

Stress Reorganization and Response in Active Solids

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We present a microscopic model of a disordered viscoelastic active solid, i.e., an active material whose long time behavior is elastic as opposed to viscous. It is composed of filaments, passive cross-links, and molecular motors powered by stored chemical energy, e.g., actomyosin powered by adenosine triphosphate. Our model allows us to study the collective behavior of contractile active elements and how their interaction with each other and the passive elastic elements determines the macroscopic mechanical properties of the active material. As a result of the (un)binding dynamics of the active elements, we find that this system provides a highly responsive material with a dynamic mechanical response strongly dependent on the amount of deformation.

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Introduction.—Active materials are condensed matter systems self-driven out of equilibrium by components that convert stored energy into movement. They have generated much interest in recent years, both as inspiration for a new generation of smart materials and as a framework to understand aspects of cell motility [1–4]. The eukaryotic cell cytoskeleton provides a paradigmatic example of such an active material. It consists of a network of protein filaments and associated proteins such as cross-links binding filaments together and molecular motors consuming chemical energy to exert forces on filaments [5]. It shows a rich variety of behaviors including mechanical tasks involved in cell locomotion and division. Because of its complexity a complete physical description of the cell cytoskeleton is not currently possible. However, a fruitful direction of progress comes from experiments on simplified *in vitro* systems of a small number of its components (namely specific filaments, cross-links, and molecular motors) [6–12].

The cytoskeleton is a viscoelastic material and the appropriateness of considering it as a liquid or solid depends on time scale. For cellular processes occurring on very long time scales, large scale network remodeling due, e.g., to (un)binding cross-links leads to fluidlike behavior. There is now a large body of theoretical work considering aspects of cytoskeletal dynamics by modeling it as an oriented active fluid, supplementing the equations of fluid mechanics with additional active stresses coupled to local orientational order [1,2,13–29]. Although appropriate for many cellular processes *in vivo*, recent mechanical experiments on simplified cytoskeletal extracts are done on time scales short compared to cross-link lifetimes, when the network behaves like a disordered solid [6–9,30,31]. To understand them requires an equivalent theoretical picture of active elastic solids [22,32–35]. To address this we develop a microscopic model of the interactions of stress generating elements (motors) and filaments in an elastic

material. Such models form an essential bridge between *in vitro* and *in vivo* observations, linking the macroscopic properties of the gel to the mechanochemical properties of its components.

We first present a generic description of the linear elasticity of an active solid, highlighting the changes in mechanical properties upon switching on activity. We then present a microscopic stochastic model of a one-dimensional disordered solid composed of both elastic and active elements, appropriate for describing a material on time scales for which the cross-links are fixed but the motor (un)binding dynamics are relevant. We investigate the collective dynamics of active and elastic elements, focusing on their steady state behavior. We obtain the statistical ground state (defined as the configuration when no external force is applied) of the active solid and also its active elastic modulus. As expected we obtain a contractile ground state but interestingly we find that taking account of (un)binding dynamics of the active elements leads to a larger contraction and a smaller elastic modulus. This has a spectacular effect on the dynamical mechanical response: for a specific range of deformation the stress response changes sign.

General linear elasticity.—For small deviations \mathbf{u} (with i th component u_i) from a ground state \mathbf{r}_0 , the free energy F of a passive linearly elastic body is quadratic in the local strain tensor $U_{ij}(\mathbf{r}) = \frac{1}{2}(\partial_j u_i + \partial_i u_j)$ (where $\partial_i = \partial/\partial x_i$) at position $\mathbf{r} = [\mathbf{r}_0 + \mathbf{u}(\mathbf{r})]$, i.e., $F = \int d\mathbf{r} [\frac{1}{2} E_{ijkl} U_{ij}(\mathbf{r}) U_{kl}(\mathbf{r})]$, where E_{ijkl} is the elastic modulus tensor. Under an external force density $\mathbf{f}(\mathbf{r})$, local force balance implies

$$\partial_j \sigma_{ij}^e = \frac{1}{2} E_{ijkl} (\partial_l \partial_j u_k + \partial_k \partial_j u_l) = -f_i(\mathbf{r}), \quad (1)$$

where $\sigma_{ij}^e(\mathbf{r}) = \delta F / \delta U_{ij}(\mathbf{r}) = E_{ijkl} U_{kl}(\mathbf{r})$ is the local stress tensor. The mechanical properties of an active material,

being out of equilibrium, cannot be obtained from a free energy. Its behavior must be constructed using dynamical arguments, respecting the conservation laws and symmetries of the system. For an isotropic active solid in a nonequilibrium steady state, the local force balance, Eq. (1), is modified by the addition of an active component σ^a to the stress tensor $\sigma = \sigma^e + \sigma^a$. This active stress for an isotropic material, has the form

$$\sigma_{ij}^a = \Delta\mu(\zeta\delta_{ij} + \mathcal{E}_{ijkl}U_{kl}) + O(U^2), \quad (2)$$

which are the only linear homogeneous terms allowed by symmetry. $\Delta\mu$ represents the chemical energy available in the system, derived from the chemical potential of adenosine triphosphate (ATP) hydrolysis and ζ and \mathcal{E}_{ijkl} are active parameters. This leads to a modification of the elastic constants \mathbf{E} to $\tilde{\mathbf{E}} = \mathbf{E} + \Delta\mu\mathcal{E}$ and the ground state strain in the unstressed state $\tilde{\mathbf{U}}_0 = -\zeta\Delta\mu\mathbf{E}^{-1}\mathbf{I}$. The change in ground state strain is due to the isotropic, pressurelike term in Eq. (2). The main aim of this work is to calculate the active parameters ζ and \mathcal{E}_{ijkl} from properties of the microscopic elements of the material. As a first step we consider a 1D model. From this model we derive the active elastic modulus \tilde{E} and ground state strain \tilde{U}_0 (in 1D we use the ground state displacement $\tilde{x}_0 = b_0\tilde{U}_0$).

Microscopic model.—We consider a 1D lattice of N sites representing passive cross-links, connected by bonds representing filaments, as depicted in Fig. 1 (bottom). Each site has one associated bond, labeled by $i = 1, \dots, N$, of length b_i and unstretched length b_0 , i.e., $x_i = b_i - b_0$ is the extension of bond i . The unstretched system length is $L_0 = Nb_0$ and undeformed volume $V = L_0A$ where A is the cross-sectional area. There are N_f filaments distributed on the bonds giving filament density as $\rho = N_f/N$. For mechanical stability in 1D, all bonds must be present to have a percolated system. Respecting this but allowing some disorder, we allow bonds to be either single, with fraction ϕ_1 , or double, with fraction $\phi_2 = 1 - \phi_1 = \rho - 1$. Assuming each filament is placed randomly the fraction of bonds with multiplicity r is given by $\phi_r = (1/N)^r (1 - 1/N)^{\rho N - r} (\rho N)! / [r!(\rho N - r)!]$. For our assumption of only single and double bonds to be valid with a 20% tolerance, the range of acceptable number densities is $1.6 < \rho < 2.2$ [36].

The filament polarity p is defined as the fraction p_R of bonds pointing right minus the fraction pointing left: $p = p_R - (1 - p_R)$. The number density of bound motors is given by $m = (\text{number of motors})/N$. Only antiparallel double bonds with a motor bound are active [32,34]. The fraction a of active bonds is therefore given by $a = 2p_R(1 - p_R)m\phi_2 = \frac{1}{2}(1 - p^2)m(\rho - 1)$. The architecture of the lattice sites and bonds is taken as constant, $\rho = \rho_0$, corresponding to fixed passive cross-links (we consider time scales short compared to their lifetimes).

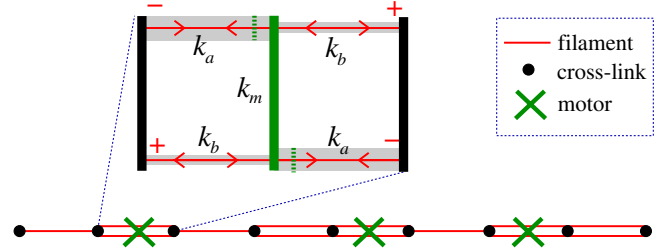


FIG. 1 (color online). Schematic diagram of a disordered 1D lattice consisting of single and double bonds representing filaments (lines), cross-links (dots), and motors (crosses). Inset: cartoon of the model of an active bond discussed in section entitled “The contractile active element.” Antiparallel filaments (horizontal lines with polarity marked by \pm) are linearly elastic with spring constants $k_{a,b}$, and arrows show filament sections under compression or extension. The motor unit (middle vertical line) can also be elastic with k_m . Dashed lines indicate initial position of the motor before stepping and extension or compression.

Discrete variable for active bonds.—We treat the dynamics of the motors explicitly by introducing a discrete occupation variable n_i for each bond i such that

$$n_i = \begin{cases} 1 & \text{if bond } i \text{ active (motor bound)} \\ 0 & \text{if bond } i \text{ passive (motor unbound)} \end{cases},$$

with stochastic switching between states $n = 0$ and $n = 1$ and the probability of being in state $n = l$ being $P_l(t) = \langle \delta_{nl} \rangle_n$ with dynamics

$$\partial_t P_1 = -k_u P_1 + k_b P_0, \quad P_0 = 1 - P_1, \quad (3)$$

where k_b and k_u are the binding and unbinding rates, respectively. We ignore the effect of mechanical forces on k_b and k_u but note that the stochastic dynamics of the bonds will depend on whether a motor is bound or not.

The microstates of our system are then the set of displacements $\{x_i\}$ and motor occupation numbers $\{n_i\}$ of the bonds $i \in \{1, \dots, N\}$. The probability of finding the system in a particular microstate is denoted $P(\{x_i\}, \{n_i\}, t)$. If the dynamics of n_i (binding and unbinding of motors) is the slowest process, i.e., fluctuations in x_i relax faster, then $P(\{x_i\}, \{n_i\}, t) = P(\{x_i\}|\{n_i\}; t)P(\{n_i\}, t)$, where $P(\{x_i\}|\{n_i\}; t)$ is the conditional probability of finding a set of $\{x_i\}$, given the set of occupation numbers $\{n_i\}$. We can describe the dynamics $P(\{n_i\}, t)$ using N uncoupled copies of Eq. (3) while the equation of motion for $P(\{x_i\}|\{n_i\}, t)$ is

$$\partial_t P(\{x_i\}|\{n_i\}) = - \sum_{j=1}^N \frac{\partial J_j}{\partial x_j} \quad (4)$$

with $J_j = -D\partial P/\partial x_j + P(\{x_i\}|\{n_i\})g_j/\xi$, where D is the amplitude of the displacement fluctuations and ξ is a local

friction. The current J_j has a deterministic contribution from fluxes due to the forces g_j and a contribution from the fluctuations ($\propto D$). The forces g_j have an elastic and active part: $g_j(\{x_i\}, \{n_i\}) = -\partial H_{\text{elastic}}/\partial x_j - n_j f_m$, where f_m is the contractile active force exerted by a motor and the elastic energy, $H_{\text{elastic}} = \sum_{i=1}^N \frac{1}{2} k^{\text{eff}} x_i^2$ with $k^{\text{eff}} = (\phi_1 \frac{k}{2} + \phi_2 k) = \rho_0(k/2)$ the effective spring constant ($k/2$ is the spring constant of a single bond [37]). The steady state distribution can then be calculated as $P_{ss}(\{x_i\}|\{n_i\}) = (1/\mathcal{Z}(\{n_i\})) \exp[-\beta H]$, where $\beta^{-1} = D\xi \neq k_B T$ and $\mathcal{Z}(\{n_i\}) = \int \prod_{i=1}^N dx_i P_{ss}(\{x_i\}|\{n_i\})$ with

$$H(\{x_i, n_i\}) = H_{\text{elastic}} + \sum_{i=1}^N f_m n_i x_i.$$

Averages of physical quantities are as usual: $B(t) = \langle B(\{x_i\}) \rangle = \int \prod_{i=1}^N dx_i B(\{x_i\}) P(\{x_i\}|\{n_i\}, t)$, and in the steady state they can be obtained from derivatives of the generating functional $\ln \mathcal{Z}(\{n_i\})$, which must be averaged over $\{n_i\}$.

Mechanical response.—We now consider the mechanical response of the system to a macroscopic deformation $L_0 \rightarrow L_0 + \Delta L$, with $\Delta L = Nb_0 U$, thus defining a macroscopic strain U . Hence $U = (Nb_0)^{-1} \sum_{i=1}^N x_i$ [38] and the relevant generating functional

$$\mathcal{Z}(\{n_i\}, U) = \int \prod_i dx_i e^{-\beta H} \delta\left(\frac{\sum_i x_i}{Nb_0} - U\right). \quad (5)$$

We consider the evolution of the macroscopic stress $\sigma = \langle (AN)^{-1} \sum_{j=1}^N g_j \rangle_{n_i, x_i}$ with time after a step strain U .

In performing averages over $\{n_i\}$, we consider two limits determined by the time scales k_u^{-1}, k_b^{-1} .

(i) For $t \ll k_b^{-1}, k_u^{-1}$, the motors are frozen in a particular set of $\{n_i\}$; i.e., n_i are quenched. Macroscopic quantities can be calculated from derivatives of $\ln \mathcal{Z}(\{n_i\})$ averaged over $\{n_i\}$, $\mathcal{F}_{\text{qu}} = -(1/\beta) \langle \ln \mathcal{Z}(\{n_i\}) \rangle_{n_i}$. The average is done over the initial distribution of occupation numbers $P(\{n_i\}, t=0)$, taken to be the steady-state distribution $P_{ss}(\{n_i\})$ given in the Supplemental Material [39]. This gives the stress

$$\sigma^{\text{qu}} = \frac{1}{V} \frac{d\mathcal{F}_{\text{qu}}}{dU} = \frac{Nb_0}{V} (k^{\text{eff}} b_0 U + a_0 f_m), \quad (6)$$

where $a_0 = \frac{1}{2} m_0 (1 - p_0^2) (\rho_0 - 1) = k_b (k_u + k_b)^{-1}$ is the mean fraction of active bonds. The ground state displacement $\tilde{x}_0 = b_0 U_0 = -(a_0 f_m / k^{\text{eff}})$ (where U_0 is the strain for which $\sigma = 0$) and elastic constant $\tilde{E} = V(Nb_0)^{-2} (d\sigma/dU) = k^{\text{eff}}/N$. This is equivalent to a “mean field model” in which n_i is fixed to its average value a_0 .

(ii) For $t \gg k_u^{-1}, k_b^{-1}$, the motor variable n_i is annealed. We can average over $\{n_i\}$ in Eq. (5) and hence obtain averaged quantities from derivatives of

$\mathcal{F}_{\text{an}} = -(1/\beta) \ln \langle \mathcal{Z}(\{n_i\}) \rangle_{n_i}$, also averaged over $P_{ss}(\{n_i\})$. The stress $\sigma^{\text{an}} = (1/V) (d\mathcal{F}_{\text{an}}/dU)$ is given by (see the Supplemental Material [39] for details)

$$\sigma^{\text{an}} \approx \frac{Nb_0}{V} \{ [k^{\text{eff}} - a_0(1 - a_0)\beta f_m^2] b_0 U + a_0 f_m \},$$

leading to the ground state local displacement $\tilde{x}_0^{\text{an}} = -f_m a_0 / [k^{\text{eff}} - a_0(1 - a_0)\beta f_m^2] < \tilde{x}_0^{\text{qu}}$ and elastic constant $\tilde{E}^{\text{an}} = (1/N) [k^{\text{eff}} - a_0(1 - a_0)\beta f_m^2] < \tilde{E}^{\text{qu}}$ up to $O(f_m^2)$ [40]. These results are equivalent to taking $n_i = a$, where a fluctuates with a Gaussian distribution, $P(a) = (1/\sqrt{2\pi\nu_a^2}) e^{-[(a-a_0)^2/(2\nu_a^2)]}$ with mean a_0 and variance $\nu_a^2 = a_0(1 - a_0)/N$, where finite ν_a could reflect fluctuations in the polarity p as well as number of motors m .

Our results imply a rich variety of dynamic responses depending on the amount of deformation. Initially after a deformation, the material will respond with effective elastic properties given by the quenched motor variables but on longer time scales with that of the annealed motor variables. Over time the restoring stress can increase, decrease, or even change sign as $\sigma^{\text{qu}}(U) \rightarrow \sigma^{\text{an}}(U)$, depending on the amount of deformation applied. This can lead to apparent stress hardening or softening with time. We define hardening (softening) as a stress at long times that has a greater (lower) magnitude than the initial stress. It is worth noting that the mechanical response of this material is naturally asymmetric, with stretch different from compression. The classes of behavior are schematically described in Fig. 2. It is useful to define x_+ as the deformation when $\sigma^{\text{qu}}(x_+) = \sigma^{\text{an}}(x_+)$ and x_- where $\sigma^{\text{qu}}(x_-) = -\sigma^{\text{an}}(x_-)$. For $\Delta L > x_+$, the system softens (stress decreases) and does not change sign (denoted + in Fig. 2). For $\tilde{x}_0^{\text{qu}} < \Delta L < x_+$, it hardens (stress increases) without changing sign (+). For $\tilde{x}_0^{\text{qu}} > \Delta L > x_-$, the stress changes sign but the magnitude of the final stress is larger than that of the initial stress.

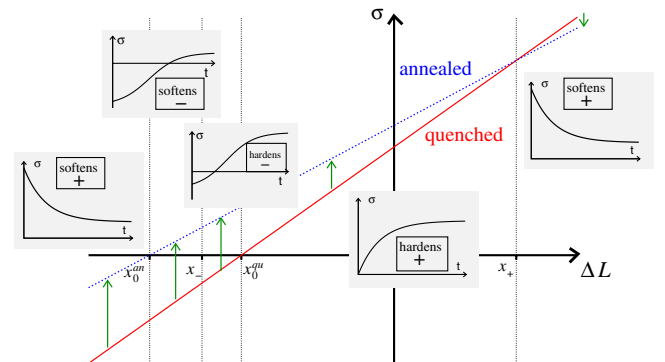


FIG. 2 (color online). Graph of the restoring stress σ versus the applied deformation ΔL . Arrows indicate direction of stress evolution. Gray insets: schematic drawings of $\sigma(t)$ showing decreasing (increasing) $|\sigma|$ over time softens (hardens) where $-$ indicates σ changes sign.

This would be perceived as dynamic hardening with a change of sign.

The contractile active element.—Finally we outline a model for the mechanics of an individual active bond in more microscopic detail. It is the linear limit of a more complex model [32]. As shown in the Fig. 1 inset, it is made up of a pair of antiparallel polar filaments linked by a motor cluster (as parallel filaments lead to sliding without force generation). In the absence of forces the filaments have length b_0 . The filaments are linearly elastic, with a segment of length l having spring constant $k(l) = k_0/l$ (springs in series). The motor cluster is made up of two motors connected by an elastic element of stiffness k_m , which we consider first as much stiffer than the filaments, $k_m \gg k$. The motors “slide” along the filaments towards the + end until the elastic forces in the cluster are equal to their stall force f_s [5]. In this stationary state, the two motors apply equal and opposite forces $\pm f_s$ to the two filaments at their respective attachment points, which each split a filament into two segments of length l_a and $l_b = b_0 - l_a$ with spring constants $k_{a,b} = k(l_{a,b})$. On average, the motor cluster is attached to the midpoint of the filaments, $l_a = b_0/2 + s$. The force f_s applied to the filaments leads to deformations $X_{a,b}$ of the two segments and a jump in the tensions $f_s = \tau_b - \tau_a$ between them, where $\tau_j = k_j X_j$ are the tensions in the respective segments $j = \{a, b\}$. Elasticity of the motor cluster implies $f_s/k_m = 2s + X_a - X_b$. When there is no external force applied ($\tau_a + \tau_b = 0$), the total deformation, $X = X_a + X_b$, is calculated as $X = -b_0 f_s^2 (4k_0^2)^{-1} [1 + 2k_0/(b_0 k_m)]$. This is negative for all finite k_0, k_m, f_s and therefore the active bond is always contractile. If $k_0 \rightarrow \infty$ (rigid filaments), $X \rightarrow 0$ as expected. The contractile force in the model above $f_m = -k^{\text{eff}} X$.

Let us now estimate typical time scales and moduli for a cytoskeletal extract such as actin-crosslinkers-myosin-ATP [6,41,42]. Segments between cross-links of typical length $b \sim 0.1 \mu\text{m}$ have a relaxation time $\tau_b \sim b^4 \eta / (k_B T l_p) \sim 10^{-6}$ s where $\eta \sim 10^{-3}$ Pa s is the viscosity of water and $l_p \sim 15 \mu\text{m}$ is the persistence length of actin [43–45]. Assuming $\tau_m \sim 1$ s [6,46], then $\tau_b \ll \tau_m$ as we have assumed above. The stall force $f_s \sim f_m \sim 2$ pN [47], $k^{\text{eff}} \sim k_B T l_p^2 / b^4$ [48], and $\beta^{-1} \sim k_B T / 10$ [6,49] can similarly be estimated.

Discussion.—We have developed and studied a microscopic stochastic model of a 1D disordered solid composed of elastic and active elements appropriate for time scales where the cross-links are fixed but the dynamics of motor (un)binding are important. We find that due to the (un)binding of motors, this active solid is a highly responsive material with a variety of different mechanical responses depending sensitively on the amount of applied deformation. This is due to the fact that the activity of motors leads to a contracted ground state and a modified elastic constant whose properties depend on the local (re)organization of

contractile elements. On time scales long compared to motor binding dynamics the contraction is greater and the material softer than on time scales shorter than the motor dynamics. This results in a variety of counterintuitive mechanical behaviors, e.g., initially after a deformation, the direction of elastic response can even be opposite in direction to that on long time scales [50]. This suggests that the rich variety of behavior shown by the cytoskeleton—its ability to adapt its properties to perform the mechanical tasks involved in cell division or cell locomotion—can be understood as a natural consequence of this type of collective dynamics.

While we have for reasons of clarity restricted ourselves to a one-dimensional model, it is natural to consider higher dimensions, in which empty bonds can be included as long as the density ρ remains above the percolation threshold for the chosen lattice. We note that if the density of filaments is reduced below the percolation threshold the system would appear to expand, since the network will break apart and lose contractility. We have studied the system to lowest order in $\Delta\mu$: to capture the behavior at high activity a number of other nonlinear effects must be considered [51]. Clearly including the force dependence of motor (un)binding rates $k_u(x_i)$, $k_b(x_i)$ can couple the rich behavior we have described above to external mechanical cues and lead to mechanical analogues of switches and logic gates. Our framework can therefore be the starting point for more complex and realistic models extended to time scales comparable to dynamics of the system architecture (lifetime of passive cross-links) and start to approach quantitative models of whole cell behavior.

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- [36] We should note that in the model described below, in the case of a large number of active bonds, there is the unphysical possibility of having more active bonds than there are double bonds. In the case of all double bonds, the distribution tail is correct; however, for $\rho < 2$ the distribution tail will not be correct.
- [37] We could include nonlinear stiffening effects of activity on the elasticity of the individual elements here by having $k^{\text{eff}} = k_0 + \Delta\mu k_1$ [32].
- [38] This argument can be made local if U varies in space over length scales much larger than the lattice spacing b_0 .
- [39] See the Supplemental Material at <http://link.aps.org/supplemental/10.1103/PhysRevLett.113.028102> for details of the generating functional, steady-state distribution of motor occupancy variables and the averaging procedures for both quenched and annealed motor variables.
- [40] Note that the second term is small compared to the first since, for linear elasticity, $\beta f_m^2/k^{\text{eff}} \sim \beta k^{\text{eff}} x^2 \ll 1$.
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