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Connecting local active forces to macroscopic stress in elastic media

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In contrast with ordinary materials, living matter drives its own motion by generating active, out-of-equilibrium internal stresses. These stresses typically originate from localized active elements embedded in an elastic medium, such as molecular motors inside the cell or contractile cells in a tissue. While many large-scale phenomenological theories of such active media have been developed, a systematic understanding of the emergence of stress from the local force-generating elements is lacking. In this paper, we present a rigorous theoretical framework to study this relationship. We show that the medium’s macroscopic active stress tensor is equal to the active elements’ force dipole tensor per unit volume in both continuum and discrete linear homogeneous media of arbitrary geometries. This relationship is conserved on average in the presence of disorder, but can be violated in nonlinear elastic media. Such effects can lead to either a reinforcement or an attenuation of the active stresses, giving us a glimpse of the ways in which nature might harness microscopic forces to create active materials.

I. INTRODUCTION

Forces in living systems are largely generated at the nanometric protein level, and yet biological function often requires them to be transmitted to much larger length scales. In the actomyosin cytoskeleton for instance, local forces exerted by myosin molecular motors on a disordered elastic scaffold of actin fibers determine the mechanical properties of the cell and help drive mitosis, cell migration and adhesion [1]. At a larger scale, contractile cells exert forces on their surroundings to participate in muscular contraction, clot stiffening [2] and wound healing [3]. Due to their physiological relevance, such systems have been extensively studied *in vitro*, and direct, dynamical imaging has recently progressed from macroscopic observations to visualizations of the networks’ microstructure [4, 5] as well as individual components [6] during contraction.

The abundance of different macroscopic behaviors generated by apparently similar microscopic components, which is particularly spectacular in the cytoskeleton, has attracted significant theoretical attention over the last decade. Two prominent theoretical strategies have emerged.

On the one hand, so-called “active gels” models emphasize macroscopic flows within the cytoskeleton, and do not formulate detailed assumptions about the microscopic interactions between motors and filaments [7–9]. Instead, they rely on symmetry considerations to derive the most general equations compatible with the problem considered, and successfully predict intricate patterns of motion resembling experimentally observed dynamical structures. While very general, these approaches involve a large number of unprescribed parameters enclosing the

relevant aspects of the microscopic dynamics; in particular, the most important, specifically active aspects of the cytoskeletal dynamics are typically described by a phenomenological “active stress tensor”.

On the other hand, length scales too small to be accurately captured by an active gel formalism have typically been modeled using both continuum [10] and discrete [16] elastic models, yielding insights into specific cellular processes such as mitotic spindle organization [12], lamellipodium growth [13] or intracellular propulsion [14]. However, although the bulk elastic properties of such models have been thoroughly investigated [15] on a general basis, force transmission from the microscopic to the macroscopic level was only considered in numerical simulations of specific geometries [16–21], and a general theoretical framework to understand this process is lacking.

In this paper, we introduce such a formalism under the form of a direct relation—termed “dipole conservation”—between the macroscopic active stress and the force dipole tensor, a local quantity describing the individual force-exerting elements. Going beyond previous special-case derivations, we show that this relation applies in both continuum (Sec. II) and discrete (Sec. III) homogeneous, linear elastic media irrespective of their shape and of the spatial distribution of the active forces. To understand the biologically relevant influence of heterogeneities, we investigate the case of random spring networks in Sec. IV, and show that although dipole conservation is violated in individual realizations of the network it still holds in an average sense provided the disorder is the same everywhere. Finally, in Sec. V we study a toy model nonlinear elastic medium and show that nonlinear elasticity can skew force transmission towards either contraction or extension. Sec. VI then discusses the applicability of this result to existing models of force transmission in tissues and the cytoskeleton.

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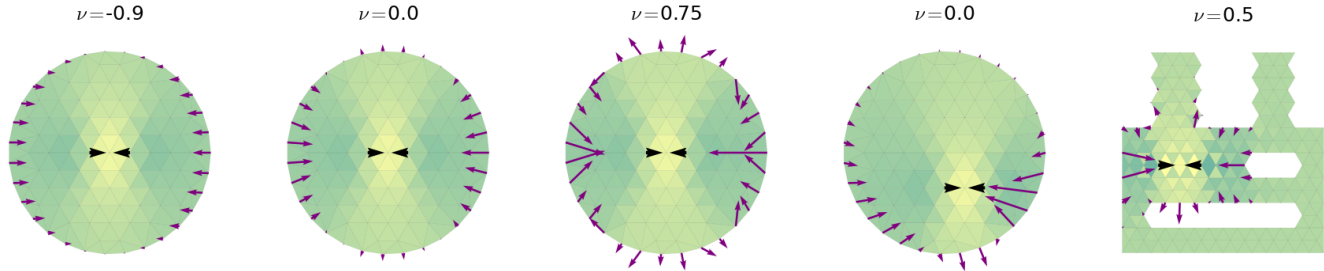


Figure 1 Boundary forces (*purple arrows*) transmitted by a two-dimensional homogeneous linear elastic medium under the influence of a localized force dipole (*black arrowheads*) computed using finite elements. The boundary force distribution is strongly influenced by both the medium’s material properties (ν denotes the Poisson ratio) and the geometry of the problem. Nevertheless, in all cases the boundary dipole tensor is equal to the body forces’ dipolar moment.

II. DIPOLE CONSERVATION IN CONTINUUM ELASTIC MEDIA

The transmission of localized active forces to the outer boundary of a continuum elastic body is a geometrically complex problem, and the distribution of transmitted forces strongly depend on the body’s shape and material properties (Fig. 1). Nevertheless, here we show that strong nonlocal constraints exist between body and boundary forces. In Sec. IIA we introduce the boundary dipole tensor, a quantity characterizing the boundary forces that is directly related to the stress tensor. Using general conditions of mechanical equilibrium, we relate this boundary dipole to the spatial distribution of body forces in Sec. IIB. Specializing our result to homogeneous linear media, we then show in Sec. IIC that the boundary dipole is exactly equal to the dipolar moment of the body force distribution, which we refer to as “dipole conservation”.

A. Boundary dipole tensor

Let us consider a general d -dimensional piece of elastic material at mechanical equilibrium, filling a domain Ω of space with boundary $\partial\Omega$ and volume V . We model the active elements embedded in the elastic body as a distribution of body forces $F_\mu(\mathbf{R})$. To quantify the macroscopic consequences of these active forces, we consider the response of the total system composed of the elastic medium and the embedded elements to an infinitesimal, affine deformation characterized by a strain tensor $\gamma_{\mu\nu}$. Under this transformation, a point belonging to the boundary $\partial\Omega$ of the elastic body with position \mathbf{R} in the resting state is displaced by a quantity $\delta R_\mu(\mathbf{R}) = \gamma_{\mu\nu} R_\nu$ (summation over repeated Greek indices is implied) [36]. Denoting the elastic stress tensor by $\sigma_{\lambda\mu}(\mathbf{R})$ and considering a surface element ds_λ lying on the boundary $\partial\Omega$, the force exerted by the outside world on the surface element reads $-\sigma_{\lambda\mu}(\mathbf{R}) ds_\lambda$. As the surface element gets

displaced by an infinitesimal δR_μ , the work performed by this force is $[-\sigma_{\lambda\mu}(\mathbf{R}) ds_\lambda] \times \delta R_\mu$. The change in energy of the total system is given by the work performed over the whole boundary:

$$\begin{aligned} \delta E &= \oint_{\partial\Omega} [-\sigma_{\lambda\mu}(\mathbf{R}) ds_\lambda] \times \delta R_\mu \\ &= -\gamma_{\mu\nu} \times \oint_{\partial\Omega} \sigma_{\lambda\mu}(\mathbf{R}) R_\nu ds_\lambda. \end{aligned} \quad (1)$$

Noting that the integral in the right-hand side of Eq. (1) is the dipolar moment of the boundary forces, we refer to this quantity as the “boundary dipole tensor” and denote it as

$$\Delta_{\mu\nu} = \oint_{\partial\Omega} \sigma_{\lambda\mu}(\mathbf{R}) R_\nu ds_\lambda. \quad (2)$$

The meaning of this new quantity becomes clear if we note that according to Eq. (1), $\Delta_{\mu\nu}$ is the derivative of the energy of the total system with respect to the boundary strain $\gamma_{\mu\nu}$. This is reminiscent of the definition of the stress tensor $\sigma_{\mu\nu}$ as the derivative of the energy density e with respect to the local strain tensor $\gamma_{\mu\nu}(\mathbf{R})$. Considering a coarse-grained approximation of the total system with a uniform bulk deformation $\gamma_{\mu\nu}$ and uniform stress $\tilde{\sigma}_{\mu\nu}$, we have $E = Ve$ with e a uniform elastic energy density and the boundary dipole tensor is directly related to the coarse-grained stress tensor:

$$\Delta_{\mu\nu} = \frac{\partial(Ve)}{\partial\gamma_{\mu\nu}} = -V\tilde{\sigma}_{\mu\nu}. \quad (3)$$

Thus $-\Delta_{\mu\nu}/V$ is the medium’s coarse-grained stress tensor and $\Delta/(Vd) = \Delta_{\mu\mu}/(Vd)$ is the analog of a hydrostatic pressure. In an active medium language, $\Delta < 0$ thus characterizes a contractile medium while $\Delta > 0$ is associated with extensility.

Note that in a system with periodic boundary condition, the boundary dipole tensor can be defined through the relation $\Delta_{\mu\nu} = -\partial E/\partial(\gamma_{\mu\nu})$, where the affine deformation can be imposed through Lees-Edwards boundary

conditions. Unless explicitly stated, all the continuum and discrete results presented in this manuscript can be rederived under periodic boundary conditions with only minimal modifications to their proofs.

B. Mean-stress theorem

As a first step towards establishing dipole conservation, here we rederive a result known as the mean-stress theorem [17, 22]. We introduce the dipolar moment of the active forces $F_\mu(\mathbf{R})$ as

$$D_{\mu\nu} = \int_{\Omega} F_\mu(\mathbf{R}) R_\nu dV. \quad (4)$$

Note that $D_{\mu\nu}$ is independent of the origin of the coordinates if the body forces sum to zero as expected for active elements embedded in an elastic medium, and that the total force dipole exerted by several active elements is equal to the sum of the individual force dipoles.

Inserting the force balance equation $\partial_\nu \sigma_{\mu\nu} = -F_\mu$ into Eq. (4) and integrating by part yields the mean stress theorem

$$D_{\mu\nu} = \oint_{\partial\Omega} \sigma_{\lambda\mu}(\mathbf{R}) R_\nu ds_\lambda + \int_{\Omega} \sigma_{\mu\nu}(\mathbf{R}) dV. \quad (5)$$

Defining the integrated stress tensor $\Sigma_{\mu\nu} = \int_{\Omega} \sigma_{\mu\nu} dV$ and using the definition of the boundary dipole Eq. (2), Eq. (5) can be cast into a compact form:

$$\Delta_{\mu\nu} = D_{\mu\nu} - \Sigma_{\mu\nu}. \quad (6)$$

This result holds irrespective of the medium's material properties, including homogeneity and linearity.

C. Dipole conservation

Despite its universality, in the general case the result of Eq. (6) involves a complicated unknown object $\Sigma_{\mu\nu}$ and is thus of limited practical use. Here we show that this limitation is lifted when considering a linear homogeneous elastic medium with fixed boundaries.

In a linear homogeneous elastic medium, stress is related to strain through a position-independent stiffness tensor: $\sigma_{\mu\nu}(\mathbf{R}) = C_{\mu\nu\alpha\beta} \gamma_{\alpha\beta}(\mathbf{R})$. Integrating this relation over space, we get

$$\Sigma_{\mu\nu} = C_{\mu\nu\alpha\beta} \Gamma_{\alpha\beta} \quad \text{with} \quad \Gamma_{\alpha\beta} = \int_{\Omega} \gamma_{\alpha\beta}(\mathbf{R}) dV, \quad (7)$$

with $\Gamma_{\alpha\beta}$ the integrated strain. Reminding ourselves that $\gamma_{\alpha\beta}(\mathbf{R}) = [\partial_\alpha u_\beta(\mathbf{R}) + \partial_\beta u_\alpha(\mathbf{R})]/2$ with $u_\alpha(\mathbf{R})$ the medium's displacement vector, integration of Eq. (7) yields a boundary integral

$$\Gamma_{\alpha\beta} = \oint_{\partial\Omega} \left[\frac{u_\beta(\mathbf{R})}{2} ds_\alpha + \frac{u_\alpha(\mathbf{R})}{2} ds_\beta \right]. \quad (8)$$

Equation (6) thus provides a decomposition of the boundary stress as a sum of a bulk term $D_{\mu\nu}$ involving active forces and a boundary term $\Sigma_{\mu\nu} = C_{\mu\nu\alpha\beta} \Gamma_{\alpha\beta}$ related to the system deformation. Note that the latter depends on the system's elastic properties through the stiffness tensor $C_{\alpha\beta\mu\nu}$, while the former does not. Now introducing the assumption of fixed boundary conditions, we find that the boundary displacements in the right-hand side of Eq. (8) vanish, implying that the whole integral vanishes. Using Eq. (7), we thus find that $\Sigma_{\mu\nu} = 0$, and thus Eq. (6) can be rewritten as the dipole conservation relation:

$$\Delta_{\mu\nu} = D_{\mu\nu} \quad (9)$$

which relates bulk and boundary forces. To understand the meaning of this equation, we decompose it into the equality of the traces, symmetric traceless parts and antisymmetric parts of the two tensors. The equality of the traces, $\Delta = D_{\mu\mu} = D$, is of particular interest for biological systems as it relates the ‘‘hydrostatic pressure’’ Δ of the medium to the local force dipole D , a quantity routinely interpreted as the amount of contractility of the active elements [11, 17, 18, 20, 23]. Next, the symmetric traceless part of each of the two dipole tensors $[(\Delta_{\mu\nu} + \Delta_{\nu\mu})/2$ and $(D_{\mu\nu} + D_{\nu\mu})/2]$ is analogous to a nematic order parameter characterizing the anisotropy of the corresponding forces, and thus their equality means that the anisotropy of the contractile forces is also conserved across scales. Finally, the equality $\Delta_{\mu\nu} - \Delta_{\nu\mu} = D_{\mu\nu} - D_{\nu\mu}$ of the antisymmetric parts is equivalent to torque balance in the elastic medium; since embedded active elements exert a vanishing total torque on the elastic medium, it simply reduces to $\Delta_{\mu\nu} - \Delta_{\nu\mu} = 0$, and thus expresses torque balance on the total system.

For systems without fixed boundaries, Eq. (9) takes the more general form

$$\Delta_{\mu\nu} = D_{\mu\nu} - C_{\mu\nu\alpha\beta} \Gamma_{\alpha\beta}, \quad (10)$$

meaning that the total coarse-grained stress $-\Delta_{\mu\nu}/V$ is the sum of an active contribution and of the elastic stress $C_{\mu\nu\alpha\beta} \Gamma_{\alpha\beta}$.

Note that Eq. (9), as well as the other dipole conservation relations presented in this paper assume a homogeneous (or statistically homogeneous in Sec. IV) elastic medium. Like these other results, it can however be generalized to cases where a piece of elastic material is removed to make space for the embedded active element by introducing a correction to the local dipole accounting for the missing piece.

III. DIPOLE CONSERVATION IN DISCRETE ELASTIC MEDIA

We now prove dipole conservation in discrete media, with similar implications as in the continuum case of

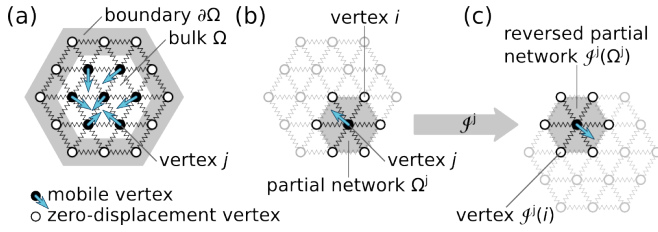


Figure 2 Parametrization and point reflection invariance in a discrete elastic system (a) Mobile bulk vertices (*solid circles*) comprised in the bulk Ω of the network are connected to each other and to zero-displacement boundary vertices belonging to the boundary $\partial\Omega$ (*open circles*). *Blue arrows* represent their displacements. (b) The partial network Ω^j is obtained by setting all displacements to zero except that of vertex j . (c) The partial network Ω^j is invariant under point reflection about vertex j even though the total network Ω (*in grey*) is not. The displacement of vertex j is reversed under this transformation.

Sec. II. Although more technically involved, this new derivation parallels the one of the previous section and its results have a similar physical interpretation. We introduce the active force dipole tensor and the boundary dipole tensor in Sec. III A and show that it satisfies a discrete mean-stress theorem in Sec. III B. Dipole conservation is then derived in Sec. III C under the assumptions of linearity and local point reflection symmetry, a variant of the homogeneity assumption used above.

A. Active force and boundary dipole tensors

We consider a d -dimensional system Ω comprised of interacting vertices i located at positions $\mathbf{R}^{(i)}$ in the reference configuration, and at $\mathbf{R}^{(i)} + \mathbf{u}^{(i)}$ in the deformed configuration characterized by the displacements $\mathbf{u}^{(i)}$. The system's boundary $\partial\Omega$ consists in a set of additional vertices whose displacements are set to zero [see Fig. 2(a)]. The active force dipole tensor and the boundary dipole tensor are thus respectively defined as

$$D_{\mu\nu} = \sum_{i \in \Omega} F_{\mu}^{(i)} R_{\nu}^{(i)}, \quad (11a)$$

$$\Delta_{\mu\nu} = \sum_{l \in \partial\Omega} f_{\mu}^{(l)} R_{\nu}^{(l)} \quad (11b)$$

where $F_{\mu}^{(i)}$ is the body force applied on the elastic network at vertex i and $f_{\mu}^{(i)}$ is the force exerted by the system on boundary vertex i .

B. Mean-stress theorem

As in the continuum case, the discrete mean-stress theorem stems from force balance. Here we consider only forces between pairs of vertices, as many-body interactions can always be decomposed into sums of pair in-

teractions. We assume these interactions to have finite range. Denoting by $f_{\mu}^{(ij)}$ the force exerted by vertex i on vertex j , the force balance condition reads

$$F_{\mu}^{(i)} = \sum_{j \sim i} f_{\mu}^{(ij)} \quad (12a)$$

$$f_{\mu}^{(i)} = \sum_{j \sim i} f_{\mu}^{(ij)} \quad (12b)$$

for bulk and boundary vertices, respectively. Here $\sum_{j \sim i}$ denotes a sum over the vertices j that interact with i .

Inserting Eq. (12a) into Eq. (11a), we obtain a double sum over vertices of the form $\sum_{i \in \Omega} \sum_{j \sim i}$. Reorganizing it into a sum over pairs of neighboring vertices and splitting the resulting expression into two sums, one over bulk pairs and the other over pairs straddling the boundary, we use Newton's third law $f_{\mu}^{(ij)} = -f_{\mu}^{(ji)}$ to find

$$\Delta_{\mu\nu} = D_{\mu\nu} + \sum_{(ij)} f_{\mu}^{(ij)} \left[R_{\nu}^{(j)} - R_{\nu}^{(i)} \right] \quad (13)$$

where the sum runs over all pairs of interacting vertices, including boundary vertices. Defining the stress associated with a pair of interacting vertices as [37]

$$\sigma_{\mu\nu}^{(ij)} = -f_{\mu}^{(ij)} \left[R_{\nu}^{(j)} - R_{\nu}^{(i)} \right] \quad (14)$$

we obtain

$$\Delta_{\mu\nu} = D_{\mu\nu} - \Sigma_{\mu\nu} \quad \text{with} \quad \Sigma_{\mu\nu} = \sum_{(ij)} \sigma_{\mu\nu}^{(ij)}, \quad (15)$$

which constitutes the discrete mean-stress theorem.

C. Dipole conservation

As in the continuum case, here we assume linear elasticity to demonstrate $\Sigma_{\mu\nu} = 0$, implying dipole conservation. Linearity implies that $\Sigma_{\mu\nu}$ is a linear function of the set $\{u_{\lambda}^{(i)}\}_{i \in \Omega}$ of equilibrium vertex displacements, which are themselves unspecified functions of the active forces. Therefore, the integrated stress in the network can be decomposed into a sum over fictitious partial networks Ω_j where all displacements but that of vertex j are set to zero [Fig. 2(a-b)]:

$$\Sigma_{\mu\nu} \left(\{u_{\lambda}^{(i)}\}_{i \in \Omega} \right) = \sum_{j \in \Omega} \Sigma_{\mu\nu}^{\Omega_j} \left(u_{\lambda}^{(j)} \right), \quad (16)$$

where $\Sigma_{\mu\nu}^{\Omega_j}$ is the integrated stress in partial network Ω_j .

To demonstrate dipole conservation, we show that the partial integrated stress $\Sigma_{\mu\nu}^{\Omega_j}$ vanishes for all j in networks invariant under local point reflection. Considering a specific partial network Ω_j , we first note that reversing the

vertex displacement also reverses the integrated stress by linearity:

$$\Sigma_{\mu\nu}^{\Omega_j}(-u_\lambda^{(j)}) = -\Sigma_{\mu\nu}^{\Omega_j}(u_\lambda^{(j)}). \quad (17)$$

We next introduce the assumption that each partial network Ω_j is invariant under local point reflection about vertex j . The result of this transformation is illustrated in Fig. 2(c), and we denote the symmetric of vertex i by $\mathcal{I}^j(i)$. Since stresses are proper tensors, the integrated stress is unchanged under this transformation:

$$\Sigma_{\mu\nu}^{\mathcal{I}^j(\Omega_j)}\left(\mathcal{I}^j\left(u_\lambda^{\mathcal{I}^j(j)}\right)\right) = \Sigma_{\mu\nu}^{\Omega_j}\left(u_\lambda^{(j)}\right), \quad (18)$$

meaning that the point-reversed image of a system under, *e.g.*, overall compression is a system under the same amount of overall compression. Since vertex j is its own image under this transformation, its displacement is reversed:

$$\mathcal{I}^j\left(u_\lambda^{\mathcal{I}^j(j)}\right) = \mathcal{I}^j\left(u_\lambda^{(j)}\right) = -u_\lambda^{(j)}. \quad (19)$$

Noting that local point reflection means that the partial network Ω_j is invariant under \mathcal{I}^j , *i.e.*, $\mathcal{I}^j(\Omega^j) = \Omega^j$, Eq. (18) becomes

$$\Sigma_{\mu\nu}^{\Omega_j}(-u_\lambda^{(j)}) = \Sigma_{\mu\nu}^{\Omega_j}(u_\lambda^{(j)}). \quad (20)$$

Combining Eqs. (17) and (20), we find that $\Sigma_{\mu\nu}^{\Omega_j} = 0$ for any j , which we insert into Eqs. (15) and (16) to prove dipole conservation in the original, full network Ω :

$$\Delta_{\mu\nu} = D_{\mu\nu} \quad (21)$$

Although superficially different from the translational invariance used in Sec. II, our local point reflection symmetry has a similar physical meaning. Indeed, it states that from any point of observation, the elastic medium looks the same to two observers looking in opposite directions. It is however more restrictive than translational symmetry, as it does not apply to, *e.g.*, the honeycomb and diamond lattices—we do however believe that dipole conservation could be established in these lattices by considering discrete rotational symmetries. Local point reflection symmetry is nevertheless fulfilled by most usual lattices, including the triangular, square, simple-, face-centered- and body-centered-cubic lattices, and thus the discrete dipole conservation relation Eq. (21) remains of wide practical interest. Furthermore, in a regular lattice with periodic boundary conditions translational invariance is sufficient to prove dipole conservation (with a proof similar to that presented in Sec. IV A).

IV. AVERAGE DIPOLE CONSERVATION IN RANDOM ELASTIC MEDIA

In this and the next section, we investigate how relaxing the assumptions of homogeneity and linearity respectively affect dipole conservation. As shown in Fig. 3, inhomogeneous elastic properties significantly affect dipole

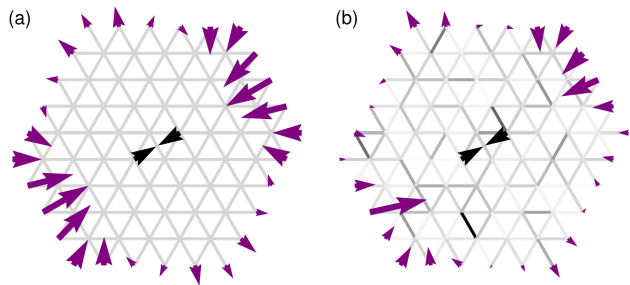


Figure 3 Force transmission in a linear spring network is strongly affected by elastic inhomogeneities. Here the opacity of a bond is proportional to its stiffness, and black arrowheads (purple arrows) represent body (boundary) forces. (a) In a homogeneous network, dipole conservation $\Delta = D$ is satisfied to the numerical precision. (b) In a random spring network, dipole conservation is typically violated; in this specific example, $\Delta/D \approx 0.60$. Here the spring constants are drawn from a lognormal law with standard deviation $\delta\alpha = 0.8$.

transmission in a spring network. Nevertheless, we show in Sec. IV A that in a random spring network with periodic boundary conditions dipole conservation is preserved in an average sense. Sec. IV B then shows numerically that fixed boundary conditions spoil this result, although deviations from it are small and go to zero for large-size systems. Finally, in Sec. IV C we use an effective medium (*i.e.*, mean-field) approach to quantify the sample-to-sample variations in the amount of transmitted force dipole, and find that it is proportional to the amplitude of the local spring disorder.

A. Average dipole conservation in periodic geometry

Consider the linear response of a regular lattice of independent, identically distributed random springs with periodic boundary conditions subjected to a distribution of body forces $F_\mu^{(i)}$ of zero sum (*i.e.*, $\sum_i F_\mu^{(i)} = 0$ as expected for active elements embedded in an elastic medium). Let $G_{\mu\nu\alpha}^{(i)}$ be the sample-dependent linear response function relating the body force at site i to the integrated stress:

$$\Sigma_{\mu\nu} = \sum_i G_{\mu\nu\alpha}^{(i)} F_\alpha^{(i)}. \quad (22)$$

Denoting averages over lattice disorder by a bar, this equation implies

$$\bar{\Sigma}_{\mu\nu} = \sum_i \overline{G_{\mu\nu\alpha}^{(i)} F_\alpha^{(i)}} = \overline{G_{\mu\nu\alpha}} \sum_i F_\alpha^{(i)}, \quad (23)$$

where the second equality stems from the statistical equivalence of all sites in the network, implying that the average response function $\overline{G_{\mu\nu\alpha}^{(i)}}$ is independent of

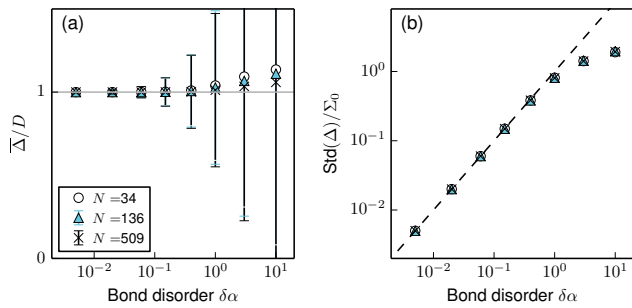


Figure 4 Deviations from average dipole conservation and sample-to-sample fluctuations in random spring networks. (a) The average dipole conservation condition $\bar{\Delta}/D = 1$ (grey line) is well respected for systems with large enough number of mobile vertices N . Bars represent the standard deviation of this ratio, thus indicating the magnitude of sample-to-sample fluctuations. Each point in this figure represents data averaged over $\mathcal{O}(10^5)$ samples, ensuring that the plotted deviations in the average $\bar{\Delta}$ are statistically significant. (b) Standard deviation of the boundary force dipole, Δ [proportional to the length of the bars in panel (a)] normalized by the second moment of the effective medium stress Σ_0 (see Appendix A) as a function of disorder. We find good agreement with the small-disorder effective medium theory prediction Eq. (26) (dashed line) up to $\delta\alpha \simeq 1$.

i. Finally, inserting our assumption of vanishing sum of the body forces into Eq. (23) yields $\bar{\Sigma}_{\mu\nu} = 0$, and thus through Eq. (15) the force dipole is conserved on average:

$$\bar{\Delta}_{\mu\nu} = D_{\mu\nu}. \quad (24)$$

This result is valid in any system where all vertices are equivalent, and thus also holds in infinite lattices.

B. Violations of average dipole conservation in the presence of fixed boundaries

To investigate the influence of finite domain size on the average dipole conservation Eq. (24), we numerically study the linear response to a force dipole of a finite hexagonal system with fixed boundary conditions, as pictured in Fig. 3(b). The network is a two-dimensional triangular lattice of independent identically distributed random hookean springs of unit rest length. The spring constant of the bond joining two neighboring sites i and j is denoted $\alpha^{(ij)}$ and drawn from a distribution $dP(\alpha)$ with average $\bar{\alpha} = 1$ and variance $\text{Var}(\alpha) = \delta\alpha^2$.

Assuming a lognormal form for $dP(\alpha)$, we minimize the elastic energy of systems of different sizes using a conjugate gradient algorithm. Our procedure uses displacements of order 10^{-100} times the lattice constant, thus guaranteeing that nonlinear effects are not present in our results. Fig. 4(a) shows that average dipole conservation is violated for small systems, but that these violations vanish for larger system sizes.

C. Influence of network disorder on the reliability of force transmission

While in large enough systems the boundary dipole becomes equal to the local force dipole *on average*, Fig. 4(a) shows that significant fluctuations *around this average* subsist even in infinite systems. Physically, this stems from the fact that the configuration of the immediate surroundings of the force-exerting active element can strongly amplify or attenuate the local force dipole. These near-field distortions are then faithfully propagated to long distances by the more distant regions of the network, which tend to transmit forces in a more dipole-conserving way. Therefore, due to their local origin these distortions are not cured by increasing the system size. The resulting boundary dipole fluctuations have a clear practical significance, as they represent an intrinsic limitation on the reliability of force transmission through disordered elastic networks and thus represent a challenge for biological systems.

To better understand the magnitude of this effect in relation to the amount of network disorder, we compute a mean-field-type approximation of the boundary dipole fluctuations through an effective medium theory [27]. As detailed in Appendix A, effective medium theories assimilate the effect of bond disorder in a fully random network to that of a single random bond with spring constant α immersed in an effective regular network. The spring constant α_m associated with this effective network is chosen so that the average of the displacement v of the random bond in the regular network is equal to the elongation v_m of the non-random bonds, *i.e.*, $\bar{v} = v_m$. This formalism allows us to calculate an approximation of the tension of each random bond, allowing us to compute the integrated stress Σ . We find that the tension of the random bond is equal to the bond tension in a fully regular medium plus a quantity proportional to $v - v_m$. Since the integrated stress in the ordered medium vanishes [Eq. (21)], our approximate system has $\Sigma \propto v - v_m$. Now averaging this relation and using $\bar{v} - v_m = 0$, we find

$$\bar{\Sigma} = D - \bar{\Delta} = 0, \quad (25)$$

i.e., the effective medium theory predicts average dipole conservation irrespective of boundary conditions. Going beyond this vanishing average stress, we further compute the variance $\bar{\Sigma}^2$ of the integrated stress, which is proportional to $\overline{(v - v_m)^2}$. For small disorder, the typical mismatch $v - v_m$ between the random bond and its deterministic neighbors is moreover proportional to the mismatch $\alpha - \alpha_m$ of their spring constants, and thus to the amplitude $\delta\alpha$ of the disorder. This finally yields

$$\text{Std}(\Sigma) = \text{Std}(\Delta) = \Sigma_0 \delta\alpha, \quad (26)$$

where the geometry-dependent prefactor Σ_0 in the right-hand side is given in Appendix A. Comparing this effective medium prediction with the numerical data of Sec. IV B, we find an excellent agreement up to a bond

disorder $\delta\alpha \simeq 1$, following which our small-disorder expansion breaks down [Fig. 4(b)].

This proportionality of dipole fluctuations $\delta\Sigma$ to the network disorder $\delta\alpha$ suggests that reliable dipole transmission is only possible in well-ordered media. However, due to the linearity of the elastic medium, the fluctuations stemming from many small contractile elements scattered through space average out to zero. This scattered geometry is reminiscent of the structure of force-generating cytoskeletal networks.

V. BREAKDOWN OF DIPOLE CONSERVATION IN NONLINEAR ELASTIC MEDIA

Unlike the elastic disorder discussed above, nonlinear elastic behavior introduces systematic violations of force dipole conservation, as illustrated here on a simple example. We consider a spherical, three-dimensional cavity of radius R_1 filled with a continuum homogeneous elastic medium with elastic energy density

$$e = \frac{\lambda}{2} (\text{Tr}\gamma)^2 + \mu \text{Tr}(\gamma^2) + \frac{\beta}{3} (\text{Tr}\gamma)^3, \quad (27)$$

where γ is the strain tensor, λ and μ are Lamé parameters that characterize the linear response of the material, and β is a nonlinear compressibility, with $\beta > 0$ describing softening upon compression. We impose a radial displacement u_0 at radius R_0 , resulting in a radial displacement

$$u_R(R) = AR + \frac{B}{R^2} \quad (28)$$

with

$$A = \begin{cases} u_0/R_0 & R < R_0 \\ -u_0R_0^2/(R_1^3 - R_0^3) & R_0 < R < R_1 \end{cases} \quad (29a)$$

$$B = \begin{cases} 0 & R < R_0 \\ u_0R_0R_1^3/(R_1^3 - R_0^3) & R_0 < R < R_1 \end{cases}. \quad (29b)$$

Although Eq. (28) matches the linearized solution of the elastic problem, it is actually valid to arbitrary nonlinear order for the specific form of the strain energy of Eq. (27) [28, 29].

Restricting ourselves to small displacements, we can use the usual Cauchy strain tensor $\gamma_{\mu\nu} = \frac{1}{2}(\partial_\mu u_\nu + \partial_\nu u_\mu)$ and derive the resulting radial stress

$$\sigma_{RR}(R) = 3\lambda A + 2\mu \left(A - \frac{2B}{R^3} \right) + 9\beta A^2, \quad (30)$$

which we use to compute the local and boundary force

dipoles

$$\begin{aligned} D &= 4\pi R_0^3 [\sigma_{RR}(R_0^+) - \sigma_{RR}(R_0^-)] \\ &= u_0 (\lambda + 2\mu) \frac{12\pi R_1^3 R_0^2}{R_1^3 - R_0^3} + \beta u_0^2 \frac{36\pi R_1^3 R_0 (R_1^3 - 2R_0^3)}{(R_1^3 - R_0^3)^2} \\ \Delta &= 4\pi R_1^3 \sigma_{RR}(R_1) \\ &= u_0 (\lambda + 2\mu) \frac{12\pi R_1^3 R_0^2}{R_1^3 - R_0^3} - \beta u_0^2 \frac{36\pi R_1^3 R_0^4}{(R_1^3 - R_0^3)^2} \\ &\underset{R_0 \ll R_1}{\sim} D - 36\pi\beta u_0^2 R_0. \end{aligned} \quad (31)$$

Thus the nonlinear elasticity of the material renormalizes the local force dipole by a quantity $-36\pi\beta u_0^2 R_0$ which becomes negligible in the linear limit $\beta u_0 \ll \lambda, \mu$. This violation of dipole conservation favors contraction ($\Delta < 0$) for a material that softens under compression ($\beta > 0$) as further discussed below.

VI. DISCUSSION

Stress-generating, active materials are essential constituents of the cell, and their biological design is strongly constrained by the physical laws governing force transmission in elastic media. As shown here, these laws take a simple, geometry-independent form in homogeneous linear elastic media, whereby the force dipole is an invariant of linear elasticity. More specifically, the macroscopic force dipole tensor exerted by the medium on its boundaries is equal to the sum of the microscopic force dipoles exerted on it by embedded active elements. This dipole conservation relation is valid both for continuum media and for discrete media with unspecified finite range interactions, making it relevant for popular biological fiber network models with stretching and bending energies [15]. It also holds true in anisotropic media. Due to its generality, dipole conservation is a powerful tool to relate widely used macroscopic descriptions of the cytoskeleton, sometimes termed active gels theories, to the underlying microscopic phenomena. For instance, in a homogeneous linear elastic medium with a density ρ of embedded elements each exerting a force dipole $d_{\mu\nu}$, the active stress $\sigma_{\mu\nu}$ —the central object of active gel theories—is simply given by $\sigma_{\mu\nu} = -\rho d_{\mu\nu}$ [see Eqs. (3) and (9)].

Considering more biologically relevant, disordered elastic media, we show that in a discrete linear system where the disorder probability distribution is position-independent, dipole conservation is satisfied on average. This result again applies to fiber network models, but can be violated in small systems where the influence of the boundary conditions is not negligible. Dipole conservation is moreover not generally respected in every statistical realization of the system, and fluctuations are proportional to the amplitude of the disorder; they are however self-averaging, leading to reliable, deterministic stress generation in large enough systems.

Unlike disorder, nonlinearities have a systematic effect on force transmission. Indeed, we show that a material that softens under compression tends to favor contraction, reminiscent of the enhanced contractility observed in bundles and networks of filaments prone to buckling under compressive stresses [30–32]. A similar effect has been predicted in shear stiffening materials [10]. It is moreover worth keeping in mind that nonlinear behavior in elastic materials is not limited to constitutive nonlinearities in the material properties, as nonlinear elasticity can also stem from geometrical effects [33]. Importantly, such geometrical nonlinearities are more prevalent in disordered than homogeneous networks [34], implying that disorder might significantly affect contractility by lowering the threshold to nonlinear behavior. As a result, a reliable understanding of contraction in active biological materials requires a good characterization of the nonlinear property of the underlying elastic ma-

trix. Given impressive recent experimental advances in this area, we believe that model-independent, rigorous theoretical studies such as this one will be valuable in analyzing new data and thus understanding the relation between molecular motors and cell-wide force generation.

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 [36] Throughout this article, the positions \mathbf{R} can be chosen to refer to either the undeformed or deformed state, provided that the correct form of the stress (nominal vs. Cauchy) is used. The mean-stress theorem holds for arbitrary deformations in both cases.
 [37] Several different conventions can be chosen to generalize the stress tensor to discrete systems [24–26]. Here we chose to localize the stress on the bonds of the network, yielding a mean-stress theorem with a concise expression.

Appendix A: Effective medium theory for disordered spring networks

Here we derive the results of Sec. IV C by developing an effective medium theory, following Ref. [27]. In this approach the disordered network described in Sec. IV is approximated by an effective homogeneous network where every bond has a spring constant α_m . When subjected to the same body forces and boundary conditions as the original network, the effective network deforms so that the bond joining adjacent vertices i and j has elongation $v_m^{(ij)}$ with respect to its rest length. To determine the value of α_m , we introduce a third system obtained by replacing bond (ij) by a random spring with constant α drawn with probability law $dP(\alpha)$. This induces a change in the deformation field, and the elongation of the considered bond in the single-random-bond system is denoted $v^{(ij)} = v_m^{(ij)} + \delta v^{(ij)}$. Mechanical equilibrium then imposes

$$\delta v^{(ij)} = v_m^{(ij)} \frac{\alpha_m - \alpha}{q\alpha_m + \alpha} \quad (\text{A1})$$

where $q = z/2d - 1$ with z the network connectivity and d the spatial dimension. The effective spring constant α_m is fixed by imposing

$$\overline{\delta v^{(ij)}} = v_m^{(ij)} \int \frac{\alpha_m - \alpha}{q\alpha_m + \alpha} dP(\alpha) = 0, \quad (\text{A2})$$

where the average is taken over the distribution of α .

To compute the integrated stress Σ , we note that displacements in our single random bond system are the same as in a homogeneous lattice of α_m springs with an active force dipole of amplitude $(\alpha - \alpha_m)v^{(ij)}$ applied along bond (ij) . We further note that the integrated stress in this homogeneous, linear system vanishes according to Eq. (21). Since stresses in this system are identical to those in our single-random-bond system except at bond (ij) , the integrated stress in the latter is equal to the integrated stress in the former (*i.e.*, zero) plus the contribution of bond (ij) :

$$\Sigma = 0 + (\alpha - \alpha_m)v^{(ij)} = \frac{z\alpha_m}{2d} \delta v^{(ij)} \quad (\text{A3})$$

where Eq. (A1) was used. Inserting Eq. (A2) into Eq. (A3), we obtain $\overline{\Sigma} = 0$, *i.e.*, the average dipole conservation equation Eq. (25).

Denoting $\sigma_m^{(ij)} = \alpha_m v_m^{(ij)}$ and $\delta\sigma^{(ij)} = \sigma_m^{(ij)} + \delta\sigma^{(ij)}$, we plug Eq. (A1) into Eq. (A3) and compute $\overline{[\delta\sigma^{(ij)}]^2} = C \left[\overline{\sigma_m^{(ij)}} \right]^2$, where

$$C = \int \left[\frac{\alpha_m - \alpha}{(1 - 2d/z)\alpha_m + 2d\alpha/z} \right]^2 dP(\alpha). \quad (\text{A4})$$

In the spirit of the effective medium theory, we approximate the fully random lattice as a superposition of single random bond lattices and sum the bond stresses $\sigma^{(ij)}$ as independent identically distributed variables:

$$\overline{\Sigma^2} = \sum_{(ij)} \overline{[\delta\sigma^{(ij)}]^2} = C \Sigma_0^2, \quad (\text{A5})$$

where $\Sigma_0^2 = \sum_{(ij)} \left[\overline{\sigma_m^{(ij)}} \right]^2$ can be computed from the stress field in the homogeneous system with appropriate boundary conditions and active body forces. This procedure is used to obtain the normalization factor of Fig. 4(b). Note that C takes a simple form in the weak disorder limit $\text{Var}(\alpha) = \delta\alpha^2 \ll \bar{\alpha}^2$. Indeed, setting $\bar{\alpha} = 1$ Eq. (A2) yields

$$\alpha_m = 1 - \frac{2d}{z}(\delta\alpha)^2 + \mathcal{O}[(\delta\alpha)^3], \quad (\text{A6})$$

and the numerical factor becomes $C = \delta\alpha^2 + \mathcal{O}[(\delta\alpha)^3]$, yielding Eq. (26).