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# Patterns and intrinsic fluctuations in semi-dilute motor-filament systems

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**Abstract** – We perform Brownian dynamics simulations of molecular motor-induced ordering and structure formations in semi-dilute cytoskeletal filament solutions. In contrast to the previously studied dilute case where binary filament interactions prevail, the semi-dilute regime is characterized by multiple motor-mediated interactions. Moreover, the forces and torques exerted by motors on filaments are intrinsically fluctuating quantities. We incorporate the influences of thermal and motor fluctuations into our model as additive and multiplicative noises, respectively. Numerical simulations reveal that filament bundles and vortices emerge from a disordered initial state. Subsequent analysis of motor noise effects reveals: i) Pattern formation is very robust against fluctuations in motor force; ii) bundle formation is associated with a significant reduction of the motor fluctuation contributions; iii) the time scale of vortex formation and coalescence decreases with increases in motor noise amplitude.

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**Introduction.** – The dynamics and structural properties of out-of-equilibrium complex liquids, such as the cytoplasm of living cells, pose formidable challenges for fundamental physics and biology research. Moreover, the ability to predict and orchestrate self-assembly of biological filaments into desired microstructures is an important requirement for further development of hybrid biomechanical systems. Recently, pattern formation and intrinsic nonequilibrium dynamics in the cytoskeleton have been investigated both experimentally [1–9] and theoretically [10–18]. The main components of the cytoskeleton are protein filaments (rigid microtubules and semiflexible actin filaments), associated molecular motors (*e.g.* various types of kinesin or dynein motors for microtubules, myosin minifilaments for actin [19]), and the energy agent Adenosine Triphosphate (ATP). The chemical energy of ATP, converted by molecular motors into mechanical energy, enables motors to march on filaments and exert forces and torques that reorganize the filament networks.

A transition to a locally ordered state with a nonzero mean filament orientation – the isotropic-polar transition – occurs when a combination of motor and filament densities surpasses a certain threshold; the structures found experimentally in cytoskeletal solutions, like bundles, asters, and vortices, can be interpreted as the result of this ordering transition [13]. In the dilute limit, binary interaction models have proven efficient in describing the qualitative effects of motors on filament self-organization [13,20–22]. However, when the number of filaments per volume is larger than  $1/L^d$ , with  $L$  the filament length and  $d$  the spatial dimension, the semi-dilute regime is reached [23]. In this region, binary interaction models are insufficient because motors can bind a filament to several other filaments. Alternative macroscopic (hydrodynamic) models have been formulated [11,24] to study such systems, but they do not demonstrate a sufficient connection between the phenomenological parameters and the underlying microscopic mechanisms. Moreover, the validity of taking a macroscopic approach is in question as there is no rigorous scale separation between

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the size of the elementary object (filament) and the scale of the pattern.

In this study, we bridge the gap by formulating a model for the spatially inhomogeneous semi-dilute regime. A model for the spatially homogeneous case has been proposed and studied in ref. [25]. There, the authors show that an isotropic-polar transition can be either second or first order depending on the importance of a force-dependent, motor detachment rate. The model developed in this paper, however, accounts both for spatial degrees of freedom and for intrinsic motor force fluctuations. Most models of filament ordering dynamics incorporate noise, usually additive and thermal, which leads to diffusion and smoothening of concentration inhomogeneities. Active processes, by contrast, favor order; when motor forces overwhelm thermal fluctuations, an orientational transition occurs resulting in pattern formation. The assumption that motors always favor ordering, however, is not obvious; motors are microscopic objects (of scale 30 nm) that undergo intrinsic fluctuations in step time and force. These stepping fluctuations result in an additional noise which is *intrinsically multiplicative*. It has been estimated [15,16] (and evaluated by Brownian dynamics simulations [17]) that the fluctuation strength due to motors may exceed the thermal fluctuations by one or even two orders of magnitude. It is also known that single motor fluctuations are of the order of the mean force [26]. The effect of these substantial fluctuations on filament self-organization and broader cytoplasm dynamics is an important issue to be resolved.

In this work we assess the extent to which multiplicative noise affects the overall evolution of multi-filament networks. Using a Brownian dynamics-type stochastic simulation, we demonstrate that our model exhibits an ordering instability in the presence of motor noise, resulting in the emergence of bundles and vortices from initially disordered filament solutions. We show that both types of patterns are strongly affected by motor affinity and motor force fluctuations. Remarkably, in the course of bundle formation, the contribution of the motor fluctuations rapidly decreases and finally vanishes in the fully ordered state. Secondly, the rate of coarsening of smaller vortices into larger ones is shown to increase substantially as the mean amplitude of motor fluctuations increases. These findings suggest that active noises can encourage pattern formation. Such counterintuitive behavior is a novel illustration of the potential benefit of noise on biological functionality. The classical example in this framework, usually related to sensing, is the well-known stochastic resonance present in a variety of biological systems, *e.g.*, in hair cell stimulation in crayfish or predatory sensors in crickets [27]. Our work similarly delineates nontrivial effects of the intrinsic fluctuations of motor forces (or “active temperature”) on the macroscopic behavior of motor-filament solutions.

**Model of filament organization.** – A semi-dilute solution of microtubules (or short actin filament bundles)

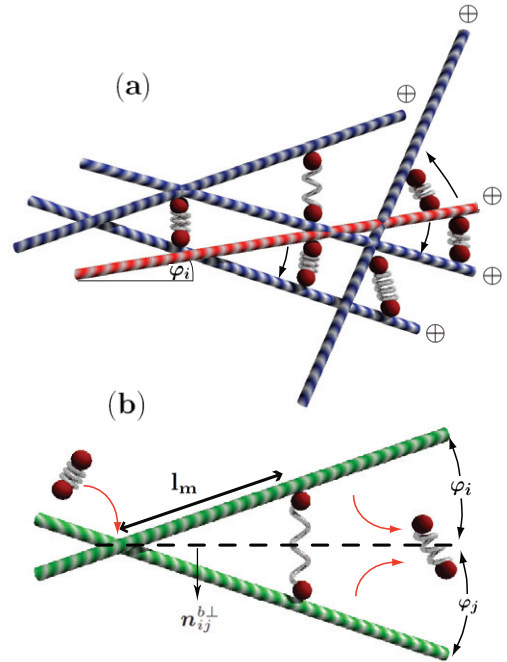


Fig. 1: (Colour on-line) (a) Illustration of a multi-filament configuration showing the interaction of the  $i$ -th microtubule (marked in red) with all other microtubules in motor contact. Respective forces acting on this filament are sketched as arrows. (b) Motor-mediated, binary microtubule interaction: motors attach at the rods' intersection point, zip across the rods causing alignment, and detach.

interacting via molecular motors is modeled as a collection of  $N$  stiff rods of fixed length  $L$ . For the sake of simplicity (and since most experiments are carried out in a quasi-two-dimensional geometry) we restrict our modeling to two spatial dimensions; the orientation of filament  $i$  can be described by a unit vector  $\mathbf{n}_i = (\cos \varphi_i, \sin \varphi_i)$ , or by the angle  $\varphi_i$  (with respect to the  $x$ -axis, see fig. 1). The position of the center of mass of the  $i$ -th filament is denoted by  $\mathbf{r}_i$ . For a system of  $i = 1 \dots N$  interacting filaments, we can write the equations of motion in the following Langevin-type form:

$$\dot{\varphi}_i = \zeta_r^{-1} \left[ l_m \mathbf{n}_i \times \sum_{j, i \cap j} \mathbf{n}_{ij}^{b\perp} F_{ij}^m + \xi_i^r \right], \quad (1)$$

$$\dot{\mathbf{r}}_i = \mathbf{M}(\varphi_i) \zeta^{-1} \mathbf{M}(-\varphi_i) \left[ \sum_{j, i \cap j} \mathbf{n}_{ij}^{b\perp} F_{ij}^m + \boldsymbol{\xi}_i \right]. \quad (2)$$

Equations (1) and (2) represent torque and force balances, respectively;  $F_{ij}^m$  is the magnitude of the force due to motor action on the filament pair  $(i, j)$  and is specified below. The force is assumed to be perpendicular to the bisecting line of two intersecting filaments  $(i, j)$ ; *i.e.* its direction is given by  $\mathbf{n}_{ij}^{b\perp} = (\sin \varphi_{ij}, -\cos \varphi_{ij})$ , where  $\varphi_{ij} = \frac{\varphi_i + \varphi_j}{2}$  is the bisector angle. In eq. (1),  $\zeta_r$  is the rotational drag coefficient and  $l_m$  is the average motor run length. The torque  $\xi_i^r$  is due to thermal

fluctuations that lead to rotational diffusion. In eq. (2), the term in brackets represents the sum of forces due to motor action and thermal fluctuations; these forces balance with the viscous drag, which is anisotropic due to the rod-like shape of filaments.  $\zeta^{-1}$  is the diagonal inverse friction matrix with components  $\zeta_{\parallel}^{-1}$  and  $\zeta_{\perp}^{-1}$ .  $\mathbf{M}(\varphi)$  is the rotation matrix which expresses parallel and perpendicular components in Cartesian components.  $\xi_i$  is the force due to thermal fluctuations, leading to translational diffusion. The sum,  $\sum_{j,i \cap j}$ , is taken over all intersecting filaments; motors are assumed to be attached close to the filament intersection points. In the derivation of eq. (1) we use a fixed “lever arm”  $l_m$  to compute the motor torques [28]. This simplification establishes an average motor forcing location at a distance  $l_m$  from the filament intersection point.

For the motor force we write

$$F_{ij}^m = \sigma_{ij} (\kappa l_m + \xi_j^m) \sin(\psi_{ij}), \quad (3)$$

with  $\psi_{ij} = \frac{\varphi_i - \varphi_j}{2}$  the angle between a filament and the bisecting line of the pair.  $\sigma_{ij}$  is the number of motors spanning the filament pair  $(i, j)$ . The first term in brackets is the average (*i.e.* deterministic) strength of the motor force and the stochastic term  $\xi_j^m$  describes fluctuations around the average. These fluctuations, unlike the thermal noise represented by  $\xi_i^r$  and  $\xi_i$ , are *intrinsically multiplicative*. For simplicity, we have assumed that every intersection of two filaments is symmetric; *i.e.* that motors act perpendicular to the bisecting line, see fig. 1b). For filament pair interactions, such configurations are rapidly achieved (see the discussions in refs. [20,25,28].) The number of motors  $\sigma_{ij}$  of the pair  $(i, j)$  includes an additional exponential form,  $\sigma_{ij} = \sigma_0 \exp(-E_{st}/k_B T)$ , where  $\sigma_0$  is the average number of motors per microtubule. The argument of the exponential represents the ratio of the motor stretching energy,  $E_{st} = \kappa a l |\sin(\frac{\varphi_i - \varphi_j}{2})|$ , to the thermal energy. This form is motivated by experimental studies [29] and was developed in ref. [30]. The stretching energy was estimated by using a typical distance  $l$  (of order 100 nm; along the microtubule) between the motor position and the intersection point of the two filaments [28].  $\kappa$  is the motor spring constant, known to be of the order of 200–400 pN/ $\mu\text{m}$  [31] for kinesin motors, and  $a$  is a molecular length scale (a few nm).

The torque  $\xi_i^r$  is due to thermal fluctuations which give rise to rotational diffusion [23] with diffusion coefficient  $D_r = \frac{k_B T}{\zeta_r}$  and  $k_B T$  the thermal energy. Analogously,  $\xi_i$  leads to anisotropic translational diffusion with  $D_{\parallel}$  and  $D_{\perp}$ . For these stochastic torques/forces we assume zero ensemble average and Gaussian distribution,  $\langle \xi_i^* \rangle = 0$  and  $\langle \xi_i^*(t) \xi_j^*(t') \rangle = 2k_B T \zeta_* \delta(t-t') \delta_{ij}$ , with  $* = r, \parallel, \perp$ . The active motor noise is motivated by experiments, *e.g.*, on actin-myosin systems [8], which showed that motor fluctuations shift the system away from thermodynamic equilibrium behavior. The effect of motor noise is captured in our model by the noise term  $\xi_j^m$ , which enters the motor

force. The respective fluctuation strength can be described by an effective temperature that exceeds the equilibrium thermodynamic temperature [8,15,17,18]. We assume  $\langle \xi_i^m(t) \rangle = 0$  and  $\langle \xi_i^m(t) \xi_j^m(t') \rangle = 2 \frac{k_B T_a \zeta_r}{l_m^2} \delta(t-t') \delta_{ij}$ . Note that the noise amplitude contains  $T_a$ , which is the effective (or active) temperature; it can be estimated as  $T_a = \frac{\langle F \rangle \langle L \rangle}{k_B}$ , with the mean motor force  $\langle F \rangle$  and the motor step length  $\langle L \rangle$ . Using experimental values for kinesin,  $\langle F \rangle = 5$  pN and  $\langle L \rangle = 8$  nm [32], one estimates  $T_a \simeq 10T$  in agreement with refs. [8,15,17].

**Evolution of multi-filament state.** – In this section, we focus on the question of whether polar structures—bundles and vortices—form in the presence of active motor fluctuations. The model given by eqs. (1) and (2) represents a system of  $3N$  equations that is highly nonlinear and nonlocal. We evolve the system using a stochastic simulation procedure. First, the independent variables are rescaled as follows,  $\tilde{\mathbf{r}}_i = \mathbf{r}/L$  and  $\tilde{t} = (k_B T/\zeta_r) t$ . Drag coefficients<sup>1</sup> have been scaled by  $\zeta = \zeta_{\parallel}$  and we introduced the rescaled motor stiffness  $\tilde{\kappa} = (l_m L/k_B T) \kappa$ .

The dimensionless versions of eqs. (1) and (2) are then investigated as follows. First, the system is initialized by randomly distributing  $N$  filaments (of unit length due to rescaling) on a circle. Typical radii used in simulations are in the range  $R = 10$ –12. To study the semi-dilute regime,  $N$  should be chosen so that initially, there are multi-filament intersections. Typically a random configuration of 1000–4000 filaments on a circle of  $R = 12$  initially produces an average of 1–3 intersections per filament. For the time evolution of the multi-filament state, the following algorithm is implemented: for every time step, all filament intersections are located. Next, we compute the total force,  $\mathbf{F}_i = \sum_{j,i \cap j} \mathbf{n}_{ij}^{\perp} F_{ij}^m$ , and the total torque,  $l_m \mathbf{n}_i \times \mathbf{F}_i$ , acting on each filament  $i$ , which accounts for all motor-mediated interactions, including the fluctuating motor forces. Finally, the filament orientations and center-of-mass positions are updated according to eqs. (1) and (2), accounting for the thermal noise contributions and the rotation matrices.

Simulations show two dominant modes of filament reorganization: first, if few filaments are interacting, *e.g.* a pair, they rotate to decrease the intersection angle while the center of mass of the pair remains constant. These dynamics are anticipated from binary interaction models and have been extensively discussed (including the explicit effects of multiple motors in ref. [28]). A second collective mode of reorganization occurs when a local preferred orientation prevails, given by several filaments pointing in a similar direction. One (or a few) additional filament(s) interacting with this locally oriented state will effectively be transported over this region until it finally,

<sup>1</sup>The drag coefficients are defined as [23]:  $\zeta_r = \frac{\pi \eta L^3}{3 \ln(L/b)}$ ,  $\zeta_{\parallel} = \frac{2\pi \eta L}{\ln(L/b)}$  and  $\zeta_{\perp} = 2\zeta_{\parallel}$ . Here,  $\eta \approx 0.005$  pNs/ $\mu\text{m}^2$  is the solvent viscosity,  $L \approx 10$ –15  $\mu\text{m}$  and  $b = 24$  nm are the microtubule’s length and diameter, respectively.

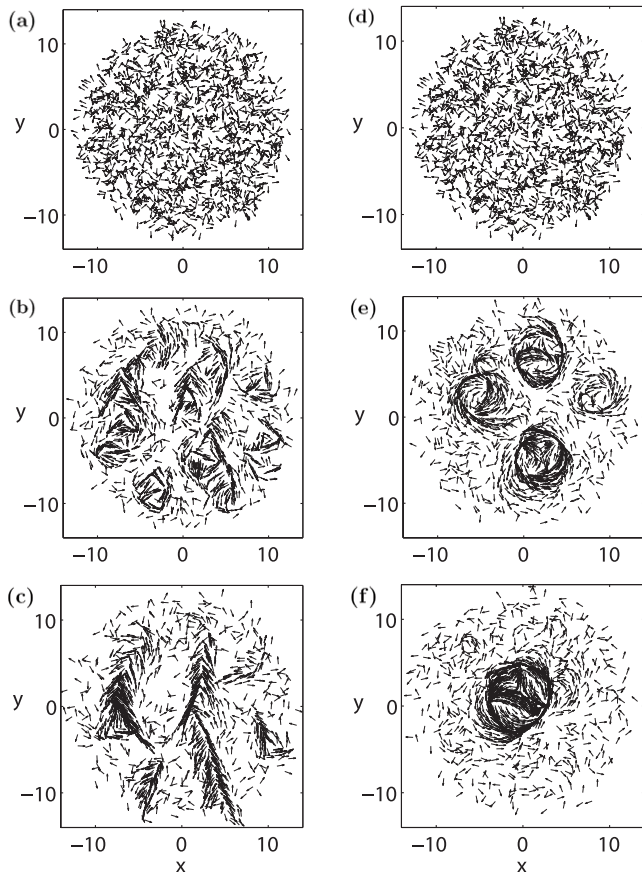


Fig. 2: Select simulation results: (a)–(c) snapshots of bundle formation at times (a)  $t=0$ , (b)  $t=180$  and (c)  $t=450$ . Simulation parameters are  $\tilde{\kappa}=300$ ,  $\sigma_0=0.5$ ,  $l_m/L=0.1$  and  $T_a/T=10$ . Bundles tend to form for larger values of the motor affinity parameter  $l_m/L$ . (d)–(f) Simulation of vortex formation and coarsening for smaller values of the motor affinity parameter,  $l_m/L=0.005$ . Snapshots are taken at times (d)  $t=0$ , (e)  $t=170$  and (f)  $t=370$ . Other parameters are as in (a)–(c).

when reaching the boundary of the oriented region, aligns with the oriented state or escapes.

**Pattern formation in the presence of motor noise.** – Figures 2(a)–(c) and 2(d)–(f) show bundles and vortices formed from an initially disordered semi-dilute filament solution—even in the presence of substantial ( $T_a/T=10$ ) motor fluctuations. The patterns formed are much more pronounced and stable as compared to those obtained from models accounting for only binary interactions, cf. the recent Monte Carlo simulation study [33].

Vortices in particular tend to coarsen and finally coalesce in the course of time. The self-organization dynamics and the types of patterns are very sensitive to the choice of parameters within the physical ranges. We have found that the primary control parameter governing the *type* of pattern formed is  $l_m$ , which describes the typical (average) distance between the motors’ position and the actual filament intersection point. In the model

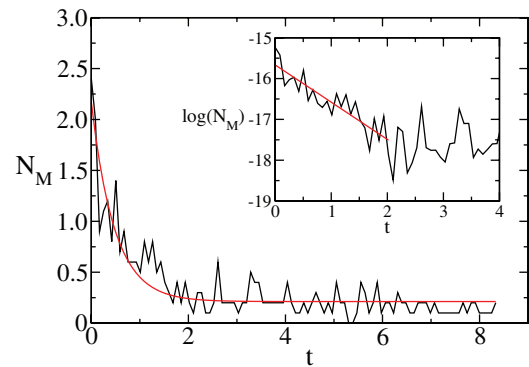


Fig. 3: (Colour on-line) Time evolution (in units of the rotational time) of active fluctuations  $N_m$  during the course of bundle formation. For the given parameters, small bundles form within twice the rotational time and concomitantly the fluctuation magnitude decreases approximately exponentially. For longer times, bundles slowly aggregate and the noise decreases slowly toward a small, constant value.

for multiple motors on a filament pair developed in ref. [28], it corresponds to the typical extension of the cluster of multiple motors around filament intersection points and is thus also related to the average number of motors per filament. The parameter  $l_m$ , referred to in the following as the “motor affinity parameter”, enters both the motor torque, where it acts as the lever arm, and the motor force, where it determines the motor extension. If this distance is small with respect to the filament length, vortices prevail while high values lead to bundles. There is, however, a sizeable range of  $l_m$ -values ( $l_m/L \approx 0.01$ – $0.1$  for the parameters given in fig. 2) that leads to intermediate vortices followed by long time bundle formation.

The rescaled motor stiffness  $\tilde{\kappa}$  affects the *size* of patterns formed (recall that  $\tilde{\kappa} = (l_m L/k_B T) \kappa$ ): low  $\tilde{\kappa}$  yields smaller structures (comprised of 10–20 filaments) which slowly coarsen, while large  $\tilde{\kappa}$  induces fast formation of large structures (comprised of hundreds to thousands of filaments). Finally, low initial filament densities (small  $N/\pi R^2$ , but still semi-dilute) and low average numbers of motors per filament  $\sigma_0$  (*i.e.* smaller total motor number) both lead to slow coarsening dynamics of the structures, of similar type as studied in ref. [22]. These assertions are hard to quantify due to the magnitude of noises. The trends, however, prevail in a large region of the parameter space:  $\kappa = 1$ – $500$ ,  $\sigma_0 = 0.1$ – $5$ ,  $l_m/L \approx 0.001$ – $0.7$ .

Another interesting phenomenon is the evolution of the overall motor fluctuation strength in the course of time. The square of the total force fluctuations (total fluctuation power) can be extracted from eq. (2) and is given by

$$N_m = \sum_{i,j} \left( \sigma_{ij} \frac{l_m}{L} \frac{T_a}{T} \sin \psi_{ij} \cos \psi_{ij} \right)^2. \quad (4)$$

Figure 3 indicates that this measure for the overall fluctuation strength decays rapidly as bundles form. Such

behavior suggests that larger motor forcing fluctuations (represented by a large multiplicative noise amplitude) are not likely to destroy pattern formations. By contrast, increases in thermal fluctuations slow down and eventually destroy structures. We verified this prediction for bundle formation with active fluctuations in the range of  $T_a/T = [1, 1000]$ . For vortices, the question is more subtle since vortices are comprised of filaments with a preferred angle with respect to each other, and thus the active fluctuations do not decay as rapidly, and can even increase. Our simulations do show, however, that the coarsening of smaller vortices into larger ones occurs on a faster time scale with increased multiplicative noise amplitude. The largest increase in coarsening speed is seen for  $T_a/T$  growing in the range of 1–100. This trend is seen until  $T_a/T$  crosses an upper threshold and destroys all pattern formations.

Finally, we have found that vortices are less pronounced or disappear completely if the anisotropy in viscous friction is neglected (*i.e.* if one chooses  $\zeta_{\parallel} = \zeta_{\perp}$ ). This behavior has been predicted by binary interaction models [20] and remains true in the semi-dilute regime. The parameter ranges for vortex and bundle formation found in our model are in good agreement with *in vitro* experiments and previous binary interaction models. Specifically, experiments on self-organization in protein-filament systems have shown that bundles form at high concentrations of motor and cross-linking proteins while vortices form at low concentrations [2,3]. Simulations of binary interaction models have displayed similar trends [21]. We do not see asters in our simulations because our models do not account for interaction anisotropy when describing motor-induced alignment.

**Conclusions.** – The effects of both active and thermal fluctuations on self-organization have been studied within the context of active cytoskeletal processes. In this study, we focused on the emergence of coherent structures from initially disordered, semi-dilute motor-filament solutions. We developed a model that accounts for multiple motors binding a filament to several other filaments, in contrast to dilute solutions with binary interactions. A generic multiplicative noise – due to intrinsic fluctuations in motor forcing – was incorporated into the model in a natural way.

Stochastic simulations revealed that filament bundles and vortices emerge in the presence of substantial motor noise. The types of structures are governed primarily by the “motor affinity parameter,” which enters through the motor-mediated forces and torques between filaments. The patterns are in qualitative agreement with previous binary interaction models [13,20–22] and *in vitro* experiments [2–4]. Additional analysis of the ordering dynamics showed a qualitative difference between the action of multiplicative motor force fluctuations and additive thermal fluctuations. Specifically, we found that bundle formation was accompanied by a rapid decay in the motor fluctuation strength. Moreover, the characteristic speed of vortex formation and coalescence increased

substantially as the motor fluctuation amplitude  $T_a/T$  increased; this behavior prevailed until a threshold was crossed and pattern formation was inhibited. These findings imply a counter-intuitive conclusion: substantial multiplicative motor fluctuations do not inhibit but rather promote pattern formation by helping filaments to explore the space and create new filament intersections. In contrast, an increase in the additive (thermal) noise consistently slows down or destroys structure formations.

Several open questions remain. First, our current model does not produce aster patterns that have been experimentally observed [2]. This is due to the absence of an interaction anisotropy [13], which can be included in further studies. Second, further analytical treatment of the proposed model may help to determine whether the switch from a continuous to a discontinuous transition to alignment persists in the spatially inhomogeneous case. This phenomenon related to the force-dependent detachment of motors has been suggested recently by a model for the homogeneous case [25]. Finally, the influence of intrinsic multiplicative noise on pattern formation and the modeling formalisms developed in this study have potential applications to several other physical problems. A few examples include the self-assembly of charged nano-particles or vibrated granular materials [34]. Further refinement and modifications of the proposed modeling framework could provide deeper insight into a wide range of physical problems.

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