Fluctuation-induced features of topological defects in passive nematics

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Topological defects are increasingly being identified in various biological systems, where their characteristic flow fields and stress patterns are associated with continuous active stress generation by biological entities. Here, using numerical simulations of continuum fluctuating nematodynamics we show that even in the absence of any activity, both noise in orientational alignment and hydrodynamic fluctuations can independently result in flow patterns around topological defects that resemble the ones observed in active systems. Remarkably, hydrodynamic fluctuations alone can reproduce the experimentally measured stress patterns around topological defects in epithelia. We further highlight subtle differences between noise in orientation and hydrodynamic fluctuations based on defect trajectories and persistence time. Our simulations show the possibility of both extensile-and contractile-like defect motion due to fluctuations and reveal the defining role of passive elastic stresses in establishing fluctuation-induced defect flows and stresses.

There is now a growing evidence of the emergence of liquid crystalline features in biological systems (see [1] for a recent review). Significant among others is the nematic orientational order, manifest in the form of collective alignment along particular axes [2], which is observed in subcellular filaments [3–6], bacterial biofilms [7–9], and cell monolayers [10–11]. For a 2-dimensional nematic, the fully-aligned nematic phase has quasi long-range order at nonzero temperature, meaning that order decays algebraically as follows from the Mermin-Wagner-Berezinskii theorem [12]. Increasing the temperature (rotational noise), leads to the breakdown of the orientational order onto an isotropic state via the Berezinskii–Kosterlitz–Thouless (BKT) transition [12–13]. Such a transition is characterized by the appearance of topological defects, singular points in the orientation field, which break the quasi long-range order. Due to the head-tail symmetry of the nematic particles, the lowest energy defects are of topological charge ±1/2, meaning that as one traces a loop around the defect, the particles rotate by ±π. Topological defects in nematics have recently been found to be at the core of many biological functions, e.g. cell extrusion in mammalian epithelia [10], neural mound formation [14] and limb origination in the simple animal Hydra [6] (see [1–15] for recent reviews on physical and biological significance of topological defects).

What sets these biological nematics apart from their passive counterparts is the presence of activity: each constituent element of living matter is capable of producing work and injecting energy locally by means of active stress generation [17]. While the existence of quasi long-range order has also been proven for active nematics [18–19], the dynamical properties of defects is expected to be different from the passive case since as a consequence of activity the +1/2 defects with polar symmetry can self-propel and move along their axis of symmetry [20]. For an extensile active stress, which extends along the elongation direction of active particles, the resulting motion of +1/2 defects is along the head, while the opposite holds for contractile active stresses that tend to point inwards along the elongation axis of active particles [20]. This persistent movement, both in the direction of the head and the tail of the ±1/2 defect, has been observed in various biological systems, e.g. contractile in fibroblasts [11] and extensile in epithelial monolayers [10]. Recently it has even been shown that perturbing the adhesion between cells can result in a switch between extensile and contractile behaviours in epithelial cell layers [21]. While the emergence of extensile or contractile behaviour of topological defects has been widely associated to the activity of these systems, here we show that fluctuations can lead to similar patterns of flows around topological defects and result in both extensile and contractile defect behaviour.

Fluctuations, represented by temperature in classical models, are known to drive many phase transitions, and are of particular importance in biological systems [22–25]. Noise is known to drive the BKT transition, in which spontaneously generated topological defects break the order, in a 2-dimensional passive, dry nematic, shown analytically by renormalisation group analyses [13] and computationally for a lattice model with finite size scaling [20], and for a dry, freely moving, particle-based model for various length to width ratios [27–28]. Similar BKT type transition was also reported in a discrete model of active nematics [29].

Drawing analogies with the BKT transition in passive nematics, it has been shown that in over-damped active nematics, where hydrodynamic flows are dominated and suppressed by frictional screening, self-propulsion of ±1/2 topological defects can lead to the defect pair un-binding, destroying any (quasi) long-range orientational order [30]. Introducing fluctuating forces coupled to the nematic alignment field, it was lately shown that such specific fluctuations can result in an effective extensile stresses in passive nematics [31]. More recently, combining discrete, vertex-based, simulations of model cellular layers with analytical treatment of linearised ne-

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FIG. 1. Fluctuation-induced nucleation and annihilation of defect pairs. (a) Snapshots from simulation with hydrodynamic noise (50 × 50 zoom in) depicting defect pair creation at $t = t_0$ (1st column), movement (2nd column), before (3rd column) and after (4th column) annihilation. Red circles: $+\frac{1}{2}$ defects, blue triangles: $-\frac{1}{2}$ defects. Here, $\tau = \eta/C$ is the characteristic time, $u_{KB} = 0.05$, and $\xi = 1$. The defect pair of interest are marked in magenta (positive) and cyan (negative). Black solid lines show the director field. (b) Same as (a) but for rotational noise with $Q_{KB} = 0.04$.

matohydrodynamics equations, it has even been argued that any fluctuations can result in the self-propulsion of comet-shaped, $+\frac{1}{2}$ topological defects [32]. Similarly, cell shape fluctuations in a cell-based, phase-field, model of cell monolayer has been shown to affect self-propulsive features of topological defects [33]. Notwithstanding these recent works, the dynamics and flow features of topological defects in the presence of fluctuations remain poorly understood. Moreover, it is not clear how different sources of fluctuations in hydrodynamic flows and in particle alignment affect the creation, annihilation, and motion of topological defects in the absence of any active stresses and whether fluctuations alone can explain experimental observations of contractile- and extensile-like defect motions in cellular layers.

Using a numerical implementation of hydrodynamic fluctuations and rotational noise in a hybrid lattice Boltzmann simulation, we investigate the effects of noise on a continuum nematohydrodynamics representation of passive liquid crystals. We employ a 2-dimensional continuum nematohydrodynamic model [20, 34, 35]. The nematic order parameter, $Q$, evolves according to: $\partial_t Q + \vec{v} \cdot \nabla Q = S$, where $\nabla$ is the molecular field, describing the relaxation towards minimum of the free energy that includes Landau-de Gennes bulk free energy plus the Frank elastic free energy. The rotational viscosity, $\gamma$, controls the relaxation. $S$ is the co-rotation term, which captures the particle response to the gradient of flow and is a function of the flow alignment parameter, $\xi$. The velocity field, $\vec{v}$, evolves according to the incompressible Navier-Stokes equations:

$$\rho(\partial_t \vec{v} + \vec{v} \cdot \nabla \vec{v}) = \nabla \cdot \Pi, \quad \nabla \cdot \vec{v} = 0,$$

where $\rho$ is the density and $\Pi$ is a general stress term that includes pressure, viscous and elastic stresses, defined as $\Pi_{\text{elastic}} = 2\xi(Q+I/2) - \xi H \cdot (Q+I/2) - \xi Q \cdot H - \nabla Q : \delta F \delta \nabla Q + Q \cdot H - H \cdot Q$. The elastic stress, $\Pi_{\text{elastic}}$, shows a dependence on the order parameter, $Q$, and derived quantities. This coupling, known as backflow [36], has been numerically and experimentally shown to be relevant to $\pm 1/2$ defect annihilation dynamics in passive nematics [37, 38]. For the rotational fluctuations, white noise with the strength $Q_{KB}$ is added to the two independent elements of the nematic tensor, $Q_{xz}$ and $Q_{yx}$, at the beginning of each LB step. Hydrodynamic fluctuations with the strength $u_{KB}$ are implemented at the level of the lattice Boltzmann density distribution following [39, 40] (see supplementary material for details of implementations and governing equations).

We begin by qualitatively assessing the impact of rotational noise and hydrodynamic fluctuations on the spatio-temporal patterns of nematic director field in passive nematics (Fig. 1). Fluctuations result in the nucleation of pairs of $\pm 1/2$ topological defects. The defects have a finite lifetime. For the rotational noise, the nucleated defects are short-lived and disappear shortly after their creation, only for the process to repeat itself (Fig. 1).
FIG. 2. Fluctuation-induced defect kinematics. Left and right columns compare the defect motion between the systems with hydrodynamic fluctuations \((u_{kBT} = 0.05, \xi = 1)\) and rotational noise \((Q_{kBT} = 0.04, \xi = 1)\), respectively. (a) Trajectories of +1/2 defects (red) and −1/2 defects (blue) from creation time to annihilation. (b) Log-log plot of the mean-square-displacement of defects vs time. The black line denotes slope equal to 1. Averaged over 10 realisations.

Remarkably, the nucleated pairs of defects in the presence of hydrodynamic fluctuations show a qualitatively similar behaviour to active extensile systems: after the nucleation, the +1/2 defect breaks away from the −1/2 counterpart, moving along its comet-head through the system, until it is annihilated by another −1/2 defect (Fig. 1b). This persistent motion of the +1/2 defect, in contrast to the displacement of short-lived +1/2 defect for rotational noise, is best evident in the temporal trajectory plots and the mean-square-displacement measurements of defects motion (Fig. 2). As opposed to the rotational noise, hydrodynamic fluctuations lead to the emergence of distinct speeds for +1/2 and −1/2 topological defects: at short times +1/2 defects move faster than their −1/2 counterparts, while at longer times the motion of both defects becomes dominated by interactions with other defects and thus shows diffusive nature. Such diffusive behavior for both defect types is in contrast with the predictions of active nematohydrodynamic theories [41, 43], that expect propulsive +1/2 and diffusive −1/2 defect motions as observed in dense colonies of motile bacteria [43]. Remarkably, the defects motion observed here for hydrodynamic fluctuations is consistent with experimental characterisation of the mean-squared-displacements of ±1/2 topological defects in the human-bronchial-cells (HBC) [44], where both defect times showed diffusive behaviour at long times, and suggests that the defect motions in such epithelial layers could be simply dominated by hydrodynamic fluctuations.

We next asked how the averaged flow fields of fluctuation-induced topological defects compare with the flow fields that have been extensively measured in experiments for different cell layers [10, 11, 44] and with the theoretical predictions from active nematics [41, 45]. Interestingly, averaged flow fields around the +1/2 defects for both the rotational noise and for hydrodynamic fluctuations show the typical flow jet at the defect centre, pointing towards the head, accompanied by a vortex pair around the defect’s axis of symmetry (Fig. 3), which is the expected flow field for motile +1/2 defects in extensile active nematics [20, 41, 43] and is observed in experiments on epithelial cell layers [10, 44] and neural progenitor stem cells [13].

In addition to a characteristic flow pattern, experiments and active nematic theories have measured the isotropic stresses \((\sigma_{iso} = \frac{1}{2} \text{Tr}(\Pi))\) around the defects to characterise the tensile and compressive forces around defect structures. In active nematics, an extensile defect has a region of positive isotropic stress (compression) at the head, and negative isotropic stress (tension) at the tail, inverted for a contractile defect [20]. This stress pattern has been linked to functional behaviour in governing cell death and extrusion in epithelia [10]. Remarkably, only for hydrodynamic fluctuations, the corresponding isotropic stress patterns demonstrate the compression at the head of the defect and the tension at the tail region.

FIG. 3. Fluctuation-induced defects flow and isotropic stresses. Left and right columns compare the averaged flows and isotropic stresses between the systems with hydrodynamic fluctuations \((u_{kBT} = 0.05, \xi = 1)\) and rotational noise \((Q_{kBT} = 0.04, \xi = 1)\), respectively. (a) Averaged velocity field around +1/2 defects. (b) Averaged isotropic stress fields around +1/2 defects (colormap) and the corresponding director fields (black solid lines).
FIG. 4. Extensility of +1/2 defects. The dependence of the extensility, $\mathcal{E}$ on (a) the flow-aligning parameter $\xi$ with hydrodynamic fluctuations with $u_{b\alpha T} = 0.05$ (purple), rotational strength with $Q_{\kappa B T} = 0.04$ (orange), and (b) fluctuation strength at $\xi = 1$. Dotted line in (a) denotes $\xi = 7/9$. Averaged over 10 realisations (20 for $\mathcal{E}(Q_{\kappa B T})$).

(Fig. 3), further reinforcing the idea that such experimentally observed patterns could be fluctuation-induced.

Our numerical results clearly show a tendency for the emergence of active extensile-like features around +1/2 defects, but it is not clear what determines such defect features. To answer this question, we next investigated the impacts of flow-aligning parameter and passive elastic stresses on the fluctuation-induced topological defect features, since in passive nematics the former characterises the orientation response to flow gradients [37], and the latter couples the orientation field to the flow [37]. Starting with the flow-aligning parameter, we observed disappearance of any coherent flow around defects for $\xi = 0.0$. Moreover, the direction of flow around the +1/2 defect switches sign for negative values of the flow-aligning parameter, resembling contractile-like flows observed for monolayers of mouse fibroblasts [11] and epithelial cells with weakened cell-cell adhesion [21].

To quantify the extensile- or contractile-like flow features around +1/2 defects we define the extensility parameter, $\mathcal{E}$, based on the averaged flow field around the defects, $\langle \vec{u} \rangle = (\langle u_x^d \rangle, \langle u_y^d \rangle)$, as:

$$\mathcal{E} := \frac{\langle |u_y^d| \rangle}{\langle |u_x^d| \rangle},$$

where we rotate all defects such that their comet-shaped head points in the $+y$-direction. The extensility parameter goes from $\mathcal{E} = -1$ for a purely contractile defect over $\mathcal{E} = 0$ for no movement or isotropic movement to $\mathcal{E} = 1$ for a purely extensile defect. For both sources of fluctuations, the results show that the flow aligning parameter $\xi$ plays a significant role in determining the extensility of the defects (Fig. 4a). Moreover, there is a saturation value of extensility, $\mathcal{E}$, which, for both types of noise, coincides with the crossover from flow tumbling to flow-aligning behaviour that is expected at $|\xi| > \frac{3q_\text{eq}^2}{4q_\text{eq}}$, where using approximation of the nematic order magnitude with its equilibrium value $q_\text{eq} = 1.0$ leads to $|\xi| \gtrsim 7/9$. Therefore, orientation response of nematic particles to flow gradients is integral to contractile- or extensile-like behaviour of +1/2 defects. Not only flow-aligning is necessary for the establishment of fluctuation-induced, active-like defect features, the back coupling of the orientation to flow field through passive elastic stresses is also required. This is evident from the results of simulations, where passive elastic stresses are turned off (Fig. 4b; black solid line). It is important to note that for both cases of $\xi = 0.0$ and $\Pi_{\text{elastic}} = 0.0$ fluctuations both in orientation field and in hydrodynamics lead to defect formation, but the resulting defects do not show active-like flow and stress features. Additionally, we numerically confirmed that the directed motion of the +1/2 defects is governed only by the contribution of the flow-aligning parameter, $\xi$, in the passive stress and not by the $\xi$-dependent co-rotation term in the $Q$ equation. Therefore, the mechanism of extensile- or contractile-like +1/2 defect behaviour can be understood as follows: rotational noise or hydrodynamic fluctuations continuously create pairs of +1/2 topological defects; once created, passive elastic stresses generate flow fields around +1/2 defects that for positive (negative) values of flow-aligning parameter, $\xi$, show extensile-like (contractile-like) flow and stress features.

Finally, we quantify the impact of the strength of fluctuations on the active-like defect behaviour. As evident from Fig. 4a,b,c the extensility parameter increases from zero after the magnitude of noise passes above a certain threshold. This is true for both types of the noise and occurs at the point where fluctuation-induced topological defects are first nucleated.

Our results show that the fluctuation-induced extensile- and contractile-like defects crucially depend on the sign and magnitude of the flow-aligning parameter through its contribution to the passive elastic stresses. The value of the flow-aligning parameter depends on the size, aspect ratio, magnitude of the order, and also interactions between the nematogens. Indeed, the few attempts to extract the flow-aligning parameters, for the wing epithelium of Drosophila [17] and for mouse fibroblast cells [48], have shown that it can have a range of values and even become negative. Therefore it would not be surprising if different experimental systems show distinct behaviours associated with flow-tumbling or flow-aligning behaviour. However, to our knowledge, the role...
of this parameter has been only marginally explored in most theoretical works and experiments. The emergence of fluctuation-induced extensile- and contractile-like defects in passive nematics questions whether systems previously described as active nematics must necessarily be active. Experimental active matter systems operate at nonzero temperature and therefore must necessarily be active. Future studies should focus on effective ways for discerning the activity-induced from fluctuation-induced effects in the experiments on biological matter.

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