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Abstract. We discuss general features of noise and fluctuations in active polar gels close to and away from equilibrium. We use the single-component hydrodynamic theory of active polar gels built by Kruse and coworkers to describe the cytoskeleton in cells. Close to equilibrium, we calculate the response function of the gel to external fields and introduce Langevin forces in the constitutive equations with correlation functions respecting the fluctuation-dissipation theorem. We then discuss the breakage of the fluctuation-dissipation theorem due to an external field such as the activity of the motors. Active gels away from equilibrium are considered at the scaling level. As an example of application of the theory, we calculate the density correlation function (the dynamic structure factor) of a compressible active polar gel and discuss possible instabilities.

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1 Introduction

Active systems are driven out of equilibrium by a constant energy consumption that can be dissipated as heat or used to produce work. Typical examples are gels driven by chemical reactions [1], vibrated granular materials [2], coordinated motion of self-propelling agents such as bird flocks or fish pools [3], the cell cytoskeleton and tissues [4]. Although such systems have very different characteristic length scales or time scales, they share general features in a coarse-grained limit where conservation laws and symmetries govern hydrodynamic behaviors which are therefore generic. In recent years, coarse-grained descriptions have been proposed in very different contexts [5, 6]. However, since they are largely based on symmetries, they all share a similar structure. The values of coefficients describing system properties can however differ in their orders of magnitude for specific realizations.

Within this framework, we have developed a hydrodynamic gel theory of the cell cytoskeleton in references [7, 8]. In this theory, we consider in particular the acto-myosin cytoskeleton as an active gel of rigid filaments with a polar order parameter which describes the average orientation of actin filaments within a volume element. These filaments are rod-like objects with a vectorial symmetry.

An energy flux is provided to the system by the action of myosin molecular motors walking on the actin filaments, and also by the polymerization-depolymerization process of actin. These motors transduce, into mechanical work, the chemical energy of the hydrolysis of Adenosine Triphosphate (ATP), which is the motors fuel. In the hydrodynamic limit, the activity of motor molecules gives rise to active stresses characterized by the new phenomenological material coefficient ζ . This macroscopic description is independent of many microscopic details and therefore does not provide a relationship between the activity coefficient ζ and the microscopic properties of molecular motors and active filaments. Such a relationship can only be obtained from theories which are based on a microscopic description of the components on the molecular scale. From such microscopic descriptions, the hydrodynamic limit can in principle be obtained by systematic coarse-graining [9–12]. Recent mesoscopic descriptions of the actin-myosin cytoskeleton which are based on specific molecular processes can provide estimates of the macroscopic transport coefficients used in the hydrodynamic theory. The hydrodynamic theory of active gels has recently been used to describe some dynamic cellular processes such as lamellipodium motion [13] or instabilities of the cortical actin layer [14].

Active polar gels have been shown to have unusual flow properties: in many instances a spontaneous flow appears

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even in the absence of any external pressure or external forces, due to the inherent activity [15]. As a consequence, an active macroscopic gel often does not have static steady states: a homogeneous thin film of active gel becomes unstable at a finite thickness with respect to more complex dynamic states.

The description of active polar gels has been developed as a mean-field theory to describe average behaviors of the system. Cells are highly fluctuating systems and many processes are strongly influenced by fluctuations. Noise in cells has two origins: At short time scales, fluctuations can be linked to degrees of freedom that are equilibrated at a temperature T and are thus thermal in nature. At time scales of cellular processes mediated by conformational changes of proteins which are driven by chemical reactions, the stochastic nature of these processes is the source of non-equilibrium fluctuations [16, 17]. In particular, the polymerization kinetics of the actin filaments and the associated treadmilling are stochastic phenomena with an intrinsic noise not associated with thermal fluctuations. Similarly the motion of molecular motors and the production of forces and active stresses in the cytoskeleton are associated to transitions between different states of motor proteins which also have an intrinsic noise. It is therefore important to include noise in the description of active gels in order to have an accurate description of the mechanical properties of the cytoskeleton.

From more formal point of view, a cell in general and the cytoskeleton are non-equilibrium systems. A strong test to decide whether a system is at thermodynamic equilibrium is the violation of the fluctuation-dissipation theorem. The violation of the theorem has been recently tested experimentally by Mizuno *et al.* [18]. The validity of the fluctuation-dissipation theorem is important to study within the framework of the hydrodynamic theory of active gels.

The aim of this paper is to build a fluctuating hydrodynamic description of the actin cytoskeleton. By starting close to equilibrium, we first characterize thermal noise and then discuss how effects of non-thermal noise can be introduced in the framework of our hydrodynamic theory of active gels.

An important issue when considering noise is the fluctuation-dissipation theorem [19]. In a system at thermal equilibrium, the fluctuation-dissipation theorem relates the noise directly to the linear response of the system to external fields. The violation of this theorem is a criterion to determine whether a system is out of equilibrium and thus active. Cells and the actin cytoskeleton are expected to be non-equilibrium systems which are driven out of equilibrium by the ATP field and thus do not satisfy a fluctuation-dissipation theorem.

In order to clarify the underlying concepts and characterize thermal noise, we first discuss in Section 2 fluctuations in a physical gel described by the Maxwell model of viscoelasticity [20]. Our description of active gels is based on this model. Considering thermal noise, we show that the two possible thermodynamic ensembles at constant external stress or constant velocity gradient lead to the

same stochastic equations. In Section 3, we use the same approach to discuss thermal fluctuations in active gels. We show that the correlations of the various noise terms only depend on the dissipative transport coefficients such as the viscosities and therefore that they cannot be affected by the geometrical non-linearities that we introduce in the theory. Section 4 is devoted to the discussion of the violation of the fluctuation-dissipation theorem. We show that this violation is due to the existence of finite external fields such as the ATP source and that it occurs at second order in these fields. In Section 5 we discuss general features of fluctuations of an active gel far from equilibrium resulting from the intrinsic stochasticity of molecular motors. Finally, in Section 6, we calculate the density correlations in a compressible active polar gel and we show that the gel can become unstable. This result is consistent with earlier results of Voituriez *et al.* [21]. The last section presents a discussion of our results and some concluding remarks.

2 Fluctuating Maxwell model

Fluctuating hydrodynamic theories are well established for simple fluids [22]. The introduction of noise terms in the constitutive equations of active gels requires a particular care when viscoelasticity is considered. As a simple example, we therefore discuss first thermal noise in the special case of the Maxwell model of viscoelastic materials. The Maxwell model for a simple viscoelastic fluid is defined by constitutive equations which relate the mechanical stress to the local velocity gradient, the cross-over between elastic and viscous behavior involving a single relaxation time τ . We discuss here how noise terms can be added in such a way that the fluctuation-dissipation theorem is satisfied. We obtain results similar to those of reference [23].

2.1 Maxwell model

We consider for simplicity an incompressible fluid with a shear viscosity denoted by η . The constitutive relations of the Maxwell model then read

$$\left(1 + \tau \frac{D}{Dt}\right) \sigma_{\alpha\beta} = 2\eta v_{\alpha\beta}, \quad (1)$$

where $v_{\alpha\beta} = \partial_t u_{\alpha\beta} = (\partial_\alpha v_\beta + \partial_\beta v_\alpha)/2$ denotes the strain rate tensor which is the time derivative of the deformation tensor $u_{\alpha\beta}$, and $\sigma_{\alpha\beta}$ is the symmetric part of the total stress tensor. In the most general version of the Maxwell model, the time derivative in the constitutive equation is a convected corotational derivative of a tensor [20]

$$\frac{D}{Dt} \sigma_{\alpha\beta} = \frac{\partial}{\partial t} \sigma_{\alpha\beta} + v_\gamma \partial_\gamma \sigma_{\alpha\beta} + [\omega_{\alpha\gamma} \sigma_{\gamma\beta} + \omega_{\beta\gamma} \sigma_{\gamma\alpha}], \quad (2)$$

where $\omega_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta - \partial_\beta v_\alpha)$ is the vorticity of the flow. The hydrodynamic equations follow from the constitutive

relations by taking into account conservation laws for momentum and mass. Momentum conservation implies the force balance

$$\partial_\beta \sigma_{\alpha\beta} - \partial_\alpha P = 0, \quad (3)$$

where P denotes hydrostatic pressure.

Decomposing the stress into a dissipative part σ^d and a reactive part σ^r as $\sigma_{\alpha\beta} = \sigma_{\alpha\beta}^d + \sigma_{\alpha\beta}^r$, the constitutive equations of the Maxwell model can be written as

$$\begin{aligned} \left(1 - \tau^2 \frac{D^2}{Dt^2}\right) \sigma_{\alpha\beta}^d &= 2\eta v_{\alpha\beta}, \\ \sigma_{\alpha\beta}^r &= -\tau \frac{D}{Dt} \sigma_{\alpha\beta}^d. \end{aligned} \quad (4)$$

We add a noise term $\xi_{\alpha\beta}$ by first considering the linearized constitutive equation. This can be done most conveniently in the frequency representation where

$$(1 - i\omega\tau)\sigma_{\alpha\beta} = 2\eta v_{\alpha\beta} + \xi_{\alpha\beta}, \quad (5)$$

with the convention of the Fourier transform $\sigma(\omega) = \int dt \sigma(t) e^{i\omega t}$. Stress fluctuations can then be described by rewriting this equation as

$$\sigma_{\alpha\beta} = \frac{2\eta}{1 - i\omega\tau} v_{\alpha\beta} + s_{\alpha\beta}. \quad (6)$$

Here, the stress in linear response is determined as a function of a given shear rate and the stress fluctuations are given by $s_{\alpha\beta} = \xi_{\alpha\beta}/(1 - i\omega\tau)$. In order to determine the structure of the noise, we now make use of the fluctuation-dissipation theorem.

2.2 Fluctuation-dissipation theorem

The noise correlations can be determined from the fluctuation-dissipation theorem as follows: Consider a set of variables ϕ_i and their thermodynamically conjugated forces f_i such that the entropy production rate is $T\dot{S} = \sum_i \dot{\phi}_i f_i$ and ϕ_i and f_i have the same signature under time-reversal. The Fourier modes at angular frequency ω obey the linear response relation

$$\phi_i(\omega) = \chi_{ij}(\omega) f_j(\omega). \quad (7)$$

The linear response function can be decomposed into real and imaginary parts as $\chi_{ij} = \chi'_{ij} + i\chi''_{ij}$. The correlation functions

$$\langle \phi_i(\omega) \phi_j(\omega') \rangle = 2\pi C_{ij}(\omega) \delta(\omega + \omega') \quad (8)$$

and the linear response functions must obey the fluctuation-dissipation relation

$$C_{ij}(\omega) = \frac{2k_B T}{\omega} \chi''_{ij}(\omega). \quad (9)$$

Therefore, the Langevin equation can be written in the frequency representation as

$$\phi_i = \chi_{ij}(\omega) f_j + \xi_i, \quad (10)$$

with a noise term that has zero average and

$$\langle \xi_i(\omega) \xi_j(\omega') \rangle = 2\pi \frac{2k_B T \chi''_{ij}(\omega)}{\omega} \delta(\omega + \omega'). \quad (11)$$

2.3 Fluctuating stresses

We consider the ensemble where the stress tensor fluctuates and the deformation is imposed. The entropy production is then $\int dt \sigma_{\alpha\beta} \partial_t u_{\alpha\beta} = -\int dt (\partial_t \sigma_{\alpha\beta}) u_{\alpha\beta}$, such that we identify the negative stress $\sigma_{\alpha\beta}$ with the fields ϕ_i and the deformations $u_{\alpha\beta}$ with the forces f_i . In this case, the linear response $-\sigma_{\alpha\beta} = \chi_{\alpha\beta\gamma\delta} u_{\gamma\delta}$ with $v_{\alpha\beta} = -i\omega u_{\alpha\beta}$ is, according to equation (6), given by

$$\chi_{\alpha\beta\gamma\delta} = (\delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma}) \frac{i\omega\eta}{1 - i\omega\tau}. \quad (12)$$

The appropriate noise fluctuations which ensure that the FDT is satisfied are

$$\begin{aligned} \langle s_{\alpha\beta}(\omega, \mathbf{x}) s_{\gamma\delta}(\omega', \mathbf{x}') \rangle &= 2\pi \frac{2k_B T \eta}{1 + \omega^2 \tau^2} (\delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma}) \\ &\quad \times \delta(\omega + \omega') \delta(\mathbf{x} - \mathbf{x}'). \end{aligned} \quad (13)$$

Note that the Maxwell model is purely elastic for short times. As a consequence, the noise strength in (13) vanishes for large ω . In a real system the large-frequency limit is determined by the solvent viscosity which is neglected in the Maxwell model.

By transforming back to the time representation, we note that the convective and corotational non-linearities in equation (1) cannot affect the noise which is only linked to dissipative terms. Therefore, the constitutive equations of the fluctuating Maxwell model can be written as

$$\left(1 + \tau \frac{D}{Dt}\right) \sigma_{\alpha\beta} = 2\eta v_{\alpha\beta} + \xi_{\alpha\beta}, \quad (14)$$

where the noise correlation is given by

$$\begin{aligned} \langle \xi_{\alpha\beta}(t, \mathbf{x}) \xi_{\gamma\delta}(t', \mathbf{x}') \rangle &= 2k_B T \eta (\delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma}) \\ &\quad \times \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'). \end{aligned} \quad (15)$$

The same result is obtained if we use the conjugate ensemble where the deformation tensor fluctuates. This is explicitly shown in Appendix A.

3 Fluctuations of active gels

Starting from the constitutive material equations for viscoelastic active and polar gels, which have been derived elsewhere, we can systematically add noise terms such that the FDT is obeyed by correlation and response functions. This leads to a description of fluctuations in such systems in the vicinity of a thermodynamic equilibrium.

The constitutive equations are expressed in terms of conjugate thermodynamic fluxes and forces. In addition to the pair $\sigma_{\alpha\beta}$ and $v_{\alpha\beta}$, we consider the rate of change of the orientation field Dp_α/Dt and its thermodynamic conjugate $h_\alpha = -\delta F/\delta p_\alpha$ which derives from a free energy F . We furthermore take into account the local rate r of the consumption of ATP molecules per unit volume which plays the role of a fuel. The conjugate variable to r is the chemical potential difference $\Delta\mu$ between fuel and reaction products.

In order to discuss shear and compression separately for a compressible system, we write the total stress tensor as $\sigma_{\alpha\beta}^{\text{tot}} = \sigma_{\alpha\beta} + \sigma_{\alpha\beta}^a - P\delta_{\alpha\beta}$, where $\sigma_{\alpha\beta}$ is symmetric and P is the thermodynamic pressure. The antisymmetric part of the stress tensor is given by $\sigma_{\alpha\beta}^a = \frac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha)$. We further decompose the symmetric stress $\sigma_{\alpha\beta} = \bar{\sigma}_{\alpha\beta} + \frac{1}{3}\sigma_{\gamma\gamma}\delta_{\alpha\beta}$ in the traceless part $\bar{\sigma}_{\alpha\beta}$ and the trace $-p = \frac{1}{3}\sigma_{\gamma\gamma}$. We thus have

$$\sigma_{\alpha\beta}^{\text{tot}} = \bar{\sigma}_{\alpha\beta} + \frac{1}{2}(p_\alpha h_\beta - p_\beta h_\alpha) - (P + p)\delta_{\alpha\beta}. \quad (16)$$

Similarly, we write $\partial_\alpha v_\beta = \tilde{v}_{\alpha\beta} + \omega_{\alpha\beta} + \frac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}$, where the traceless symmetric part of the velocity gradient tensor is given by $\tilde{v}_{\alpha\beta} = v_{\alpha\beta} - \frac{1}{3}v_{\gamma\gamma}\delta_{\alpha\beta}$. We have again defined $v_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta + \partial_\beta v_\alpha)$ and $\omega_{\alpha\beta} = \frac{1}{2}(\partial_\alpha v_\beta - \partial_\beta v_\alpha)$.

The constitutive equations of an active polar gel can be expressed separately for the reactive and for the dissipative parts of the fluxes. We introduce the traceless quadrupolar tensor

$$q_{\alpha\beta} = \left(p_\alpha p_\beta - \frac{1}{3}p_\gamma p_\gamma \right) \delta_{\alpha\beta} \quad (17)$$

describing the anisotropy of the orientation field. The constitutive relations for the reactive fluxes then read

$$\begin{aligned} \tilde{\sigma}_{\alpha\beta}^r &= -\tau \frac{D}{Dt} \tilde{\sigma}_{\alpha\beta}^d + \zeta \Delta \mu q_{\alpha\beta} \\ &\quad + \frac{\nu_1}{2} \left(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta} \right), \end{aligned} \quad (18)$$

$$-p^r = -\tau \frac{D}{Dt} p^d + \bar{\zeta} \Delta \mu + \bar{\nu}_1 p_\gamma h_\gamma, \quad (19)$$

$$\begin{aligned} \frac{D}{Dt} p_\alpha^r &= \tau \frac{D}{Dt} \left(\frac{1}{\gamma_0} \delta_{\alpha\beta} + \frac{1}{\gamma_a} q_{\alpha\beta} \right) h_\beta \\ &\quad - \nu_1 p_\beta \tilde{v}_{\alpha\beta} - p_\alpha v_{\beta\beta}, \end{aligned} \quad (20)$$

$$r^r = \zeta q_{\alpha\beta} \tilde{v}_{\alpha\beta} + \bar{\zeta} v_{\alpha\alpha}. \quad (21)$$

Note that these reactive constitutive equations do not contribute to the noise and therefore no noise terms are added. The constitutive relations for the dissipative fluxes are given by

$$\left(1 - \tau^2 \frac{D^2}{Dt^2} \right) \tilde{\sigma}_{\alpha\beta}^d = 2\eta \tilde{v}_{\alpha\beta} + \xi_{\alpha\beta}^{(\sigma)}, \quad (22)$$

$$-\left(1 - \tau^2 \frac{D^2}{Dt^2} \right) p^d = \bar{\eta} v_{\gamma\gamma} + \xi, \quad (23)$$

$$\begin{aligned} \frac{D}{Dt} p_\alpha^d &= \left(\frac{1}{\gamma_0} \delta_{\alpha\beta} + \frac{1}{\gamma_a} q_{\alpha\beta} \right) h_\beta \\ &\quad + \lambda_1 p_\alpha \Delta \mu + \xi_\alpha^{(p)}, \end{aligned} \quad (24)$$

$$r^d = \lambda_1 p_\alpha h_\alpha + \Lambda \Delta \mu + \xi^{(r)}. \quad (25)$$

Here, we have added the noise terms $\xi_{\alpha\beta}^{(\sigma)}$, ξ , $\xi_\alpha^{(p)}$ and $\xi^{(r)}$. We have introduced two dissipative coefficients for the dynamics of the orientation field: the isotropic coefficient γ_0 and the coefficient describing γ_a anisotropic dissipation.

Note that in equations (22) and (23) we have ignored, for simplicity, anisotropic dissipative terms in the viscosity.

Combining the reactive and dissipative fluxes, we obtain the full constitutive equations with noise. In the following, we consider the simpler case where the modulus of the orientation field does not fluctuate and is $p_\gamma p_\gamma = 1$. In this case,

$$\begin{aligned} \left(1 + \tau \frac{D}{Dt} \right) \left\{ \tilde{\sigma}_{\alpha\beta} + \zeta \Delta \mu q_{\alpha\beta} + \frac{\nu_1}{2} \right. \\ \left. \times \left(p_\alpha h_\beta + p_\beta h_\alpha - \frac{2}{3}p_\gamma h_\gamma \delta_{\alpha\beta} \right) \right\} = 2\eta \tilde{v}_{\alpha\beta} + \xi_{\alpha\beta}^{(\sigma)}, \end{aligned} \quad (26)$$

$$\left(1 + \tau \frac{D}{Dt} \right) \{-p + \bar{\zeta} \Delta \mu + \bar{\nu}_1 p_\gamma h_\gamma\} = \bar{\eta} v_{\gamma\gamma} + \xi, \quad (27)$$

$$\begin{aligned} \frac{D}{Dt} p_\alpha &= \left(1 + \tau \frac{D}{Dt} \right) \frac{1}{\gamma_1} h_\alpha^\perp \\ &\quad - \nu_1 (\delta_{\alpha\beta} - p_\alpha p_\beta) p_\gamma \tilde{v}_{\beta\gamma} + \xi_\alpha^\perp, \end{aligned} \quad (28)$$

$$r = \lambda_1 p_\alpha h_\alpha + \Lambda \Delta \mu + \zeta q_{\alpha\beta} \tilde{v}_{\alpha\beta} + \bar{\zeta} v_{\alpha\alpha} + \xi^{(r)}, \quad (29)$$

where $1/\gamma_1 = 1/\gamma_0 - 1/(3\gamma_a)$. Note that in this case there is no longitudinal equation for the polarization. The transverse parts of the field h_α and of the orientation noise $\xi_\alpha^{(p)}$ are given by $h_\alpha^\perp = (\delta_{\alpha\beta} - p_\alpha p_\beta) h_\beta$ and $\xi_\alpha^\perp = (\delta_{\alpha\beta} - p_\alpha p_\beta) \xi_\beta^{(p)}$.

We study here a one-component active gel within the framework of a linear theory. The equations that we obtain only on symmetry grounds do not contain any polar term and would be identical for a system with nematic ordering. Note that the constitutive equations of references [11, 12] obtained from microscopic considerations contain real polar terms in the constitutive equation for the polarization. We consider these terms here as non-linear terms and we ignore them. Polar terms also arise in the generalization of the theory to multicomponent systems done in reference [24].

Using the linear response functions which follow from these constitutive equations, we can determine the noise correlations such that the FDT is satisfied. The response functions are given in Appendix B. The noise correlations are thus given by

$$\begin{aligned} \langle \xi_{\alpha\beta}^{(\sigma)}(t, \mathbf{x}) \xi_{\gamma\delta}^{(\sigma)}(t', \mathbf{x}') \rangle &= 2k_B T \eta \left[(\delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma}) \right. \\ &\quad \left. - \frac{2}{3} \delta_{\alpha\beta} \delta_{\gamma\delta} \right] \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'), \end{aligned} \quad (30)$$

$$\langle \xi_\alpha^\perp(t, \mathbf{x}) \xi_\beta^\perp(t', \mathbf{x}') \rangle = 2 \frac{k_B T}{\gamma_1} [\delta_{\alpha\beta} - p_\alpha p_\beta] \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'), \quad (31)$$

$$\langle \xi^{(r)}(t, \mathbf{x}) \xi^{(r)}(t', \mathbf{x}') \rangle = 2k_B T \Lambda \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'), \quad (32)$$

$$\langle \xi(t, \mathbf{x}) \xi(t', \mathbf{x}') \rangle = 2k_B T \bar{\eta} \delta(t - t') \delta(\mathbf{x} - \mathbf{x}'). \quad (33)$$

All the cross-correlations between the various noise terms vanish.

For the simplifications used so far, namely ignoring the anisotropy of the friction η as well as neglecting longitudinal fluctuations of p_α , all friction terms are independent of the state variables. In this case, the corresponding

noises which obey the fluctuation-dissipation theorem are additive with constant noise strength. If the anisotropy of friction is taken into account or if both transverse and longitudinal fluctuations of p_α are discussed, friction becomes state dependent. The fluctuation-dissipation theorem then imposes noise amplitudes which are also state dependent. Such multiplicative noise requires a more careful treatment. The consequences of state-dependent dissipation are discussed in Appendix D.3.

4 Breaking of the fluctuation-dissipation theorem

The fluctuation-dissipation theorem is a consequence of causality, microscopic reversibility and thermodynamics close to equilibrium. If the system is driven by thermodynamic forces further away from equilibrium, the FDT (9) breaks down and the noise correlations are no longer fixed by thermodynamic arguments. This can be discussed in a general context using the symmetry of the noisy equations with respect to time-reversal.

We consider the simple case where the linear response relations (7) can be written in time domain as a first-order differential equation

$$\dot{\phi}_i = A_{ij}f_j + \xi_i. \quad (34)$$

Note that the thermodynamic forces in general derive from a potential F , $f_i = -\partial F/\partial\phi_i + f_i^{\text{ext}}$, where f_i^{ext} denote externally applied forces.

The probability of a trajectory $\phi_i(t)$ of the dynamics then is of the form [25]

$$P[\phi_i(t)] \sim \exp\{-S[\phi_i(t)]\} \quad (35)$$

with the action

$$S[\phi_i(t)] = \frac{1}{4} \sum_{ik} \int dt \left(\dot{\phi}_i - \sum_j A_{ij}f_j \right) \times B_{ik} \left(\dot{\phi}_k - \sum_l A_{kl}f_l \right), \quad (36)$$

see Appendix C. The weight $\exp(-S[\phi_i(t)])$ forms the basis of a Path Integral representation of the stochastic process. Here, the symmetric matrix $B_{ij} = B_{ji}$ describes noise correlations

$$\langle \xi_i(t)\xi_j(t') \rangle = 2(B_{ij})^{-1}\delta(t-t'). \quad (37)$$

Decomposing the matrix $A_{ij} = A_{ij}^s + A_{ij}^a$ symmetric and antisymmetric parts A_{ij}^s and A_{ij}^a , thermodynamics imposes that $A_{ij}^s B_{jk} = \beta\delta_{ik}$, where $\beta = 1/(k_B T)$. The matrix $B_{ij} = 0$ if the time-reversal signatures ϵ_i and ϵ_j of variables ϕ_i and ϕ_j differ. Furthermore, $A_{ij} = A_{ji}\epsilon_i\epsilon_j$, has antisymmetric and symmetric parts, depending on the time-reversal signature of the variables. This implies that B_{ij} and A_{ij} have the block representations given in equations (C.5) and (C.7).

At thermodynamic equilibrium, the time-reversal invariance of the dynamics $P[\phi_i(t)] = P[\epsilon_i\phi_i(-t)]$ implies that the action is invariant under time-reversal $S[\phi_i(t)] = S[\epsilon_i\phi_i(-t)]$. If the system is driven away from equilibrium, time-reversal invariance is broken

$$S[\phi_i(t)] - S[\epsilon_i\phi_i(-t)] = -\beta W_{\text{diss}}, \quad (38)$$

where

$$W_{\text{diss}} = F(\phi_i(t_0)) - F(\phi_i(t_{\text{max}})) + \int_{t_0}^{t_{\text{max}}} \sum_i \dot{\phi}_i f_i^{\text{ext}} dt \quad (39)$$

is the dissipated work performed on the system. From this property of the action under time-reversal follows the fluctuation theorem [26–28]

$$\frac{P[\phi_i(t)]}{P[\epsilon_i\phi_i(-t)]} = \exp\{\beta W_{\text{diss}}\}. \quad (40)$$

In the limit of vanishing W_{diss} , the fluctuation theorem (40) reduces to the FDT [29,30]. Further away from equilibrium, the FDT is broken, see Appendix C.

We can use this framework to describe fluctuations and FDT breaking in the active gel by generalizing these arguments to a linear dynamics with memory kernels, see Appendix C.3. We identify the variables $\dot{\phi}_i$ with $\sigma_{\alpha\beta}$, $\partial p_\alpha/\partial t$ and r , respectively. With this choice, the f_i are $u_{\alpha\beta}$, h_α and $\Delta\mu$. The time-reversal signatures are $\epsilon_\sigma = -1$, $\epsilon_p = 1$ and $\epsilon_r = 1$.

5 Fluctuations away from thermal equilibrium

If the system is driven away from thermodynamic equilibrium, the fluctuation-dissipation theorem breaks down and the form and amplitude of noise correlations are no longer fixed by the requirement that the FDT must be satisfied.

In this case, we can estimate the form and strength of noise terms using physical arguments as already done in reference [31] in a different context for hair cells of the inner ear. In active gels, active stresses are generated for example by motor proteins which are driven by the hydrolysis of a fuel ATP. The chemical energy transduced per ATP molecule under physiological conditions is about $\Delta\mu \simeq 20k_B T$. Because this significantly exceeds $k_B T$, we expect that athermal noise that violates the FDT can become relevant in realistic cellular situations. We can estimate the strength of non-equilibrium fluctuations of the stress that result from fluctuations of the force generation of motor proteins. In the simple case of an isotropic gel, such active stress fluctuations can be described by a noise $\bar{\xi}_{\alpha\beta}^{(\sigma)}$ with zero average and [31]

$$\langle \bar{\xi}_{\alpha\beta}^{(\sigma)}(t, \mathbf{x}) \bar{\xi}_{\gamma\delta}^{(\sigma)}(t', \mathbf{x}') \rangle = p(1-p)c_m f_0^2 a^2 e^{-|t-t'|/\tau_m} \times \cos(\omega_0 t) \left[(\delta_{\alpha\gamma}\delta_{\beta\delta} + \delta_{\alpha\delta}\delta_{\beta\gamma}) - \frac{2}{3}\delta_{\alpha\beta}\delta_{\gamma\delta} \right] \delta(\mathbf{x}-\mathbf{x}'). \quad (41)$$

Here, a denotes the mesh size of the gel, c_m is the concentration of independently acting force generators (these could be individual motors or small aggregates of motors) and f_0 is the stall force of such force generators. Force generation is associated with a characteristic time scale τ_m . The probability for a force generator to be active and generate a force is p . The force fluctuation of a force generator is of order f_0^2 and it is correlated over a time τ_m . In general, groups of motors can generate noisy oscillations of frequency ω_0 [32] which leads to the oscillations in the relaxation. The force generators being independent, the stress correlation is proportional to their density. The average active stress can be expressed in these quantities as $\zeta \Delta \mu \simeq c_m a f_0 p$. For $\omega_0 = 0$, the noise fluctuations can be approximated on long time scales as

$$\langle \bar{\xi}_{\alpha\beta}^{(\sigma)}(t, \mathbf{x}) \bar{\xi}_{\gamma\delta}^{(\sigma)}(t', \mathbf{x}') \rangle \simeq p(1-p) c_m f_0^2 a^2 \tau_m \times \left[(\delta_{\alpha\gamma} \delta_{\beta\delta} + \delta_{\alpha\delta} \delta_{\beta\gamma}) - \frac{2}{3} \delta_{\alpha\beta} \delta_{\gamma\delta} \right] \delta(t-t') \delta(\mathbf{x}-\mathbf{x}'). \quad (42)$$

By comparing these noise strengths to the thermal noise equation (33), we can define the effective temperatures for active shear noise

$$k_B T_{\text{eff}} \simeq p(1-p) \frac{c_m f_0^2 a^2 \tau_m}{2\eta}. \quad (43)$$

An alternative way to obtain fluctuation correlations far from equilibrium which is followed in reference [33] would be to introduce the dependence of the activity coefficient ζ as a function of the local density and to retain the associated non-linear terms. This will be the subject of a future publication

6 Density fluctuations

As an illustration of the general equations for noisy active gels presented in the previous sections, we now discuss the correlation function of density fluctuations in a compressible active polar gel. Note that, as in the whole paper, we consider here the gel as a one-component compressible system and that we therefore ignore any permeation of the solvent with respect to the gel. Our analysis could also be valid for an incompressible active gel film treated as a two-dimensional system, the thickness fluctuations of the film are then equivalent to fluctuations in the two-dimensional density. The relaxation modes of an active film have been calculated in reference [21] using the same hydrodynamic approach and give the singularities of the density correlation function. The gel has an average density ρ_0 and we only consider small fluctuations around this density with a local density $\rho_0 + \rho$. We consider the case where the polarization p_α has a unit modulus and a uniformly polarized system where the average polarization is oriented along the z -direction. The free energy of the active gel depends on the density fluctuation ρ and on the local polarization p_α . We write it as

$$F = \int d\mathbf{x} \left[\frac{K}{2} (\nabla p_\alpha)^2 - \frac{1}{2} h_\parallel \mathbf{p}^2 + \alpha \rho \nabla \cdot \mathbf{p} + \frac{\chi}{2} \rho^2 \right]. \quad (44)$$

We use here an approximation where the three Frank constants describing the rotational elasticity of the polarization are equal. The field h_\parallel is a Lagrange multiplier insuring the normalization of the polarization. The compressibility of the gel, at constant polarization field configuration, is $1/(\chi \rho_0)$. For a polar system there is a coupling between the density fluctuations and the divergence of the polarization characterized by the parameter α . From this free energy, one can calculate the orientational field $h_\alpha = -\frac{\delta F}{\delta p_\alpha} = K \nabla^2 p_\alpha + \alpha \partial_\alpha \rho$ and the pressure field $P = \chi \rho + \alpha \partial_\alpha p_\alpha$.

We decompose all quantities in Fourier components both in space and in time $\rho(\mathbf{x}) = \int \frac{d\omega}{2\pi} \frac{d\mathbf{q}}{(2\pi)^3} \tilde{\rho}(\mathbf{q}, \omega) \exp(i\mathbf{q}\mathbf{x} - \omega t)$ and similarly for the components of the velocity and the polarization. The calculation of the density correlation function is straightforward although lengthy. The density correlation function is defined as $S(\mathbf{x}, t) = \langle \rho(\mathbf{x}, t) \rho(\mathbf{0}, 0) \rangle$. We first calculate its Fourier transform $\tilde{S}(\mathbf{q}, \omega) = \langle \tilde{\rho}(\mathbf{q}, \omega) \tilde{\rho}^*(\mathbf{q}, \omega) \rangle$ where $*$ denotes a complex conjugate.

The calculation of the dynamic correlation function requires the solution of dynamic equations for the variables $\tilde{\rho}$, \tilde{p}_α and \tilde{v}_z . The equations for the velocity are obtained by inserting the constitutive equation (6) in the force balance equation $\partial_\alpha (\sigma_{\alpha\beta} - P \delta_{\alpha\beta}) = 0$. The density is related to the velocity by the mass conservation equation $\partial_t \rho + \partial_\alpha (v_\alpha \rho) = 0$. We obtain a set of equations linear in $\tilde{\rho}$, \tilde{p}_α and \tilde{v}_z , with source terms provided by the noises ξ , $\xi_{\alpha\beta}^{(\sigma)}$, ξ_α^\perp . The expression for $\tilde{\rho}$ reads

$$\tilde{\rho}(\mathbf{q}, \omega) = \frac{1}{\Delta} \left[\left(\frac{Kq^2}{\tilde{\gamma}_1} + \frac{\zeta \Delta \mu}{\tilde{\eta}} - i\omega + \frac{i\alpha q_z}{\tilde{\eta}} \right) \times (iq_\alpha q_\beta \xi_{\alpha\beta}^{(\sigma)} + iq_\alpha q_\alpha \xi) - (((\nu_1 K q^2 + 2\zeta \Delta \mu) q_z) + i\alpha q^2) \times \left[\frac{1}{\tilde{\eta}} (iq_\beta \xi_{z\beta}^{(\sigma)} + iq_z \xi) + iq_\alpha \xi_\alpha^\perp \right] \right], \quad (45)$$

with

$$\Delta = \left[\left(\chi q^2 + i \left(\tilde{\eta} + \frac{4}{3} \eta \right) \omega q^2 - i\nu_1 q_z q_\perp^2 \alpha \right) \times \left(\omega - \frac{\alpha q_z}{\tilde{\eta}} + i \left(\frac{Kq^2}{\tilde{\gamma}_1} + \frac{\zeta \Delta \mu}{\tilde{\eta}} \right) + ((\nu_1 K q^2 + 2\zeta \Delta \mu) q_z) + i\alpha q^2 \right) \times \left(q_z \omega \left(\frac{\nu_1 + 1}{2} + \frac{\tilde{\eta} + \frac{4}{3} \eta}{\tilde{\eta}} \right) - \frac{\alpha q_\perp^2}{\tilde{\gamma}_1} - i \frac{\chi q_z}{\tilde{\eta}} \right) \right], \quad (46)$$

$$\frac{1}{\tilde{\eta}} = \frac{((\nu_1 - 1) q_\perp^2 - (\nu_1 + 1) q_z^2)}{2\eta q^2} = \frac{((\nu_1 - 1) \cos^2 \theta - (\nu_1 + 1) \sin^2 \theta)}{2\eta}, \quad (47)$$

$$\frac{1}{\tilde{\gamma}_1} = \frac{1}{\gamma_1} + \frac{1}{\tilde{\eta}} \frac{(\nu_1 - 1)}{2}, \quad (48)$$

where $\frac{q_z}{q} = \sin \theta$ and $\frac{q_\perp}{q} = \cos \theta$. For simplicity we have chosen units where $\rho_0 = 1$.

For any finite $\zeta\Delta\mu$, there is always a scale at which the system becomes unstable. The instability arises when $\Delta(\mathbf{q}, \omega) = 0$, *i.e.* when both the real and the imaginary parts of Δ vanish.

The small- q limit is particularly simple to discuss and turns out to be the only case relevant to the small- $\zeta\Delta\mu$ regime we consider here. One obtains for angles θ sufficiently different from $\frac{\pi}{4}$ an activity threshold at finite wave vector given by

$$\zeta\Delta\mu_c = - \left(\frac{\tilde{\eta}}{\tilde{\gamma}_1} - \nu_1 \cos^2 \theta \right) \frac{(K - \frac{\alpha^2 \cos^2 \theta}{\chi})}{\cos 2\theta} q^2, \quad (49)$$

with a characteristic frequency

$$\omega_c = - \frac{\alpha q}{\chi} \left(\frac{1}{\tilde{\eta}} - \frac{2}{\tilde{\gamma}_1} \right) \sin \theta \cos^2 \theta \zeta\Delta\mu_c. \quad (50)$$

The instability is a convective instability occurring at a finite frequency in which the perturbation travels with an amplitude growing as it travels. The ultimate behavior of the system depends on non-linear terms and on the boundary conditions. For a gel slab of thickness L with its polarization orthogonal to the lateral surfaces, $\theta = \frac{\pi}{2}$, $q_\perp = 0$, $q_z = \frac{\pi}{L}$, one recovers the threshold derived in [15] and $\omega_c = 0$: the system becomes unstable with respect to a steady state in which both a shear and a polarization gradient set in. Note that, at threshold, no density heterogeneity appears. For a gel slab with a polarization parallel to the lateral surfaces, a similar instability is obtained. In that case the density couples linearly at threshold to the polarization field deformation and to the shear.

For θ close to $\frac{\pi}{4}$, more precisely $|\frac{\chi \cos 2\theta}{\tilde{\eta}}| < |\frac{\alpha^2 q^2 \sin^2 \theta \cos^2 \theta}{\chi} (\frac{1}{\tilde{\eta}} - \frac{2}{\tilde{\gamma}_1}) (\nu_1 \cos^2 \theta + \frac{\tilde{\eta} + \frac{3}{2}\eta}{\tilde{\eta}})|$, the activity threshold $\zeta\Delta\mu_c$ takes a value which is independent of the wave vector q . Since the threshold in this case has no reason to remain small, it will typically be outside the validity range of the small $\zeta\Delta\mu$ regime discussed here.

The correlation function $\hat{S}(\mathbf{q}, \omega)$ can be calculated in a straightforward way using equation (45) and the noise correlations (30, 33). Its expression is somewhat lengthy. Power counting arguments show that the equal-time correlation function $S(\mathbf{q}, t = 0)$ is finite for any q , $\zeta\Delta\mu$ values such that the instability threshold is not reached. Upon approaching the threshold, $S(\mathbf{q}, t = 0)$ diverges like $\frac{1}{\zeta\Delta\mu - \zeta\Delta\mu_c}$ upon varying activity or like $\frac{1}{q - q_c}$ as a function of q vectors. In the limit where $q_z = 0$, $\alpha = 0$, the activity does not play any role and $S(\mathbf{q}, t = 0)$ is given by the thermodynamic result $S(\mathbf{q}, t = 0) = kT/\chi$. This result implies that the prefactor of the diverging term goes to zero in that limit. It can be checked explicitly that it is proportional to α^2 .

Although they are related, the instability that we find is different from that obtained by Simha *et al.* [5] who predict a divergence at low wave vectors as $S(\mathbf{q}, t = 0) \sim 1/q^2$. This is due to the different dynamics of the density field. We consider here a one-component system where the variation of the density is driven by the velocity field whereas they implicitly consider a two-component system where the change in density is driven by diffusion.

7 Concluding remarks

The aim of this paper is to propose a generalized hydrodynamic theory of polar active gels including fluctuations to describe active properties of the cytoskeleton on mesoscopic scales. This theory has been constructed by introducing noise terms in the hydrodynamic equations proposed in references [7, 8].

As a first step we considered only thermal noise. Thermal noise can be introduced in a systematic way by imposing that close to thermal equilibrium the system satisfies the fluctuation-dissipation theorem. All dissipative kinetic coefficients are then directly linked to fluctuation amplitudes by a generalized Einstein relation. In the simpler case where the polarization has a fixed modulus and only the orientation fluctuates, all the noise correlations are local in time and in space and depend only on the dissipative transport coefficients such as the translational and rotational viscosities.

The systematic and very general analysis of Section 3 shows that the fluctuation-dissipation theorem is violated at second order in $\Delta\mu$. Only in the absence of external driving is time-reversal invariance obeyed. In the limit of small $\Delta\mu$, we have calculated the density fluctuations in the gel. They diverge at a contractility threshold $\zeta\Delta\mu_c$ which goes to zero like wave vector squared. This divergence signals an instability in general towards traveling waves and towards sheared steady states for $\theta = 0$ and $\frac{\pi}{2}$. The equal-time correlation function reflects these divergences, the $\frac{1}{\zeta\Delta\mu - \zeta\Delta\mu_c}$ or $\frac{1}{q - q_c}$ diverging terms being proportional to the square of the coupling constant α . Therefore, an active polar gel is always unstable in the thermodynamic limit. Only a finite system in which the critical wavelength is suppressed can be stable. This is consistent with our previous results obtained in references [15, 21].

When the system is driven far from thermal equilibrium, fluctuations on large scales have a noticeable contribution coming from the stochasticity of active processes such as the action of motor molecules. In this case, there is no general principle which imposes conditions on the correlation functions of the stress fluctuations. However, typical features of the fluctuations can be estimated from microscopic pictures for the active processes in the gel. The simple scaling arguments given in Section 5 estimate the noise strength based on the motor density, the gel density and the characteristic times of motor action. In general on the mesoscopic scale oscillations could occur which are reflected in a general correlation function by a frequency ω_0 . For the non-oscillating case or for long times we can define, from these estimates, an effective temperature for the shear correlations which is larger than the ambient temperature if active noise dominates. This implies the existence of larger fluctuations as compared to thermodynamic equilibrium as observed by [18].

The stochastic differential equations for the hydrodynamic fluctuations presented here are simple as long as kinetic coefficients remain independent of the state variables themselves. In such a linear response case, noise is additive. In a general hydrodynamic theory which is obtained by a systematic expansion in terms of thermody-

dynamic forces and fields, kinetic coefficients can become state-dependent. In active gels this is the case because viscosity is anisotropic in oriented gels and the friction of the orientation field is itself anisotropic. Furthermore, reactive coefficients also become state-dependent such as those which describe anisotropic active stresses. State-dependent friction induces state-dependent or multiplicative noise and in addition generates new drift terms in the dynamic equations. Similarly, state-dependent reactive terms also induce additional drift but do not contribute to fluctuations.

The results given in this paper provide a framework to study the fluctuations of the cytoskeleton in cells and in *in vitro* acto-myosin systems on mesoscopic scales where many motors and filaments cooperate. Recent experiments have, for example studied in great details the motion of beads in an actin gel containing myosin motors [18]. We are presently using this generalized hydrodynamic theory to describe fluctuations observed in such experiments.

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Appendix A. Maxwell model in the fluctuating velocity ensemble

In the ensemble where the shear deformations fluctuate, we identify the stress $\sigma_{\alpha\beta}$ with forces f_i and the deformation tensor $u_{\alpha\beta}$, where $du_{\alpha\beta}/dt = v_{\alpha\beta}$ (or $-i\omega u_{\alpha\beta} = v_{\alpha\beta}$), with the conjugate variables ϕ_i . Writing

$$v_{\alpha\beta} = \frac{1 - i\omega\tau}{2\eta} \sigma_{\alpha\beta} + \bar{\xi}_{\alpha\beta}, \quad (\text{A.1})$$

where $\bar{\xi}_{\alpha\beta} = (1 - i\omega\tau)\xi_{\alpha\beta}/(2\eta)$. The response function $\partial u_{\alpha\beta}/\partial\sigma_{\gamma\delta}$ is given by

$$\bar{\chi}_{\alpha\beta\gamma\delta} = (\delta_{\alpha\gamma}\delta_{\beta\delta} + \delta_{\alpha\delta}\delta_{\beta\gamma}) \frac{-1 + i\omega\tau}{4\eta i\omega}. \quad (\text{A.2})$$

The FDT implies that

$$\langle u_{\alpha\beta}(\omega, \mathbf{x}) u_{\gamma\delta}(\omega', \mathbf{x}') \rangle = 2\pi \frac{k_B T}{2\eta\omega^2} \times (\delta_{\alpha\gamma}\delta_{\beta\delta} + \delta_{\alpha\delta}\delta_{\beta\gamma}) \delta(\omega + \omega') \delta(\mathbf{x} - \mathbf{x}'). \quad (\text{A.3})$$

From this, we deduce that

$$\langle \bar{\xi}_{\alpha\beta}(\omega, \mathbf{x}) \bar{\xi}_{\gamma\delta}(\omega', \mathbf{x}') \rangle = 2\pi \frac{k_B T}{2\eta} \times (\delta_{\alpha\gamma}\delta_{\beta\delta} + \delta_{\alpha\delta}\delta_{\beta\gamma}) \delta(\omega + \omega') \delta(\mathbf{x} - \mathbf{x}'), \quad (\text{A.4})$$

which is equivalent to equation (15).

Appendix B. Linear response functions of active polar gels in frequency domain

The imaginary parts of the linear response functions determine the noise correlations required such that FDT is obeyed. For an active polar gel, the response functions have the following form. The linear response between $\sigma_{\alpha\beta}$ and $u_{\alpha\beta}$ in frequency domain is given by

$$\chi_{\alpha\beta\gamma\delta}^{\sigma u} = \frac{i\omega\eta}{1 + i\omega\tau} \left[(\delta_{\alpha\gamma}\delta_{\beta\delta} + \delta_{\alpha\delta}\delta_{\beta\gamma}) - \frac{2}{3}\delta_{\alpha\beta}\delta_{\beta\gamma} \right]. \quad (\text{B.1})$$

The cross terms on the linear response

$$\chi_{\alpha\beta\gamma}^{\sigma h} = -\frac{\nu_1}{2} \left(p_\alpha \delta_{\beta\gamma} + p_\beta \delta_{\alpha\gamma} - \frac{2}{3} p_\gamma \delta_{\alpha\beta} \right) \quad (\text{B.2})$$

and $\chi^{\sigma\delta\mu}$ are both real. Furthermore, we have

$$\chi_{\alpha\beta}^{p\perp h} = \frac{1 - i\omega\tau}{-i\omega\gamma_1} \delta_{\alpha\beta} \quad (\text{B.3})$$

and $\chi_{\alpha}^{p\perp\Delta\mu} = 0$, while χ^{pu} is real. Finally, $\chi^{r\Delta\mu} = i\Lambda/\omega$ and $\chi^{rh} = i\lambda_1 p_\alpha/\omega$, while χ^{ru} is real.

Appendix C. Breaking of time-reversal invariance

Appendix C.1. Time-reversal symmetry

We consider the behavior of the system under time-reversal transformations

$$\phi_i(t) \rightarrow \phi'_i(t) = \epsilon_i \phi_i(-t), \quad (\text{C.1})$$

where $\epsilon_i = \pm 1$ describes the time-reversal signature of the variable ϕ_i . For example, a displacement variable has $\epsilon = 1$, while for a velocity $\epsilon = -1$. The probability of the time-reversed path is described by the action

$$S[\epsilon_i \phi_i(-t)] = \frac{1}{4} \int dt \left[\sum_{ij} \epsilon_i \epsilon_j B_{ij} \dot{\phi}_i \dot{\phi}_j + \sum_{ijk} \epsilon_i \epsilon_k (B_{ij} A_{jk} + B_{ji} A_{jk}) \dot{\phi}_i f_k + \sum_{ijkl} \epsilon_j \epsilon_l A_{ij} B_{ik} A_{kl} f_j f_l \right], \quad (\text{C.2})$$

where we have used that $\dot{\phi}'_i(t) = -\epsilon_i \dot{\phi}_i(-t)$ and the forces transform as $f'_i(t) = \epsilon_i f_i(-t)$ with the same time-reversal signatures as the corresponding fields. We first discuss the case where external forces are absent, $f_i^{\text{ext}} = 0$. If the system is at thermodynamic equilibrium, the reversibility of microscopic processes becomes manifest at mesoscopic and macroscopic scales and the process becomes invariant with respect to time-reversal. This implies that if the variables ϕ_i return to their initial values, $\phi_i(t_0) = \phi_i^A$ and $\phi_i(t_{\text{max}}) = \phi_i^A$, the probability of the forward and backward trajectories are the same: $P[\phi_i(t)] = P[\epsilon_i \phi_i(-t)]$.

This implies that the action is invariant under time-reversal: $S[\phi_i(t)] = S[\epsilon_i \phi_i(-t)]$.

This invariance of the action under time-reversal imposes conditions on the matrices B_{ij} and A_{ij} which we can determine by comparing the action of the time-reversed path $S[\epsilon_i \phi_i(-t)]$ with

$$S[\phi_i] = \frac{1}{4} \int dt \left[\sum_{ij} B_{ij} \dot{\phi}_i \dot{\phi}_j - \sum_{ijk} (B_{ij} A_{jk} + B_{ji} A_{jk}) \dot{\phi}_i f_k + \sum_{ijkl} A_{ij} B_{ik} A_{kl} f_j f_l \right]. \quad (\text{C.3})$$

Time-reversal symmetry first requires that

$$B_{ij} = B_{ij} \epsilon_i \epsilon_j. \quad (\text{C.4})$$

This implies that $B_{ij} = 0$ if $\epsilon_i \epsilon_j = -1$. The matrix B_{ij} thus only links those variables ϕ_i with the same time-reversal signature ϵ_i .

If the variables ϕ_i are grouped such that ϕ_α with $\alpha = 1, \dots, p$ and ϕ_μ with $\mu = p+1, \dots, N$, such that $\epsilon_\alpha = 1$ and $\epsilon_\mu = -1$, the matrix B has the block representation

$$B_{ij} = \left(\begin{array}{ccc|ccc} B_{11} & B_{21} & \dots & B_{p1} & 0 & \dots & 0 \\ B_{21} & B_{22} & \dots & B_{p2} & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & & \vdots \\ B_{p1} & B_{p2} & \dots & B_{pp} & 0 & \dots & 0 \\ \hline 0 & 0 & \dots & 0 & B_{p+1,p+1} & \dots & B_{N,p+1} \\ \vdots & \vdots & & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 0 & B_{N,p+1} & \dots & B_{N,N} \end{array} \right). \quad (\text{C.5})$$

Since B_{ij} is symmetric and since each block can be inverted independently, the inverse $(B_{ij})^{-1}$ has the same block structure. From this argument it follows that time-reversal symmetry requires that only noise variables with the same time signature can be correlated.

While the matrix B_{ij} is symmetric, A_{ij} is considered to be a general matrix without specific symmetry requirements. It is convenient to decompose $A_{ij} = A_{ij}^s + A_{ij}^a$ in a symmetric and antisymmetric part, $A_{ij}^s = A_{ji}^s$ and $A_{ij}^a = -A_{ji}^a$. In addition to equation (C.4), two further conditions have to be imposed on the matrix A_{ij} for time-reversal symmetry to be satisfied. We first state these conditions and then demonstrate that these conditions generically lead to a time-reversal invariant theory.

The first condition on A_{ij} can be written as

$$A_{ij} = A_{ji} \epsilon_i \epsilon_j. \quad (\text{C.6})$$

Condition (C.6) implies that A_{ij} is symmetric if $\epsilon_i = \epsilon_j$ and antisymmetric if $\epsilon_i \neq \epsilon_j$. A_{ij} thus has the block

structure

$$A_{ij} = \left(\begin{array}{cccc|cccc} A_{11}^s & A_{21}^s & \dots & A_{p1}^s & -A_{p+1,1}^a & \dots & -A_{N,1}^a \\ A_{21}^s & A_{22}^s & \dots & A_{p2}^s & -A_{p+1,2}^a & \dots & -A_{N,2}^a \\ \vdots & \vdots & \ddots & \vdots & \vdots & & \vdots \\ A_{p1}^s & A_{p2}^s & \dots & A_{pp}^s & -A_{p+1,p}^a & \dots & -A_{N,p}^a \\ \hline A_{p+1,1}^a & A_{p+1,2}^a & \dots & A_{p+1,p}^a & A_{p+1,p+1}^s & \dots & A_{N,p+1}^s \\ \vdots & \vdots & & \vdots & \vdots & \ddots & \vdots \\ A_{N,1}^a & A_{N,2}^a & \dots & A_{N,p}^a & A_{N,p+1}^s & \dots & A_{N,N}^s \end{array} \right). \quad (\text{C.7})$$

The second condition is

$$\sum_j B_{ij} A_{jk}^s = \beta \delta_{ik}, \quad (\text{C.8})$$

where β is an arbitrary parameter. Time translation invariance requires that all terms in the action are invariant. For the last term in (C.3) this implies

$$\sum_{ijkl} A_{ij} B_{ik} A_{kl} f_j f_l = \sum_{ijkl} \epsilon_j \epsilon_l A_{ij} B_{ik} A_{kl} f_j f_l. \quad (\text{C.9})$$

This relation indeed follows from the three conditions (C.4, C.6) and (C.8).

The remaining second term in (C.3) consists of two parts which we discuss separately. With conditions (C.4, C.6) and (C.8), we find

$$\int_{t_0}^{t_{\max}} dt \sum_{ijk} B_{ij} A_{jk}^s \dot{\phi}_i \partial_k F = \beta (F(\phi_i(t_{\max})) - F(\phi_i(t_0))) \quad (\text{C.10})$$

and

$$- \int_{t_0}^{t_{\max}} dt \sum_{ijk} \epsilon_i \epsilon_k B_{ij} A_{jk}^s \dot{\phi}_i \partial_k F = -\beta (F(\phi_i(t_{\max})) - F(\phi_i(t_0))). \quad (\text{C.11})$$

In addition, the equivalent term involving the antisymmetric part of A_{ij} automatically satisfied time-reversal invariance because only terms with $\epsilon_i \epsilon_k = -1$ contribute

$$\sum_{ijk} \epsilon_i \epsilon_k B_{ij} A_{jk}^a \dot{\phi}_i f_k = - \sum_{ijk} B_{ij} A_{jk}^a \dot{\phi}_i f_k. \quad (\text{C.12})$$

From (C.10) and (C.11), we see that time-reversal invariance $P[\phi_i(t)] = P[\epsilon_i \phi_i(-t)]$ is ensured if the initial and final states are identical, $\phi_i(t_{\max}) = \phi_i(t_0)$. The structure of the kinetic coefficients given by (C.7) reflects the Onsager symmetry relations. Dissipative couplings (with $\epsilon_i = \epsilon_j$) are symmetric ($A_{ij}^s = A_{ji}^s$) and contribute to the noise ($B_{ij}^{-1} = A_{ij}^s \beta^{-1}$), while reactive coupling are antisymmetric ($A_{ij}^a = -A_{ji}^a$) and do not contribute to the noise.

Appendix C.2. Time-reversibility and fluctuation theorems

We have shown that if equations (C.4, C.6) and (C.8) are satisfied, the action is invariant with respect to time-reversal $S[\phi_i(t)] = S[\epsilon_i \phi_i(-t)]$ in the absence of external forces. This corresponds to thermodynamic equilibrium.

Using the results from the previous section, we can generalize this in out-of-equilibrium situations. If external forces are applied and paths end at different points in phase space as they start,

$$S[\phi_i(t)] - S[\epsilon_i \phi_i(-t)] = -\beta W_{\text{diss}}, \quad (\text{C.13})$$

where the dissipated work is given by

$$W_{\text{diss}} = F(\phi_i(t_0)) - F(\phi_i(t_{\text{max}})) + \int_{t_0}^{t_{\text{max}}} \sum_i \dot{\phi}_i f_i^{\text{ext}} dt. \quad (\text{C.14})$$

This implies furthermore

$$\frac{P[\phi_i(t)]}{P[\epsilon_i \phi_i(-t)]} = \exp\{\beta W_{\text{diss}}\}. \quad (\text{C.15})$$

This is a simple form of a general fluctuation theorem (FT) which we have thus derived [26–28]. In the limit of small perturbations from equilibrium, the FT becomes the FDT which fixes the parameter β .

At equilibrium, we have the distribution $P_0[\phi_i(t)]$ which obeys $P_0[\phi_i(t)] = P_0[\epsilon_i \phi_i(-t)]$. Close to equilibrium, we write $P[\phi_i(t)] = P_0[\phi_i] + \delta P[\phi_i(t)]$. For small dissipative work (small forces f_i^{ext}), we can expand both sides of the fluctuation theorem (assuming for simplicity $\phi_i(t_0) = \phi_i(t_{\text{max}})$) to linear order in δP and W_{diss}

$$\delta P[\phi_i(t)] - \delta P[\epsilon_i \phi_i(-t)] \simeq \beta P_0[\phi_i(t)] \int_{t_0}^{t_{\text{max}}} dt' \sum_i \dot{\phi}_i f_i^{\text{ext}}. \quad (\text{C.16})$$

We define the linear response function at equilibrium

$$\begin{aligned} \langle \delta \phi_i(t) \rangle &= \int \mathcal{D}\phi_1 \dots \mathcal{D}\phi_N \phi_i(t) \delta P[\phi_i] \\ &\simeq \int_{t_0}^{t_{\text{max}}} dt' \sum_j \chi_{ij}(t-t') f_j^{\text{ext}}(t') \end{aligned} \quad (\text{C.17})$$

and the linear response of the time-reversed action

$$\begin{aligned} \langle \delta \bar{\phi}_i(t) \rangle &= \int \mathcal{D}\phi_1 \dots \mathcal{D}\phi_N \phi_i(t) \delta P[\epsilon_k \phi_k(-t)] \\ &\simeq \int_{t_0}^{t_{\text{max}}} dt' \sum_j \epsilon_i \epsilon_j \chi_{ij}(-t+t') f_j^{\text{ext}}(t'). \end{aligned} \quad (\text{C.18})$$

With the definition $C_{ij}(t) = \langle \phi_i(t+\tau) \phi_j(\tau) \rangle$, with $C_{ij}(t) = C_{ji}(-t)$, the FT, equation (C.15) implies

$$\chi_{ij}(t) - \epsilon_i \epsilon_j \chi_{ij}(-t) \simeq -\beta \frac{d}{dt} C_{ij}(t). \quad (\text{C.19})$$

This is equivalent to the FDT

$$k_B T \chi_{ij}(t) = -\theta(t) \frac{d}{dt} C_{ij}(t) \quad (\text{C.20})$$

if $\beta = (k_B T)^{-1}$, where $\theta(t)$ denotes the Heavyside function. This equivalence follows using the time-reversal symmetry of $C_{ij}(t) = \epsilon_i \epsilon_j C_{ij}(-t)$.

Thus, the FDT is broken by the quadratic terms in the force in the FT equation (C.15). The FT, however, is valid also for large forces f_i^{ext} and thus far beyond linear response.

Appendix C.3. Generalization to time-dependent linear response

We now consider the generalized Langevin equation

$$\dot{\phi}_i = \int_{-\infty}^t dt A_{ij}(t-t') f_j(t') + \xi_i, \quad (\text{C.21})$$

with noise correlation

$$\langle \xi_i(t+\tau) \xi_j(\tau) \rangle = 2(B_{ij})^{-1}(t) \quad (\text{C.22})$$

and probability

$$P[\xi_i(t)] = P_0 \exp \left\{ -\frac{1}{2} \sum_{ij} \int dt' dt'' \xi_i(t') B_{ij}(t'-t'') \xi_j(t'') \right\}, \quad (\text{C.23})$$

where $B_{ij}(t) = B_{ji}(-t)$.

It is most convenient to use a frequency representation

$$P[\xi_i(\omega)] = P_0 \exp \left\{ -\frac{1}{4\pi} \sum_{ij} \int d\omega \xi_i(\omega) B_{ij}(\omega) \xi_j^*(\omega) \right\}, \quad (\text{C.24})$$

with Hermitian matrix $B_{ij}(\omega) = B_{ji}^*(\omega)$ and $B_{ij}(\omega) = B_{ij}^*(-\omega)$. We can now employ the same arguments as above using

$$P[\phi_i(\omega)] = P_0 J \exp \{-S[\phi_i(\omega)]\}, \quad (\text{C.25})$$

where J is a Jacobian and

$$S[\phi_i(\omega)] = \frac{1}{4\pi} \sum_{ik} \int d\omega (-i\omega \phi_i - A_{ij} f_j) B_{ik}(\omega) (i\omega \phi_k - A_{kl}^* f_l^*). \quad (\text{C.26})$$

Now the equilibrium conditions become $B_{ij}(\omega) = \epsilon_i \epsilon_j B_{ij}(-\omega)$ and $A_{ij}(\omega) = \epsilon_i \epsilon_j A_{ij}(-\omega)$. From this it follows that $B_{ij}(\omega)$ can be brought in the block representation such that $B_{ij} = B_{ji}$ is real if $\epsilon_i = \epsilon_j$ and $B_{ij} = -B_{ji}$ if $\epsilon_i \neq \epsilon_j$. Similarly, $A_{ij}(\omega) = A_{ij}^h(\omega) + A_{ij}^a(\omega)$ can be decomposed in Hermitian dissipative parts A_{ij}^h and anti-Hermitian reactive parts A_{ij}^a . We then have

$$B_{ij}(\omega) A_{jk}^h(-\omega) = \beta \delta_{ik}. \quad (\text{C.27})$$

Appendix D. State-dependent friction

Appendix D.1. Anisotropic friction

In the presence of an orientation field p_α , the system is anisotropic and the Maxwell model needs to be generalized. The constitutive equations (26) and (27) for the stresses become

$$\begin{aligned} \left(1 + \tau \frac{D}{Dt} \right) \left\{ \tilde{\sigma}_{\alpha\beta} + \zeta \Delta \mu q_{\alpha\beta} + \frac{\nu_1}{2} \left(p_\alpha h_\beta + p_\beta h_\alpha \right. \right. \\ \left. \left. - \frac{2}{3} p_\gamma h_\gamma \delta_{\alpha\beta} \right) \right\} = 2 \tilde{\eta}_{\alpha\beta\gamma\nu} \tilde{v}_{\gamma\nu} + 2 \eta_{\alpha\beta} v_{\gamma\gamma} + \xi_{\alpha\beta}^{(\sigma)}, \\ \left(1 + \tau \frac{D}{Dt} \right) \left\{ -p + \bar{\zeta} \Delta \mu + \bar{\nu}_1 p_\gamma h_\gamma \right\} = \bar{\eta} v_{\gamma\gamma} + \bar{\eta}_{\alpha\beta} \tilde{v}_{\alpha\beta} + \xi. \end{aligned} \quad (\text{D.1})$$

Here, the viscosity tensors reflects the symmetries of the system and friction differs in longitudinal and transverse directions. We have $\eta_{\alpha\beta} = \eta_1 q_{\alpha\beta}$, $\bar{\eta}_{\alpha\beta} = \bar{\eta}_1 q_{\alpha\beta}$, and

$$\begin{aligned} \tilde{\eta}_{\alpha\beta\gamma\nu} = & \eta_2 \left(\delta_{\alpha\gamma} \delta_{\beta\nu} + \delta_{\alpha\nu} \delta_{\beta\gamma} - \frac{2}{3} \delta_{\gamma\nu} \delta_{\alpha\beta} \right) \\ & + \eta_3 \left(q_{\alpha\gamma} \delta_{\beta\nu} + \delta_{\alpha\gamma} q_{\beta\nu} + q_{\alpha\nu} \delta_{\beta\gamma} + \delta_{\alpha\nu} q_{\beta\gamma} \right. \\ & \left. - \frac{2}{3} (q_{\gamma\nu} \delta_{\alpha\beta} + \delta_{\gamma\nu} q_{\alpha\beta}) \right) \\ & + \eta_4 \left(q_{\alpha\gamma} q_{\beta\nu} - \frac{1}{3} q_{\delta\gamma} q_{\delta\nu} \delta_{\alpha\beta} \right). \end{aligned} \quad (\text{D.2})$$

Using this anisotropic viscosity, the fluctuation-dissipation theorem requires that the noise becomes state-dependent. Similarly, the anisotropic dissipation of the orientation field described by the coefficients γ and γ_a in equations (20) and (24) requires state-dependent noise if longitudinal fluctuations are not neglected.

Appendix D.2. Langevin equation and fluctuation-dissipation theorem

We discuss here the fluctuation-dissipation theorem for state-dependent friction following the lines of reference [34]. We consider the case without memory, $\tau = 0$ for which the dynamic equations can be written as first-order Langevin equations (34). For state-dependent friction, the mobility matrix A_{ij} depends on the state variables ϕ_i which also requires state-dependent noise [34]

$$\dot{\phi}_i = A_{ij}(\phi_1, \dots, \phi_n) \bar{f}_j + g_{ij}(\phi_1, \dots, \phi_n) \eta_j(t). \quad (\text{D.3})$$

Here, we have anticipated that for state-dependent friction the drift terms \bar{f}_i can differ from the thermodynamic forces f_i in (34) and the noises η_j are Gaussian variables with zero average and

$$\langle \eta_i(t) \eta_j(t') \rangle = \delta_{ij} \delta(t - t'). \quad (\text{D.4})$$

The fluctuation-dissipation theorem then imposes specific forms for the noise amplitudes g_{ij} . Note, however, that the stochastic differential equation (D.3) is only uniquely defined if an integration convention is specified which describes how integrals can be calculated by discretization and a continuum limit. We use the α -convention [34] which implies in the limit of small time interval Δt

$$\begin{aligned} \int_t^{t+\Delta t} dt' g_{ij}(\phi_k(t)) \eta_j(t) &= g_{ij}(\alpha \phi_k(t + \Delta t)) \\ &+ (1 - \alpha) \phi_k(t) \int_t^{t+\Delta t} dt' \eta_j. \end{aligned} \quad (\text{D.5})$$

The solutions to (D.3) depend on the parameter α . The Ito interpretation of the Langevin equation corresponds to $\alpha = 0$, while the Stratonovich interpretation is obtained for $\alpha = 1/2$.

The fluctuation-dissipation theorem ensures that the system relaxes to a thermodynamic equilibrium with a probability distribution $P^{\text{eq}}(\phi_1, \dots, \phi_n) \sim \exp\{-F/k_B T\}$, which is independent of the mobility matrix A_{ij} . Here $F(\phi_1, \dots, \phi_n)$ is the free energy and $f_i = -\partial F/\partial \phi_i$ are the thermodynamic forces. This equilibrium condition requires that the Fokker-Planck equation for the distribution function $P(\phi_1, \dots, \phi_n)$ is of the form

$$\frac{\partial P}{\partial t} = -\frac{\partial J_i}{\partial \phi_i}, \quad (\text{D.6})$$

with currents

$$J_i = A_{ij}^s \left(f_j P - k_B T \frac{\partial P}{\partial \phi_j} \right) + A_{ij}^a f_j P. \quad (\text{D.7})$$

Note that the diffusion matrix $k_B T A_{ij}^s$ is symmetric while the mobility matrix A_{ij} can have antisymmetric parts. Here, we have decomposed the matrix $A_{ij} = A_{ij}^s + A_{ij}^a$ in symmetric and an antisymmetric parts which are of the form (C.7). Furthermore, we neglect a possible state dependence of reactive coefficients, $\partial A_{ij}^a/\partial \phi_j = 0$. In this case, the reactive currents which can exist at thermodynamic equilibrium $J_i^{\text{eq}} = A_{ij}^a f_j P^{\text{eq}}$ have vanishing divergence as required, $\partial J_i^{\text{eq}}/\partial \phi_i = 0$. The consequences of state-dependent reactive terms are discussed below.

For the stochastic differential equation (D.3) with interpretation α , the corresponding Fokker-Planck equation has the current [34]

$$J_i = \left(A_{ij} \bar{f}_i + \alpha \frac{\partial g_{il}}{\partial \phi_k} g_{kl} - \frac{1}{2} \frac{\partial}{\partial \phi_j} (g_{il} g_{jl}) \right) P - \frac{1}{2} g_{il} g_{jl} \frac{\partial P}{\partial \phi_j}. \quad (\text{D.8})$$

By comparing (D.7) and (D.8), we obtain the generalized Einstein relation

$$g_{il} g_{jl} = 2 A_{ij}^s k_B T. \quad (\text{D.9})$$

Choosing the matrix $g_{ij} = g_{ji}$ symmetric, this relation uniquely specifies the noise strengths g_{ij} as functions of the state variables ϕ_i .

With these functions g_{ij} , the drifts \bar{f} can now be determined from

$$A_{ij} f_j = A_{ij} \bar{f}_j + \alpha \frac{\partial g_{il}}{\partial \phi_k} g_{kl} - \frac{1}{2} \frac{\partial}{\partial \phi_j} (g_{il} g_{jl}). \quad (\text{D.10})$$

Using the symmetric matrix $B_{ij} = 2(g_{il} g_{jl})^{-1}$ which obeys (C.8), we find

$$\bar{f}_i = f_i - k_B T \left(\alpha B_{im} \frac{\partial g_{ml}}{\partial \phi_k} g_{kl} + \frac{1}{2} B_{im} \frac{\partial}{\partial \phi_j} (g_{ml} g_{jl}) \right). \quad (\text{D.11})$$

Note that all correction terms to f_i in the drift are proportional to $k_B T$ because they are generated by fluctuations. With these expressions for \bar{f}_i and g_{ij} , the drift and noise terms are specified which have to be used in the stochastic differential equation (D.3) with state dependent friction, where A_{ij} is the mobility matrix and f_j the thermodynamic forces discussed in the main text.

Appendix D.3. State-dependent reactive terms

If both dissipative and reactive terms, A_{ij}^s and A_{ij}^a depend on the state variables ϕ_i , the Fokker-Planck current takes the form [35]

$$J_i = A_{ij}^s \left(f_j P - k_B T \frac{\partial P}{\partial \phi_j} \right) + \left(A_{ij}^a f_j - k_B T \frac{\partial A_{ij}^a}{\partial \phi_j} \right) P. \quad (\text{D.12})$$

The reactive correction term $-k_B T P \partial A_{ij}^a / \partial \phi_j$ on the right-hand side ensures that the probability density is stationary at equilibrium, $\partial J_i^{\text{eq}} / \partial \phi_i = 0$. While state-dependent reactive terms do not affect the noise strength g_{ij} , an additional term appears in the drift:

$$\bar{f}_i = f_i - k_B T \left(\alpha B_{im} \frac{\partial g_{ml}}{\partial \phi_k} g_{kl} + \frac{1}{2} B_{im} \frac{\partial}{\partial \phi_j} (g_{ml} g_{jl}) + B_{im} \frac{\partial A_{mj}^a}{\partial \phi_j} \right). \quad (\text{D.13})$$

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