

Fluctuations and hydrodynamics in active filament solutions

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1 Introduction

Soft active systems are a new and exciting class of materials to which energy is continuously supplied by internal or external sources. Biology provides many examples of such systems, including cell membranes and bio-polymer solutions driven by chemical reactions, living cells moving on a substrate, and the cytoskeleton of eukariotic cells (Howard, 2000). The cytoskeleton is a complex network of long filamentary proteins (mainly F-actin and microtubules) cross-linked by a variety of smaller proteins (Howard, 2000; Dogterom *et al.*, 1995). Among the latter are clusters of motor proteins, such as myosin and kinesin, that use chemical energy from the hydrolysis of ATP to “walk” along the filaments, mediating the exchange of forces between them (Takiguchi, 1991; Urrutia *et al.*, 1991; Nédélec *et al.*, 1997; Humphrey *et al.* 2002). This out of equilibrium chemical activity in motor-filament solutions is known to lead to complex co-operative behaviour (Nédélec *et al.*, 1997; Nakazawa and Sekimoto, 1996; Kruse and Jülicher, 2000, 2003) including pattern formation and creation of dissipative structures. In addition, even in the *absence* of macroscopic patterning the mechanical response functions of such a mixture is strongly modified by the novel microscopic dynamics occurring due to the addition of motors to a solution of filaments. In this paper I will describe some recent work (Liverpool and Marchetti, 2003, 2005) attempting to study certain aspects of these motor-filament systems.

2 Dynamical model

The filaments are modelled as rigid rods of length l and diameter $b \ll l$. Each filament is identified by the position \mathbf{r} of its centre of mass and a unit vector $\hat{\mathbf{u}}$ pointing towards the polar end. Taking into account *filament transport*, the normalised filament probability distribution function, $\Psi(\mathbf{r}, \hat{\mathbf{u}}, t)$, obeys a conservation law,

$$\partial_t \Psi + \nabla \cdot \mathbf{J} + \mathcal{R} \cdot \mathbf{J}^r = 0, \quad (1)$$

where $\mathcal{R} = \hat{\mathbf{u}} \times \partial_{\hat{\mathbf{u}}}$ is the rotation operator. The translational and rotational currents \mathbf{J} and \mathbf{J}^r have diffusive terms, contributions coming from excluded volume and active contributions coming from the motors. Following Kruse and Jülicher (2000, 2003), the active contributions are obtained from relative velocities of interacting filaments due to the motors which are parametrised by the parameters α , β and γ , the rates for the various motor-induced translations and rotations (Fig. 1). These parameters α, β, γ are proportional to motor density. The contribution proportional to α depends on the separation of the centres of the filaments and results from a difference in motor activity between the ends and mid-points of the filaments. It tends to align the centres of mass and polar heads of the pair (see Fig. 1 (a)). The contribution proportional to β vanishes for aligned filaments and can separate anti-parallel filaments, as illustrated in Fig. 1 (c). This mechanism yields both translational and rotational currents. The γ term tends to rotate filaments until they are parallel or antiparallel.

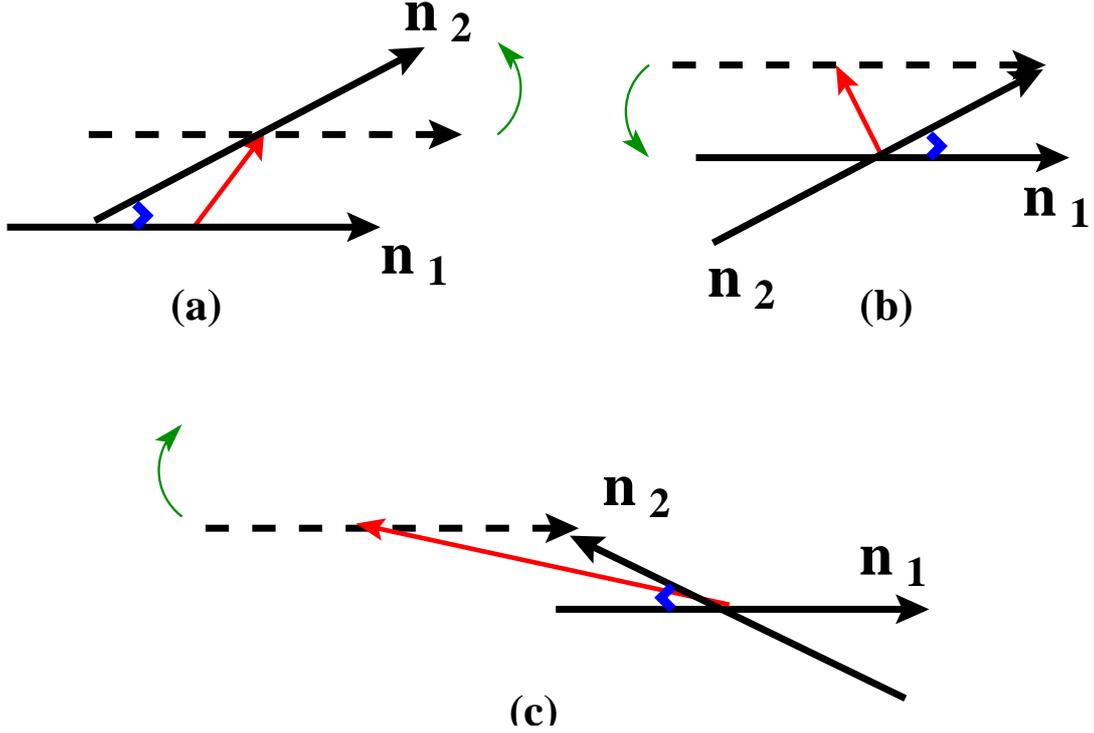


Figure 1: Cartoons of motor-induced filament interactions, viewed from the rest frame of filament 2. The angular bracket connecting each pair of filaments represents the motor. A thick and a dashed arrow show the position of filament 1 before and after translation, respectively. In each case the translation is followed by a rotation at a rate γ in the direction indicated by the curved arrow. (a) The contribution to \mathbf{v} proportional to α is along the direction of the relative displacement $\boldsymbol{\xi}$ of the centres of mass of the two filaments (thin arrow). The contribution to \mathbf{v} proportional to β is illustrated in (b) and (c) for two filaments with $\boldsymbol{\xi} = 0$ and $\hat{\mathbf{n}}_1 \cdot \hat{\mathbf{n}}_2 > 0$ (b) and $\hat{\mathbf{n}}_1 \cdot \hat{\mathbf{n}}_2 < 0$ (c). In both cases the translation at a rate β in the direction of $\hat{\mathbf{n}}_2 - \hat{\mathbf{n}}_1$ (thin arrow) tends to bring the polar heads of the two filaments to the same spatial location. In (b) the counterclockwise rotation aligns the filaments, while in (c) the clockwise rotation anti-aligns and separates them.

We focus on the filament dynamics on length scales large compared to their length, l where the filament dynamics can be described in terms of the filaments density $\rho(\mathbf{r})$, the local filament polarization $\mathbf{p}(\mathbf{r})$ and local filament 'nematic order' $\mathbf{Q}(\mathbf{r})$ defined as the first three (tensor) moments of the distribution $\Psi(\mathbf{r}, \hat{\mathbf{u}}, t)$, given by (in two dimensions)

$$\begin{pmatrix} \rho(\mathbf{r}, t) \\ \mathbf{p}(\mathbf{r}, t) \\ \mathbf{Q}(\mathbf{r}, t) \end{pmatrix} = \int d\hat{\mathbf{u}} \begin{pmatrix} 1 \\ \hat{\mathbf{u}} \\ \hat{\mathbf{u}}\hat{\mathbf{u}} - \frac{1}{2}\boldsymbol{\delta} \end{pmatrix} \Psi(\mathbf{r}, \hat{\mathbf{u}}, t). \quad (2)$$

Coarse-grained equations for ρ and \mathbf{p} can be obtained by using the expressions for the active and diffusive (passive) currents and writing the density $\Psi(\mathbf{r}, \hat{\mathbf{u}}, t)$ in the form of an exact moment expansion, and retaining only the first three moments in this expansion (Liverpool and Marchetti, 2003). Using the coarse-grained equations and linear stability analysis, we can study the phase diagram of the motor-filament system and identify the regions of parameter space for which it goes from homogeneous isotropic state to homogeneous polarized, nematic and inhomogeneous phases allowing us to obtain a phase diagram in terms of filament and motor densities for these states. We also identify new dynamic states of the non-equilibrium fluid which have no

equilibrium analogue. Finally we study the mechanical response of the filament/motor mixture to imposed deformation.

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