Actively Stressed Marginal Networks

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We study the effects of motor-generated stresses in disordered three-dimensional fiber networks using a combination of a mean-field theory, scaling analysis, and a computational model. We find that motor activity controls the elasticity in an anomalous fashion close to the point of marginal stability by coupling to critical network fluctuations. We also show that motor stresses can stabilize initially floppy networks, extending the range of critical behavior to a broad regime of network connectivities below the marginal point. Away from this regime, or at high stress, motors give rise to a linear increase in stiffness with stress. Finally, we demonstrate that our results are captured by a simple, constitutive scaling relation highlighting the important role of nonaffine strain fluctuations as a susceptibility to motor stress.

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The mechanical properties of cells are regulated in part by internal stresses generated actively by molecular motors in the cytoskeletal filamentous actin network [1]. On a larger scale, collective motor activity allows the cell to contract the surrounding extracellular matrix, consisting also of biopolymer networks. Experiments show that such active contractility dramatically affects network elasticity, both in reconstituted intracellular F-actin networks with myosin motors [2–5] and in extracellular matrices with contractile cells [6]. The dynamics and elasticity of active biopolymer networks have been studied theoretically using long-wavelength hydrodynamic approaches [7] as well as affine models [8–10]. These approaches, however, fail to describe highly disordered networks. There is also experimental evidence that cytoskeletal networks may be unstable or only marginally stable in the absence of motor activity [11]. In such cases, networks are expected to be governed by highly nonuniform, soft or floppy modes of deformation that may lead to a fundamental breakdown or failure of continuum elasticity [12]. Importantly, motor-induced contractile stresses can be expected to couple to these soft modes [13], giving rise to a nonlinear elastic response that is distinct from the nonlinearities arising from single fiber elasticity that have been considered in previous models. Moreover, such a coupling to local soft modes of the network may call into question the equivalence of internal (motor) and external stress, a tacit assumption in the analysis of recent in vitro experiments [2,4].

Here, we introduce a simple model to study the effects of motor generated stresses on the elastic properties of disordered fiber networks. Networks are formed by cross-linked straight fibers with linear stretching and bending elasticity. These fibers are organized on a face centered cubic (fcc) lattice in which a certain fraction of the bonds can randomly be removed. This allows us to explore a wide range of network connectivities, 0 ≤ z ≤ 12. Motor activity is introduced by contractile, static, and strain-independent force dipoles acting between neighboring network nodes. We find that motors can stabilize the elastic response of otherwise floppy, unstable networks. The motor stress also controls the mechanics of stable networks above a characteristic threshold, in the vicinity of which the network exhibits critical strain fluctuations. We develop a quantitative effective medium theory (EMT) to describe the elastic response of these systems. Interestingly, the network’s stiffness is controlled by a coupling of the motor induced stresses to the strain fluctuations. This coupling gives rise to anomalous regimes at the stability thresholds, at which network criticality is reflected in both divergent strain fluctuations and anomalous dependences of the network mechanics on stress. In these critical regimes, the shear modulus depends nonlinearly on both motor stress and single filament elasticity [6,13–15]. Interestingly, this dependence on internal motor stress differs qualitatively from that of an applied external stress.

A key parameter that characterizes fiber networks is the mean coordination number, z. Other network properties that have been found to affect the elastic properties of such networks include a jamming geometry [16] or a divergence of the average fiber length [17,18], neither of which is considered here. Although the network is connected above a threshold z_{cond} ≃ 2, it only becomes rigid above a higher rigidity threshold z_{r} ≃ 3.4 [12]. This threshold is due to the bending rigidity of the individual fibers and it lies below the central-force rigidity threshold, z_{CF} ≃ 6, for a spring-only network. In general, when some fraction of the bonds are under stress, additional constraints are introduced [19]. More formally, these constraints appear as scalar terms in the Hamiltonian [20] that can shift the various rigidity thresholds in the system. In random spring networks, for example, this can be realized by applying finite network deformations; this has been...
studied in spring networks [21–23] where the actual rigidity
threshold shifts continuously to lower values with the
applied external strain. Under such external deformations,
the internal stress is free to adopt the most favorable
distribution. By contrast, motors impose a fixed distribu-
tion of internal stress, which may lead to a qualitatively
different network mechanics.

To provide insight into the elasticity of fibrous networks
with contractile internal stresses, we use a model of fibers
organized on a fcc lattice. By removing lattice bonds with a
probability 1 − p, we tune the average coordination num-
ber, \( z = Zp \), where the maximum connectivity \( Z = 12 \) for
the undiluted lattice. Motors are introduced as contractile
force dipoles and are inserted randomly with a probability
\( q \). The fibers are modeled as linear elastic beams with a
stretching modulus \( \mu \) and bending rigidity \( \kappa \). Using units
in which \( \ell_0 = \mu = 1 \), the total energy can be written as

\[
H = \frac{1}{2} \sum_{(ij)} P_{ij} (|r_{ij}| - 1)^2 + \frac{\kappa}{2} \sum_{(ijk)} P_{ij} P_{jk} \left( |r_{ij} \times r_{jk}| / |r_{ij}||r_{jk}| \right)^2
+ \int \sum_{(ij)} Q_{ij} |r_{ij}|
\]

(1)

where, \( r_{ij} = r_i - r_j \) and \( r_i \) denotes the position of \( i \)-th
node, and \( P_{ij} = 1 \) for present bonds or \( P_{ij} = 0 \) for
removed bonds. The first sum extends over neighboring
pairs of vertices. The crosslinks themselves do not contrib-
ute a torsional stiffness and, thus, the second sum only
extends over coaxial nearest neighbor bonds on the same
fiber. The last term represents the work performed by the
motors, where \( Q_{ij} = 1 \) if a motor acts between nodes \( i \) and
\( j \) and \( Q_{ij} = 0 \) otherwise.

To develop a mean-field, EMT that captures the disor-
dered nature of this model—including internal stresses—
we extend the theory for the linear mechanical response of
disordered spring networks [24–26]. In our EMT approach
we ignore the bending contribution (\( \kappa = 0 \)), allowing us
to circumvent the difficulties involved in an EMT with
three-point bending interactions [12,27,28]. Our EMT is
based on a mapping between the disordered network and
an ordered one with an effective elastic constant, yet with
the same underlying lattice geometry and under the same
internal stress as the original disordered system, denoted
by \( \sigma_M \). The effective elastic constant, \( \tilde{\mu}(\sigma_M) \), is
determined by a self-consistency condition; the local distor-
tion in the effective medium induced by replacing a bond,
selected randomly from the disordered system, should
vanish on average. For a general disordered network this
procedure yields an implicit expression for the effective
stretch modulus [29]

\[
\int_0^\infty \frac{\mu_{ij} - \tilde{\mu}(\sigma_M)}{\mu_{EM} + \mu_{ij} - \tilde{\mu}(\sigma_M)} \mathcal{P}(\mu_{ij}) d\mu_{ij} = 0,
\]

(2)

where \( \mu_{EM}^{-1} \) equals the displacement of a bond in the
unperturbed effective medium due to a unit force acting
along the bond, \( \mu_{ij} \) is the stretching modulus between
nodes \( i \) and \( j \), and \( \mathcal{P}(\mu_{ij}) \) is the probability density of
the moduli in the disordered system. For the case of a
diluted fcc lattice considered here, \( \mathcal{P}(\mu_{ij}) = p \delta(\mu_{ij} - 1) +
(1-p) \delta(\mu_{ij}) \), we find an effective shear modulus

\[
G_{EM} = \frac{5\sqrt{2}}{72} \tilde{\mu}(\sigma_M) + \frac{5}{6} \sigma_M,
\]

(3)

where \( \sigma_M = \sqrt{5} q f \) within the EMT.

While the full expression for \( \tilde{\mu}(\sigma_M) \) is long [29],
the scaling predictions of the EMT are simple. Even below
the central-force isotropic point, \( z_{CF} \), motor activity induces
a finite shear modulus. Far from \( z_{CF} \), \( G \sim G_0 + \sigma_M \), where
\( G_0 \) is the shear modulus of the unstressed network [30]. By
contrast, close to \( z_{CF} \) there is an anomalous scaling regime
\( G \sim \sigma_M^{1/2} / \mu_{EM}^{1/2} \).

To test the implications of the EMT and effects of a finite
bending rigidity, we simulate fiber networks with \( \kappa > 0 \).
The shear modulus, \( G \), is determined by applying a shear
strain along the 111-plane using Lees-Edwards periodic
boundary conditions and energy minimization by a con-
jugate gradient algorithm [31]. First, we consider the high
motor density limit \( q \approx 1 \). The dependence of \( G \) on motor
stress and connectivity is shown in Figs. 1(a) and 1(b). Ex-
cept where \( G \) is governed by \( \kappa \), e.g., for connectivities
between \( z_b \) and \( z_{CF} \) and \( \sigma_M \ll \kappa \), the EMT prediction is in
good quantitative agreement with the numerical results

FIG. 1 (color online). (a) Shear modulus vs motor stress for
various values of \( z \). Symbols represent the numerical data. The
dashed line represents a linear dependence and the grey region
indicates affine predictions for all presented coordination num-
bers (see Ref. [29] for comparison with EMT). (b) \( G \) vs \( z \)
for various values of \( \sigma_M \). Symbols represent numerical data. Thin,
solid lines represent EMT predictions. The grey line indicates
the affine prediction. (c) The differential nonaffinity \( \delta G \) vs motor
stress for various values of \( z \). (d) \( \delta G / z \) vs \( z \) for various values of
\( \sigma_M \) and for \( \kappa = 10^{-5} \). Dotted vertical lines in (b),(d) represent
the two rigidity thresholds, \( z_b \) and \( z_{CF} \).

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over a range of network parameters. This is to be expected, since the EMT does not account for fiber bending stiffness. The comparison is shown in Fig. 1(b) and Ref. [29].

Moreover, in the vicinity of \( z_{\text{CF}} \) for \( \sigma_M \gg \kappa \), we find a mixed regime, in which

\[
G \sim \mu^{1-\gamma'} \sigma_M^{\gamma'}
\]

with \( \gamma' \approx 0.4 \), whereas \( \gamma' = 1/2 \) in the EMT (Fig. 2). Such mixed regimes are known to arise in the vicinity of stability thresholds when additional, stabilizing interactions or fields are added, in such diverse systems as resistor and unstressed elastic networks [12,22,32]. In this model, motor stress can be thought of as an external field that stabilizes floppy networks. Consistent with this, we find an additional anomalous regime near the bending rigidity threshold, where

\[
G \sim \kappa^{1-\gamma} \sigma_M^{\gamma}
\]

with \( \gamma \approx 0.6 \) (Fig. 2).

We gain additional physical insight into the elastic properties of active networks with a scaling argument to estimate the amount of work that is performed by the motors when the system is sheared. The characteristic deformation of a single bond in such a network will be such that it avoids energetically costly stretching contributions.

Such deformations are oriented perpendicularly to the direction of the bond: the nonaffine contribution to this deformation can be estimated by

\[
\delta U_1 \sim \gamma \sqrt{\delta \Gamma},
\]

where the differential nonaffinity parameter is defined as

\[
\delta \Gamma = \frac{1}{\gamma'}\sum_k (\delta u_k - \delta u_k^{\text{aff}})^2.
\]

Here \( \delta u_k \) is the displacement of node \( k \) under an infinitesimal external shear \( \gamma \), \( \delta u_k^{\text{aff}} \) is the affine prediction and the average is taken over all network nodes. Interestingly, however, this is not the only relevant contribution to the deformation of the bond. The component of the affine deformation perpendicular to the bond does not contribute to bond-stretching energies to harmonic order and, thus, is not avoided. Importantly however, this deformation does contribute to the motor work. Therefore, the total work performed by the internal stress resulting from such deformations scales as

\[
\delta W \sim \sigma_M^{\gamma} \delta \Gamma + \sigma_M^{2} \gamma^2,
\]

implying the following relationship for the shear modulus:

\[
G \sim G_0 + \sigma_M \delta \Gamma + \sigma_M.
\]

The nonaffinity, \( \delta \Gamma \), depends on system parameters as shown in Figs. 1(c) and 1(d). As predicted by Eq. (7), we find that \( G - G_0 - \frac{5}{6} \sigma_M \) vs \( \sigma_M \delta \Gamma \) collapses onto a single line for all system sizes, as shown in Fig. 3(a). Interestingly, the scaling in Eq. (7) also suggests that \( \delta \Gamma \) can be interpreted as a susceptibility of the shear modulus to internal stress. Consistent with this, \( \delta \Gamma \) exhibits strong peaks close to both rigidity thresholds [Fig. 1(d)], which are critical points. At these points of marginal stability, we find that \( \sigma_M \) suppresses critical fluctuations, as shown by the marked reduction in \( \delta \Gamma \) in Fig. 1(c) with increasing motor stress. This further supports the interpretation of \( \sigma_M \) as a field that takes the system away from criticality and suggests a power law dependence of \( \delta \Gamma \) on \( \sigma_M \). This dependence, taken together with Eq. (7), can account for the observed scaling of \( G \) in Eqs. (4) and (5) provided that

\[
\frac{1}{\gamma'} = \frac{1}{\gamma} + \frac{1}{\gamma'}.
\]
of the threshold stress, the network acquires a finite shear rigidity. Near a point. Concurrent with the development of a macroscopic stress. This is in contrast with the stiffening behavior of prestressed elastic networks [33,34]. However, $G$ scales sublinearly with the global stress induced by motors. Similar stress-stiffening of floppy networks below marginal stability is also found beyond a threshold in the motor density, indicating a surprising generality of critical fluctuations and divergent susceptibility for systems below the usual rigidity percolation point.

This work demonstrates that motor activity controls the elastic properties of disordered networks by coupling to the differential nonaffine fluctuations in the deformation field. This coupling makes elastic deformations more affine and stabilizes the network. Far from the elastic critical points this coupling leads to linear stiffening as a function of the motors stress, as has been observed in several studies of prestressed elastic networks [33,34]. However, $G$ scales sublinearly with the global stress induced by motors. Similar stress-stiffening of floppy networks below marginal stability is also found beyond a threshold in the motor density, indicating a surprising generality of critical fluctuations and divergent susceptibility for systems below the usual rigidity percolation point.

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$\delta \Gamma(z_b) \sim \left(\frac{K}{\sigma_M}\right)^{1-y}$ and $\delta \Gamma(z_{CF}) \sim \left(\frac{\mu}{\sigma_M}\right)^{1-y'}$.

To confirm this, we directly observe scaling of $\delta \Gamma$ consistent with Eq. (8) and the previously observed exponents $y$ and $y'$, as shown in Figs. 2(c) and 2(d).

The schematic phase diagram for the high-motor density limit is shown in Fig. 3(b). Away from the stability thresholds the shear modulus scales linearly with the active stress. This is in contrast with the stiffening behavior of externally deformed networks, for which the dependence of the differential elastic modulus goes as the square root of the external stress [22,23]. Thus, there is not necessarily a quantitative correspondence between internally and externally stressed networks, in contrast to suggestions in prior work [4].

Finally, we explore the role of inhomogeneity in the distribution of active motors, which shows that critical behavior is not limited to the critical points associated with rigidity percolation. We model inhomogeneous motors by considering the range $q<1$ for different values of $z$ well below the rigidity percolation point, $z < z_b$. In this case the motors only induce a macroscopic stress when the motor density exceeds a $z$-dependent threshold, $q_c(z)$, as shown in Fig. 4(b). Importantly, the effective connectivity at this threshold remains well below the isostatic point. Concurrent with the development of a macroscopic stress, the network acquires a finite shear rigidity. Near the threshold $q_c$, the motor-induced stress falls significantly below the mean-field prediction ($\sigma_M = \sqrt{8q f}$) and depends nonlinearly on $q$. Interestingly, in this regime ($\sigma_M \ll \sqrt{8q f}$) the nonaffine fluctuations become large [see Fig. 4(d)], diverging with motor stress with an exponent close to $-0.22$, as shown in Fig. 4(c). Such a divergence, taken together with Eq. (7), implies an anomalous, sublinear exponent 0.78, in Fig. 4(a). This happens even when the mean coordination number of the network is well below the rigidity percolation point. Thus, criticality in the form of a divergent susceptibility is not limited to the marginal points, $z_b$ and $z_{CF}$, but occurs over range of connectivities below $z_{CF}$.

FIG. 4 (color online). The role of inhomogeneity in the motor distribution for different values of $z$ [see legend in panel (a) for all plots]. (a) Shear modulus vs normal stress induced by the motors. Solid line represents the power law of 0.78, while the dashed line indicates the mean-field predictions. (b) The normal stress vs motor occupation probability $q$. Solid line represents the mean-field prediction, $\sigma_M = \sqrt{8q f}$. (c) The differential nonaffinity measure vs $\sigma_M$ for the same parameters as in (a). The solid line represents the power law of $-0.22$. (d) $\delta \Gamma$ vs $q$. For all the data in this figure $f = 10^{-4}$ and $\kappa = 10^{-5}$.

$\delta \Gamma(z_b) \sim \left(\frac{K}{\sigma_M}\right)^{1-y}$ and $\delta \Gamma(z_{CF}) \sim \left(\frac{\mu}{\sigma_M}\right)^{1-y'}$.

(8)
[30] In all scaling relationships with additive contributions, unknown numerical prefactors are omitted.