Onset of meso-scale turbulence in active nematics

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Meso-scale turbulence is an innate phenomenon, distinct from inertial turbulence, that spontaneously occurs at low Reynolds number in fluidized biological systems. This spatiotemporal disordered flow radically changes nutrient and molecular transport in living fluids and can strongly affect the collective behaviour in prominent biological processes, including biofilm formation, morphogenesis and cancer invasion. Despite its crucial role in such physiological processes, understanding meso-scale turbulence and any relation to classical inertial turbulence remains obscure. Here we show how the motion of active matter along a micro-channel transitions to meso-scale turbulence through the evolution of locally disordered patches (active puffs) from an ordered vortex-lattice flow state. We demonstrate that the stationary critical exponents of this transition to meso-scale turbulence in a channel coincide with the directed percolation universality class. This finding bridges our understanding of the onset of low-Reynolds-number meso-scale turbulence and traditional scale-invariant turbulence in confinement.
Low-Reynolds-number turbulence is established through continuous energy injection from the constituent elements of an active fluid in many biological systems, including bacterial suspensions, cellular monolayers or sub-cellular filament/motor protein mixtures. Although the inertia is negligible (Reynolds number \( \ll 1 \)) in such systems, active turbulence is characterized by a highly disordered distribution of vortices. However, in bulk, meso-scale turbulence in living fluids possesses a characteristic vortex length scale, which distinguishes it from scale-invariant inertial turbulence, and it is considered a new class of turbulent flow.

Despite extensive implications for diverse fluid dynamical systems and more than a century of research, the transition from pressure-driven laminar flow to inertial turbulence in even the simplest geometries remains one of the major unresolved problems in fluid mechanics. Elaborate experiments have recently shed new light on the nature of this transition by measuring the decay and splitting of local turbulent domains/clusters (puffs) in pipe flows and have determined the critical Reynolds number—ratio of inertial to viscous forces—at which the transition occurs. Short-range interactions between the locally turbulent puffs, which feed on surrounding laminar flow as an absorbing state, drive a continuous transition to a fully turbulent flow. Recent experimental evidence from channel and circular Couette flows, together with direct numerical simulation studies and predator–prey models, have provided evidence that the transition at the critical Reynolds number is characterized by the directed percolation universality class.

Strikingly, here we show that for a profoundly distinct class of turbulence at low Reynolds number, the transition in a channel can also be characterized by the emergence of puffs created by microscopic activity of biological fluids. Even for this low Reynolds number class of turbulent-like flows that apparently lacks a perfectly unique absorbing state, we find that the critical exponents correspond to the directed percolation critical exponents.

The marked difference between the various flow states is clearly seen in the structure of the vorticity. Therefore, to characterize the transition between the regimes, we measure the distribution of the local enstrophy \( \epsilon \), averaged across the channel. This quantity represents the strength of vortices in the flow, and has also been used for determining the nature of inertial turbulence. The vortex-lattice state possesses a well-defined peak in the enstrophy (Fig. 2b). As the active flow transitions at higher activities, the enstrophy distribution broadens, demonstrating that vorticity cascades down into meso-scale turbulence. The gradual disappearance of the peak in the enstrophy distribution (Fig. 2b) suggests a continuous transition from the vortex lattice to meso-scale turbulence. But how does the active turbulence develop from the vortex lattice?

**Critical behaviour.** Figure 1c shows a snapshot of the vorticity field in a long channel close to the transition. The vortex lattice predominately occupies the entire channel. Locally, however, we can identify regions of the channel where vortex pairs split into smaller non-ordered vortices (Fig. 1d). This coexistence of the global vortex lattice and clusters of local active turbulence controls the transition to turbulence in the channel. We term these localized domains of non-ordered vorticity active puffs, in analogy to the inertial puffs observed in the experiments on scale-invariant turbulence in long tubes. Unlike the inertial puffs that are externally initiated by perturbations to the flow field (such as induced pressure jumps), active puffs are intrinsic to our simulations.

The behaviour of these active puffs is clearly characterized in the space-time kymograph of enstrophy (Fig. 3). An active puff can split, giving birth to new puffs, or decay into the ordered vortex-lattice state. Below some critical activity number, puffs tend to decay back to the inactive vortex-lattice state (Fig. 3a). On the other hand, active puffs span the entire system when splitting occurs at a high enough rate to produce a statistical steady state at the critical activity number (Fig. 3b). At higher activities yet, the competition between splitting and decaying of puffs results in a well-defined turbulence fraction within the channel (Fig. 3c). The active flow approaches the fully turbulent state with active puffs ultimately occupying the entire channel when the decay time far exceeds the splitting time.

We thus measure the turbulence fraction, the area fraction occupied by active puffs in the channel, as a function of the activity number (Fig. 4a). Well below the critical point, active puffs have a short lifetime and rarely split (Fig. 3a), leading to a negligible turbulence fraction in the steady state (Fig. 4a). However, as the critical value of the activity is approached, puff decay becomes less likely and splitting time decreases substantially (Fig. 3b). Above the critical point, the puff population does not die out, producing a steady-state, non-zero
turbulence fraction (Fig. 3c), and we find the turbulence fraction continuously increases with a power-law dependence $\sim (A - A_{\text{cr}})^{\beta}$ (Fig. 4a). We measure the stationary exponent to be $\beta = 0.275 \pm 0.043$, which closely matches the universal critical exponent of the $(1 + 1)$ directed percolation process ($\beta = 0.276$)\textsuperscript{35} and is in agreement with the value that has recently been measured for inertial turbulence in Couette flow ($\beta = 0.28 \pm 0.03$)\textsuperscript{19}. This strong agreement is striking, as it draws a parallel between the low-Reynolds-number meso-scale turbulence in living fluids, which possesses a characteristic vorticity length scale, and high-Reynolds-number inertial turbulence, which is scale-invariant. Furthermore, the exponent is particularly surprising as active puffs are generated at a small activity-independent rate. In this way, the inactive vortex lattice is not a perfectly absorbing state, and yet there is remarkable agreement between the measured stationary exponent $\beta$ and the critical exponent of the directed percolation universality class. The agreement with the universal critical exponent from directed percolation can be understood by recognizing that the creation of puffs corresponds to a weak, non-ordering field conjugated to the turbulence fraction, which is known to have no detectable effect on the stationary exponents sufficiently close to the critical point\textsuperscript{36,37}.

To further scrutinize the critical behaviour at the transition point, we measure the spatial and temporal distributions of vortex-lattice gaps (see Methods). These distributions of the inactive state characterize correlations of the active puffs\textsuperscript{38} and obey power laws with exponents $\mu_1$, $\mu_2$ for space and time, respectively (Fig. 4b,c). The temporal exponent is measured to be $\mu_2 = 1.84 \pm 0.04$ and the spatial exponent is $\mu_1 = 1.8 \pm 0.1$. These values also correspond to the critical exponents for $(1 + 1)$ directed percolation ($\mu_2 = 1.84, \mu_1 = 1.748$)\textsuperscript{35}. The values of the exponents obtained from our measurements for meso-scale turbulence in a channel and for $(1 + 1)$ directed percolation with spontaneous site activation are summarized in Table 1 and are compared with the experimentally measured exponents for the inertial turbulence in simple shear experiments in one-dimensional geometries\textsuperscript{19}. It would be of interest to see if the critical exponents of the directed percolation universality class will continue to be found in geometries with higher effective dimensionality, as in experiments on inertial turbulence in quasi-two-dimensional passive liquid crystals\textsuperscript{39,40}, in channel flows\textsuperscript{18} and in three-dimensional quantum turbulence\textsuperscript{41}.

### Discussion

Our findings present a first concrete connection between turbulence in living fluids and classical scale-invariant turbulence, beyond a superficial visual similarity, by showing that the transitions to these two profoundly distinct types of spatiotemporal disorder in channel flows are characterized by the same
scaling behaviour, corresponding to a critical directed percolation process. While the transition to scale-invariant turbulence corresponds to a critical absorbing phase transition, our results suggest that meso-scale turbulence is driven away from criticality by rare active puff creation that corresponds to directed percolation in the presence of a conjugated field. This opens new possibilities for further investigation of the nature of meso-scale turbulence and using tools from non-equilibrium statistical mechanics to explain transitionary behaviours in biological systems. Future research should investigate the transitions
between ordered flow states, the nature of the weak conjugated field and the possibility of non-universal dynamical scaling behaviour or super-exponential dependence of puff lifetime on activity number.

**Methods**

**Active nematohydrodynamics simulations.** The spatiotemporal evolution of a living fluid is described by active nematohydrodynamics equations based on the theory of liquid crystals. This formulation has been extensively applied to biological systems including bacterial suspensions\(^\text{[21]}\), microtubule/motor protein mixtures\(^\text{[10,22,42]}\) and cellular monolayers\(^\text{[8,43]}\). The total density \(\rho\) and the velocity field \(\mathbf{u}\) of the active matter obey the incompressible Navier–Stokes equations

\[
\nabla \cdot \mathbf{u} = 0, \quad (1)
\]

\[
\rho (\partial_t \mathbf{u} + \mathbf{u} \cdot \nabla \mathbf{u}) = -\nabla P + \mathbf{F}_e + \mathbf{F}_d, \quad (2)
\]

where \(P\) is the stress tensor. While several studies of meso-scale turbulence have characterized the dynamics of the flow using only the velocity field as the relevant order parameter\(^\text{[13]}\), an additional order parameter field is required to account for the orientational order of active fluids. This is particularly important since several experiments have established the existence and pivotal role of the orientational order in the dynamics of bacterial suspensions\(^\text{[5,24]}\), microtubule bundles\(^\text{[10,11]}\), assemblies of fibroblast cells\(^\text{[44]}\) and more recently in stem cell cultures\(^\text{[7]}\). To account for the macroscopic orientational order of microscopic active and anisotropic particles, the nematic tensor \(Q^i_3 = \langle m_i - I/3 \rangle\) is considered, where \(q\) denotes the coarse-grained magnitude of the orientational order, \(n\) is the director and \(I\) the identity tensor. The nematic tensor evolves as

\[
(\partial_t + \mathbf{u} \cdot \nabla)Q - \mathbf{S} = \Gamma H, \quad (3)
\]

where \(\Gamma\) is a rotational diffusivity and the co-rotation term

\[
S = (\mathbf{E} + \Omega) \cdot \left( Q + I/3 \right) - \left( \lambda E - \Omega \right) - 2\lambda \left( Q + I/3 \right) \cdot (\mathbf{E} \times \mathbf{Q}), \quad (4)
\]

accounts for the response of the orientation field to the extensional and rotational components of the velocity gradients, as characterized by the strain rate \(\mathbf{E} = (\nabla \mathbf{u} + \nabla \mathbf{u}^T)/2\) and vorticity \(\Omega = (\nabla \times \mathbf{u})/2\) tensors, and weighted by the tumbling parameter \(\lambda\). The relaxation of the orientational order is determined by the molecular field,

\[
H = \frac{\partial F}{\partial Q} + \nabla \frac{\partial F}{\partial (\nabla Q)}, \quad (5)
\]

where \(F = F_s + F_d\) denotes the free energy. We use the Landau–de Gennes bulk free energy\(^\text{[45]}\),

\[
F_s = A Q^2 + B Q^2 + C Q^4, \quad (6)
\]

and \(F_d = \gamma \langle \nabla Q \rangle^2\), which describes the cost of spatial inhomogeneities in the order parameter, assuming a single elastic constant \(K\).

In addition to the viscous stress \(\Pi^\text{visc} = 2\gamma \mathbf{E}\), equation (2) must account for contributions to the stress \(\Pi\) from the nematic field and the activity. The nematic contribution to the stress is

\[
\Pi^\text{nematic} = -\pi I - 2\lambda (Q + I/3) \cdot (\mathbf{E} \times \mathbf{Q}) - \lambda H \left( Q + I/3 \right) - \lambda \left( Q + I/3 \right) \cdot H - \nabla Q \cdot \left( \frac{\partial F}{\partial (\nabla Q)} \right) + Q \cdot H - H \cdot Q, \quad (7)
\]

where the auxiliary pressure \(P\) (ref. 46). The active contribution to the stress takes the form \(\Pi^{\text{act}} = -\langle Q \rangle\) (ref. 47), such that any gradient in \(Q\) generates a flow field, with strength determined by the activity coefficient, \(\zeta\).

The equations of active nematohydrodynamics (equations (1–3)) are solved using a hybrid lattice Boltzmann and finite difference method\(^\text{[48–50]}\). We model a two-dimensional velocity field and nematic director\(^\text{[22]}\). While the director field can theoretically develop out-of-plane components, for active experiments and the parameter values used in this study, it does not move out of plane. Discrete space and time steps are chosen as unity and all quantities can be converted to physical units in a material–dependent manner\(^\text{[23,51,52]}\). Simulations are performed with the parameters \(A = 0, B = 0.3, C = -0.3, I = 0.34, K = 0.04, \lambda = 0.3, \rho = 1\) and \(\mu = 3/3\), in lattice Boltzmann units. Parameter fitting of the continuum equations to physical active systems remains a topic of research; therefore, we consider a generic parameter set that has been shown to reproduce the active turbulent state observed in bacteria and microtubule/motor protein suspensions\(^\text{[10,22]}\). With the largest observed average speed and vortex size, these parameters indicate a small Reynolds number \(Re \simeq 10^{-1}\). Additional details can be found in refs 48–50,53.

We use a channel with a height \(h = 25\) and length \(L = 3.000\). No-slip boundary conditions are applied to channel walls and periodic boundary conditions are used at the channel extremities. The results reported here are for strong homogeneous boundary conditions for the director field on the channel walls. In addition, we have performed simulations with homeostropic and weak anchoring boundary conditions and find that the transitions described in the main text are independent of the anchoring boundary conditions on the walls. To obtain sufficient statistics for the turbulence fraction (Fig. 4a), several instances (5–10) of each set of parameters with initially randomized fields are simulated. A warm-up of \(3 \times 10^5\) time steps is allowed to reach the stationary state. Above the critical point, this produces sample sizes of \(\gtrsim 100\) puffs.

**Directed percolation model with spontaneous activation.** To examine the behaviour of the \((1 + 1)\) directed percolation universality class, we utilized a Domany–Kinzel cellular automaton\(^\text{[54]}\) and chose probabilities to correspond to site-directed percolation. This stochastic model is a discrete system on a diagonal square lattice of linear spatial size \(L\) with periodic boundary conditions. The state \(s(i,t)\) of site \(i\) at time \(t\) can be inactive (or empty) with \(s(i,t) = 0\), or the site can be activated (or occupied) \(s(i,t) = 1\) (ref. 35). In confined active nematic flows, the inactive state corresponds to the vortex-lattice state, and the activated phase corresponds to the active puffs of meso-scale turbulence. At time \(t_0\), each site is occupied with some probability \(P\), if both backward sites (at time \(t - 1\)) are occupied, and with probability \(P_1\) if only one backward site is occupied. Site-directed percolation is recovered with the choice \(P = P_1 = P_2\) (ref. 35). When the probability \(P\) reaches the critical probability \(P_c\), the system transitions from the absorbing phase of entirely inactive states to one in which the stationary density of active sites is non-zero and this transition is known to belong to the directed percolation universality class\(^\text{[35]}\).

**Table 1 | Critical exponents for the transition to the meso-scale turbulence in a micro-channel.**

| Critical exponents | \(\beta\) | \(\mu_\perp\) | \(\mu_\parallel\) |
|---------------------|-----------|-----------|-----------|
| Active turbulence at low Reynolds number | 0.275 ± 0.043 | 1.80 ± 0.10 | 1.84 ± 0.04 |
| Couette experiments for inertial turbulence\(^\text{[19]}\) | 0.28 ± 0.03 | 1.72 ± 0.05 | 1.84 ± 0.02 |
| \((1 + 1)\) directed percolation\(^\text{[35]}\) | 0.276 | 1.748 | 1.84 |

Comparison to experimental measurements of inertial turbulence in Couette flow\(^\text{[19]}\) and directed percolation exponents\(^\text{[35]}\).
In the confined active nematic, we find a small but non-zero rate of puff creation \( P_0 \). Puff creation destroys the absorbing state, driving the system away from criticality. However, directed percolation in the presence of spontaneous site activation has been well studied, and it is known that the transition point is only weakly dependent on \( P_0 \) (ref. 35), that spontaneous site activation is equivalent to a weak external field conjugated to the order parameter \( \beta \), and that the stationary scaling exponents are not observed to change and are known to be independent of \( x_0 \). Thus, at least near the critical point, there does not appear to be a suitable control parameter for \( P_0 \). From the lattice Boltzmann simulations, we find that the rate of puff formation is \((0.54 \pm 0.10) \times 10^{-7} - 10^{-7}\), and the value is used in the main text. Although \( P_0 \) moves the system slightly away from the critical point, the directed percolation scaling exponents are not observed to change and are known to be independent of \( P_0 \) in this weak field limit\(^{33}\). Measuring \( N_x \) and \( N_y \) as for the lattice Boltzmann simulations, supplies the critical exponents reported in the main text.

Calculating the turbulence fraction. The enstrophy field \( \varepsilon(x, y, t) = \Omega \cdot \Omega \) is calculated from the vorticity field \( \Omega(x, y, t) \). The field is averaged across the channel \( \varepsilon(x, t) = \langle \varepsilon(x, y, t) \rangle \), to create a 1D dimensional kymographical space-time signal. As described in the main text, the channel-averaged enstrophy in the vortex-lattice phase shows regular periodic oscillations, while local active turbulence domains (the active puffs) exhibit fluctuating, noisy enstrophy signals (Fig. 5a). To produce the visual traces of the active puffs (Fig. 3), the kymographs are Fourier-transformed in both time and space. The primary peaks are masked in reciprocal space-time using Gaussian fits to produce the kymographs without the structured oscillations of the periodic background of the vortex lattice (Fig. 5b).

To quantitatively determine the turbulence fraction, the total simulation time is divided into \( n \) windows of size \( \tau \), creating a \( L \times n \) array of space-time intervals, with each window \( r \) ranging from \( t_{r-1} \) to \( t_r \). Each of the temporal intervals is analysed for periodicity using a discretized temporal autocorrelation function \( \alpha_k(t) = (\tau - 1)^{-1} \sum_{j=0}^{\tau-1} \delta(x, t + j) \cdot \delta(x, t + j + k) \), where \( k \) runs from 0 to \( \tau \). To probe the stability of the vortex lattice, the flow is perturbed with a vortex lattice, as for the lattice Boltzmann simulations, supplies the critical exponents reported in the main text.

Data availability. Source data and simulation materials are available from the authors upon request.

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Author contributions
A.D., T.N.S. and J.M.Y. conceived the research and supervised the project. A.D., T.N.S. and K.T. carried out the simulations. All authors contributed to interpreting the results and writing the paper.

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