaments of both orientations are linked rigidly such that they form nonpolar aggregates. As a consequence, the polarization vanishes at all times. Again, we are led to a single equation for c and tension

$$\eta^{-1} \sigma = -Dc + \frac{\bar{B}}{2} (c^2 - \bar{\lambda}^2 (\partial_x c)^2) + \bar{F} c \partial_x^2 c, \quad (15)$$

which is of the same form as eq. (8) but with $A = 0$ and $E = 0$. Here $\bar{B} = 2B_1$, $\bar{F} = F_1$ and $\bar{\lambda}^2 = -F_3/(2B_1)$. We thus recover the special case discussed above where the homogeneous state becomes unstable with respect to stationary contracted states. We thus find that in nonpolar bundles propagating solutions are suppressed.

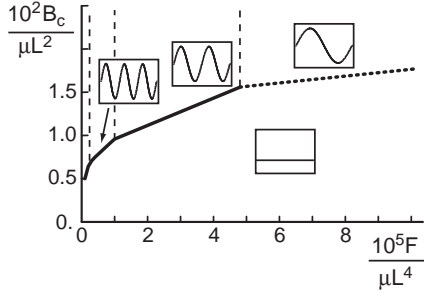


Fig. 1

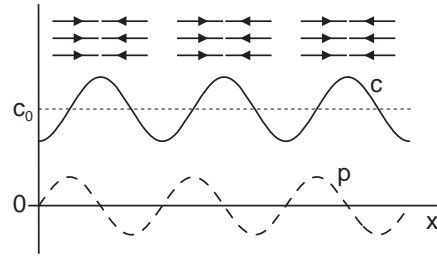


Fig. 2

Fig. 1 – Stability boundary of the homogeneous state of an active fiber in the presence of polymerization and depolymerization of filaments. Insets indicate the density profiles of the corresponding unstable modes. Along the solid line the homogeneous state loses stability via a Hopf bifurcation towards solitary waves; the dotted line indicates a pitchfork bifurcation towards contracted states. The bifurcations occur as the parameter B exceeds a critical value B_c . L is the system size, F characterizes a stabilizing nonlinearity and μ characterizes depolymerization rates. Parameters are $(A+E/\mu)/L^3 = 1.5 \cdot 10^{-3}$, $D/L^2 = 0.01$, $\epsilon/\mu L = 0.05$, $\nu = \mu$, $A = A_1$, $A_2 = 0$, $B = B_1 = B_2 = \bar{B}_1/2 = \bar{B}_2/2$, $E = E_1 = E_2 = \bar{E}_1 = \bar{E}_2 = \bar{E}_1 = \bar{E}_2$, $2F = F_1 = F_2 = F_3 = F_4 = \bar{F}_1 = \bar{F}_2 = \bar{F}_3/3 = \bar{F}_4/3$.

Fig. 2 – Density profile (solid line) and polarization profile (broken line) of an unstable mode of an active fiber with polymerization and depolymerization of filaments. The associated wavelength is smaller than the system size, leading to a periodic modulation of the unstable mode. Density and polarization display a relative phase shift of $\pi/2$. The mode thus corresponds to an arrangement of filaments, as indicated schematically.

In a general situation, we have to take into account two coupled dynamic equations for c and p . In this situation, homogeneous solutions are again stable for B smaller than a critical value. Furthermore, stable inhomogeneous stationary solutions and solitary waves exist. For $A + Ec_0 > 0$, the homogeneous state becomes unstable through a Hopf bifurcation if $\epsilon < \epsilon_c$, where ϵ has been introduced in eq. (5) and ϵ_c is a critical value. For $\epsilon > \epsilon_c$, the bifurcation is stationary.

So far, we have neglected the effects of polymerization and depolymerization of filaments represented by the source terms given by eqs. (6) and (7). These terms control the average filament concentration and polarization and lead to a coexistence of three different homogeneous steady states. These homogeneous states are given by i) $c = p = 0$, ii) $c = p = 1/(\mu + \nu)$, and iii) $c = 1/\mu$ and $p = 0$. States i) and ii) are unstable with respect to homogeneous perturbations and will not be considered further. State iii) is stable against such perturbations. As a consequence, a linear stability analysis of this state reveals a bifurcation with an unstable mode of finite wave vector q which introduces a new length scale in the system, see fig. 1. As above, this bifurcation is either stationary or of Hopf type, depending on the value of ϵ . We find that the critical mode is characterized by a phase shift of $\pi/2$ between c and p . This mode corresponds to a sarcomer-like periodic arrangement of filaments in the fiber, see fig. 2. It is also similar to polarity sorting observed in ref. [3], which can be understood if the dynamics of motor densities is taken into account [12].

The case of a fully oriented bundle needs to be discussed separately. Here, we assume that filaments of one orientation only appear in the system and that filaments of opposite orientation are not generated by polymerization events. Therefore, the dynamic solutions satisfy the condition $c = p$ for all times. In this situation, two homogeneous states with $c = p = 0$ and $c = p = 1/(\mu + \nu)$ exist. The former is always unstable while the latter becomes unstable for $B > \bar{B}_c$, where $\bar{B}_c = \mu(2\sqrt{F/\mu} + D)$. At the bifurcation, the characteristic wave

vector is given by $q^4 = (\mu + \nu)/F$ and the frequency is $\omega = A + E/(\mu + \nu)$. Therefore, as in the absence of polymerization and depolymerization, the instability of the homogeneous state occurs in general via a Hopf bifurcation.

In this paper, we have developed a generic continuum description of contractile fibers. This description is based on the idea that the mechanical tension in the fiber as well as the polarization current are fully determined by the local state of the material characterized by its density and polarization. The resulting two coupled nonlinear equations for the density and the polarization can be simplified in two limiting cases: a fully oriented bundle, where all filaments have the same orientation, and a nonpolar bundle, with no average polarization.

The dynamic equations describe the contraction of a fiber resulting from tension generated in the fiber by active processes. A fiber with constant tension and density can become unstable with respect to contracted states and solitary waves. Contracted states are inhomogeneous steady states where filaments accumulate in a region, while solitary waves occur via a Hopf bifurcation. They are propagating density profiles and lead to time-dependent stress profiles in the fiber.

If filaments polymerize and depolymerize, the density is no longer a conserved quantity. We have added source and sink terms to the dynamic equations and have focussed for simplicity on the simple case where polymerization and depolymerization depend only on the local state of the fiber. In this case, the unstable mode near a bifurcation is characterized by a wavelength which defines a new length scale in the problem. Again, both stationary contracted states and solitary-wave solutions exist.

This continuum description can be compared to the results found in a more microscopic description of filament bundles [10]. This description is based on the idea that active currents arise from interactions between filament pairs via motors. A mathematical formulation of the currents leads to nonlocal interaction terms represented by integrals over squares of the filament densities. The strength of interactions mediated by molecular motors is characterized by two coupling constants α and β . By taking the long-wavelength limit of the nonlocal dynamic equations of this model, we obtain a continuum limit which corresponds to the physical description derived here on symmetry grounds. We can calculate the coefficients of the expansions (4) and (5) for this model. We recover all terms of the generic expansion but find that $A_1 = 0$ and $A_2 = 0$, as well as $\tilde{E}_1 = \tilde{E}_2 = 0$ and $\tilde{F}_3 = \tilde{F}_4 = 0$. This implies that the corresponding terms are generated by higher-order processes where three or more filaments interact via motors. In addition, the microscopic model which is based on interactions of filament pairs imposes relations between expansion coefficients. Therefore, the resulting dynamic equations are of higher symmetry. For example, interactions of filament pairs lead to $B_1 = B_2$, $E_1 = -E_2$, and $F_1 = F_2 = -2F_3 = -2F_4$. Furthermore, $E_1 \sim \beta$. As a consequence, interactions between filament pairs do not generate oscillatory states in fully polarized bundles. Three-body interactions and higher turn the stationary instability into a Hopf bifurcation in the generic case. However, all other states that we have discussed above are generated by the microscopic model, in particular solitary waves and contracted steady states. Our microscopic model based on pairwise interactions of filaments via motors therefore provides a possible microscopic mechanism for the terms in the generic expansion.

Our theory is motivated by active cellular structures which have the form of fibers. Examples are stress fibers, contractile rings and adhesion belts. Stress fibers are formed by cells which adhere to a substrate or to neighboring cells under mechanical stimulation. They are important elements for the force generation of cells and during cell locomotion. Contractile rings are formed during cytokinesis during cell division. Finally, adhesion belts are formed in epithelial cells and serve to deform the epithelium. Active fibers in cells typically consist of actin and myosin motors. In addition, they contain other cytoskeletal proteins.

Our work suggests that propagating density profiles are in general expected to occur in active fibers and we expect such solitary waves in particular to be relevant for the dynamics of contractile rings. Our study suggests that inhomogeneous states can be stationary or propagating, depending on the values of parameters in the problem.

Oscillatory instabilities and propagating modes are suppressed in nonpolar fibers. Nonpolar fibers made of cytoskeletal elements require an architecture where filaments are arranged in such a way that the average polarization always vanishes. An example is the arrangement of filaments in muscle sarcomeres. On scales which are large compared to the sarcomere length of $2\mu\text{m}$, the specific arrangement of actin filaments attached to Z-disks corresponds to an effectively nonpolar system. We can therefore conclude that the structure of muscle sarcomeres has the ability to reduce the tendency of contractile fibers to oscillate. Muscle oscillations have, however, been observed under specific conditions in skeletal muscles [16]. Furthermore, the flight muscles of many insects generate spontaneous oscillations which are used to beat the wings [17]. Our work indicates that such oscillations are rather a consequence of instabilities of rigidly coupled myosin motors interacting with actin filaments [18, 19] than a result of the solitary-wave solutions which we discuss here in active bundles.

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