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Discontinuous fluidisation transition in assemblies of actively-deforming particles: A new paradigm for collective motion in dense active materials

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Tracking experiments in dense biological tissues reveal a diversity of sources for local energy injection at the cell scale. The effect of cell motility has been largely studied, but much less is known about the effect of the observed volume fluctuations of individual cells. We devise a simple microscopic model of ‘actively-deforming’ particles where local fluctuations of the particle size constitute a unique source of motion. We demonstrate that collective motion can emerge under the sole influence of such active volume fluctuations. We interpret the onset of diffusive motion as a nonequilibrium first-order phase transition, which arises at a well-defined amplitude of self-deformation. This behaviour contrasts with the glassy dynamics produced by self-propulsion, but resembles the mechanical response of soft solids under mechanical deformation. It thus constitutes the first example of active yielding transition.

Active matter represents a class of nonequilibrium systems that is currently under intense scrutiny [1, 2]. In contrast to externally driven systems (such as sheared materials), active matter is driven out of equilibrium at the scale of its microscopic constituents. Well-studied examples include biological tissues [3], bacterial suspensions [4] and active granular and colloidal particles [5–8].

Epithelial tissues constitute a biologically relevant active system composed of densely packed eukaryotic cells [3, 9–14]. Such tissues display a surprisingly fast and collective dynamics, which would not take place under equilibrium conditions [10]. This dynamics has been ascribed to at least three distinct active processes [13]: (i) self-propulsion through cell motility such as crawling [15], (ii) self-deformation through protrusion and contraction [16–18], and (iii) cell division and apoptosis [14]. The vertex model for tissues [12, 19, 20] includes the first two of these active processes and predicts a continuous static transition from an arrested to a flowing state [21]. Another theoretical line of research is based on self-propelled particles [22] which display at high density a nonequilibrium glass transition [23, 24] accompanied by a continuous increase of space and time correlations which diverge on approaching the arrested phase [25–27]. However, typical correlation lengthscales in tissues do not seem to diverge [9, 11, 28, 29].

To disentangle the dynamic consequences of the various sources of activity in tissues at large scale, we suggest to decompose the original complex problem into simpler ones, and to study particle-based models which only include a specific source of activity. This strategy was followed earlier for self-propulsion, but experiments are instead often modelled by complex models with many competing processes [18, 29, 30]. We argue that it is relevant to introduce a simplified model to analyse the effect of active particle deformation in a dense assembly of non-propelled soft objects. Specifically, we model a dense sys-

tem that is driven out of equilibrium locally through ‘self-deformation’ rather than self-propulsion. We study soft particles that actively change their size, while energy is being dissipated through viscous damping. As a starting point, we consider the simplest form of self-deformation, in which the diameter of each spherical particle oscillates at very low frequency, in a way that is directly inspired by experimental observations in real tissues [16]. The interest of such modelling is that activity is thus controlled by a unique adimensional parameter, a , which quantifies the relative change of the particle diameter within a deformation period. Our aim is not to propose a realistic model of a tissue, but rather to answer a more fundamental physical question regarding the role of active volume fluctuations in tissue dynamics. Despite its relevance, such a class of models has, to our knowledge, not been analysed before in a statistical mechanics context.

Our main result is the existence of a discontinuous nonequilibrium phase transition from an arrested disordered solid to a flowing fluid state at some critical activity, a_c , with no diverging timescales or lengthscales. In particular, we observe a modest increase of one order of magnitude in the relaxation times of the fluid before the system gets discontinuously trapped in an arrested phase at $a = a_c$. Our system also shows a strong hysteresis as seen in equilibrium first-order phase transitions. This scenario for the fluidisation transition differs markedly from that of self-propelled particles in which a dramatic continuous slowing down is observed [24–27]. We propose that the correct analogy for our observations is not with a glass [24] or jamming [23] transition, but rather with the yielding transition of amorphous solids [31], which start flowing irreversibly when mechanically perturbed beyond a force threshold, the yield stress. Therefore, actively-deforming particles undergo an ‘active yielding transition’, which represents a novel paradigm for the collective motion of active materials.

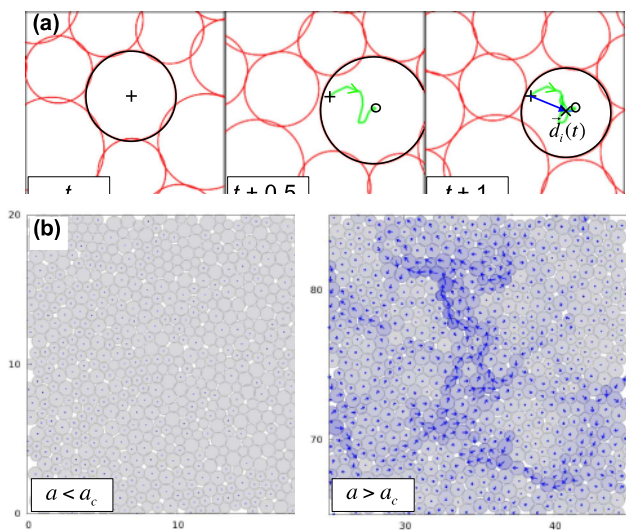


FIG. 1: (a) Snapshots of the system over one cycle of active deformation. The green curve is the trajectory of the highlighted particle during one cycle. The blue arrow represents its displacement after one cycle $\vec{d}_i(t) = \vec{r}_i(t+1) - \vec{r}_i(t)$. (b) One-cycle displacement map $\vec{d}_i(t)$ in steady state for the disordered solid phase ($a = 0.047 < a_c \approx 0.049$, left) and in the fluid phase ($a = 0.051 > a_c$, right). In the solid phase, particles approximately return to their position after each cycle. In the fluid, there are regions of large displacements where irreversible rearrangements take place. The transition between reversible and irreversible phases at a_c is discontinuous.

We consider a dense suspension of N soft circular particles at zero temperature in a two-dimensional square box of linear size L with periodic boundary conditions. The interaction between the particles is modelled by a short-ranged repulsive harmonic potential, similar to jammed foams [32]: $V(r_{ij}) = \frac{\epsilon}{2} (1 - r_{ij}/\sigma_{ij})^2 H(\sigma_{ij} - r_{ij})$, where $r_{ij} = |\vec{r}_i - \vec{r}_j|$, $\sigma_{ij} = (\sigma_i + \sigma_j)/2$, with σ_i and \vec{r}_i the diameter and position of particle i , respectively. The energy scale of the repulsive force is set by ϵ , and $H(x)$ is the heaviside function, defined such that $H(x \geq 0) = 1$. In the overdamped limit, the dynamics of each particle is described by a Langevin equation:

$$\xi \frac{d\vec{r}_i}{dt} = - \sum_{j \neq i} \frac{\partial V(r_{ij})}{\partial \vec{r}_j}, \quad (1)$$

where ξ is a friction coefficient. The dissipation timescale is $\tau_0 = \xi \sigma_0^2 / \epsilon$, where σ_0 sets the particle diameter (see below). Physically, τ_0 is the typical timescale for a system described by Eq. (1) to come at rest without forcing.

We drive the system out of equilibrium by oscillating the diameter of each particle around its mean value σ_i^0 , as shown in Fig. 1(a):

$$\sigma_i(t) = \sigma_i^0 [1 + a \cos(\omega t + \psi_i)], \quad (2)$$

where $T = 2\pi/\omega$ is the period of oscillation which we use as our time unit, and a is an adimensional parameter

which quantifies the intensity of the activity. We impose very slow oscillations, $T \gg \tau_0$, such that the system is always located near an energy minimum and inertial and hydrodynamic effects can be neglected. Specifically, we use $T = 820\tau_0$. The average diameters σ_i^0 are drawn from a bidisperse distribution of diameters $0.71\sigma_0$ and σ_0 with 3:2 proportion, in order to prevent crystallization. We use σ_0 as unit length. We have introduced in Eq. (2) a random phase ψ_i for each particle to constrain the total area fraction $\phi = \sum_i \frac{\pi \sigma_i^2(t)}{4L^2}$ to be strictly constant in time. The case with $\psi_i \equiv 0$ would correspond to affine compressions and expansions, which would then amount to studying the rheological response of the jammed solid forced at large scale, not an active material forced locally. We consider jammed systems with $\phi = 0.94$, as appropriate for confluent tissues. Most simulations were performed with a very large system of $N = 16000$ particles (typically $L \approx 100\sigma_0$). We converged to this large value using simulations with increasing sizes, seeking the disappearance of finite-size effects. We also use finite-size scaling analysis to locate the phase transition with greater accuracy. For each a value, we prepare fully random systems and apply the periodic perturbation until the system has reached steady state, either arrested or flowing. We then perform steady state measurements using averaging over time (in the flowing phase), or over initial conditions (in the arrested phase).

Figure 1(a) highlights the trajectory of a particle during one period. We define the one-cycle displacement, $\vec{d}_i(t) = \vec{r}_i(t+1) - \vec{r}_i(t)$, as shown in Fig. 1(a). Collecting the displacement of all particles we obtain the steady state one-cycle displacement map shown in Fig. 1(b) for both arrested and flowing phases. In the arrested phase, displacements are all very small and particles approximately return to the same position after each cycle, without undergoing configurational change. On the other hand, at large activity we observe regions of very large displacements where irreversible particle rearrangements occur within one cycle. These local plastic events are spatially disordered, and they coexist with regions where displacements are smaller: the dynamics is spatially heterogeneous. Clearly, Fig. 1 indicates the existence of an arrested phase where particles do not move for small a , and of a flowing phase for large a where irreversible rearrangements take place during each cycle. In the following we demonstrate that the transition between these two regimes occurs at a well-defined activity value, a_c , and that it corresponds to a first-order phase transition.

We start by showing in Fig. 2(a) the probability distribution of one-cycle displacements, $P(\delta x_i)$, where $\delta x_i = |x_i(t+1) - x_i(t)|$ (we use isotropy and average over x and y directions). In the flowing phase ($a > a_c \approx 0.049$), $P(\delta x_i)$ has a broad, nearly-exponential tail, stemming from particles involved in local rearrangements. As a result, all particles move significantly during each cycle.

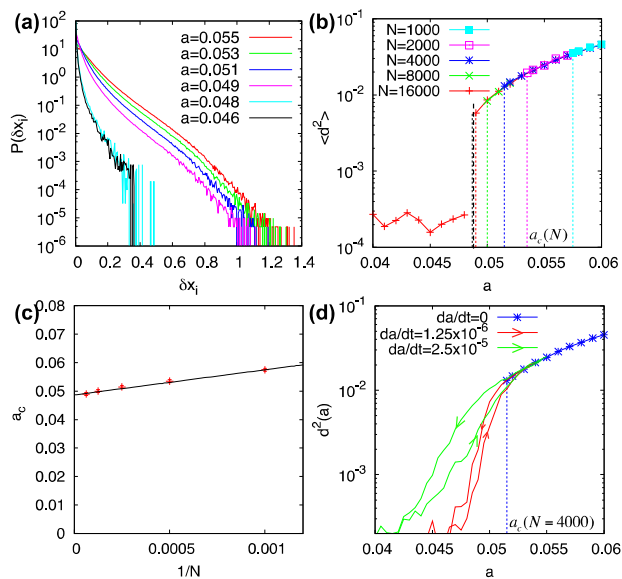


FIG. 2: (a) Probability distribution of the one-cycle particle displacements $P(\delta x_i)$ for different activities a . The distribution changes discontinuously between flowing ($a > a_c \simeq 0.049$) and arrested ($a < a_c$) phases. (b) Averaged one-cycle displacement squared at steady state for different system sizes N . $\langle d^2 \rangle$ is large above a_c , and drops discontinuously to nearly zero below a_c . The black vertical line represents $a_c(N \rightarrow \infty)$. (c) The critical activity $a_c(N)$ tends to a finite value $\simeq 0.049$ as $1/N \rightarrow 0$. (d) Evolution of $\langle d^2 \rangle$ for $N = 4000$ as the activity is cycled at finite rate between $a = a_1 > a_c$ and $a = a_2 < a_c$. The blue curve represents the steady state value. The hysteretic response gets sharper as $\frac{da}{dt}$ decreases.

As shown below, the accumulation of these local plastic events over many cycles gives rise to diffusive behaviour and structural relaxation at large times. On the other hand in the solid phase ($a < a_c$), the exponential tail in $P(\delta x_i)$ disappears and is replaced by a narrow Gaussian distribution characterized by an average displacement per cycle that is considerably smaller. We show below that these small displacements do not produce diffusive but only localised dynamics.

Crucially, the behaviour of $P(\delta x_i)$ changes abruptly when a crosses a_c . We quantify this observation using a dynamic order parameter for this phase change: $\langle d^2 \rangle = \langle |\bar{d}_i(t)|^2 \rangle$, where the brackets represent an average over time and particles in steady state. A similar quantity was defined in the context of the yielding transition in oscillatory shear [33, 34]. In Fig. 2(b), we plot $\langle d^2 \rangle$ as a function of activity for different system sizes. The flowing phase is characterized by large particle displacements with $\langle d^2 \rangle \gtrsim 0.01$, whereas in the arrested phase, $\langle d^2 \rangle$ is about 100 times smaller. Furthermore, $\langle d^2 \rangle$ jumps discontinuously at a well-defined critical activity, $a_c(N)$. To determine $a_c(N)$ we perform 8 independent simulations from different initial configurations at each activity. We

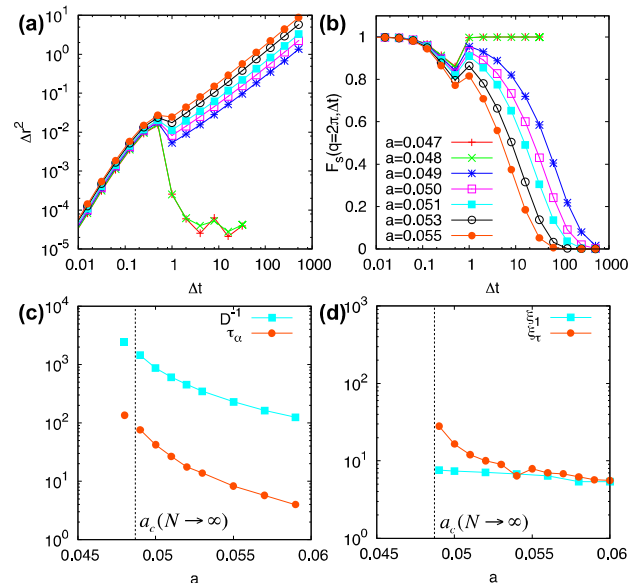


FIG. 3: (a) Mean-squared displacements are diffusive for $a > a_c$, but remain localised for $a < a_c$, with a sharp discontinuity at a_c . (b) A similar discontinuous behaviour is observed for the self-intermediate scattering function $F_s(q, \Delta t)$, which decays rapidly to 0 above a_c , but does not decay below a_c . (c) Inverse diffusion constant D^{-1} and relaxation time τ characterizing the long-time dynamics both increase modestly by about 1 decade as $a \rightarrow a_c^+$. Below a_c we find a metastable flowing phase where D^{-1} and τ can be measured (isolated points) before the system fully arrests. (d) Dynamic correlation lengthscales in the flowing phase measured over a time interval $\Delta t = 1$ (for ξ_1) and $\Delta t = \tau$ (for ξ_τ). Both lengths increase modestly towards a_c .

define a_c such that the 8 runs remain diffusive for $a > a_c$ after a large time, $t = 10^4$. In addition to the sharpness of the phase change, we also observe finite-size effects, since $a_c(N)$ decreases weakly with N . As shown in Fig. 2(c), when plotted against $1/N$, it is clear that a_c extrapolates to a finite value $a_c \approx 0.049$ when $N \rightarrow \infty$.

We substantiate further the discontinuous nature of the transition by studying hysteresis effects. In Fig. 2(d), we measure how $\langle d^2 \rangle$ changes as we slowly cycle the activity $a(t)$ between $a = a_1 > a_c$ and $a = a_2 < a_c$ at a constant rate $\frac{da}{dt}$. We obtain the evolution for $\langle d^2 \rangle$ by averaging over 10^3 such cycles. We observe hysteresis cycles that become sharper and narrower as the sweeping rate becomes slower. Such phenomenology is again representative of first-order phase transitions.

We now turn to the long-time dynamics and measure the mean-squared displacement (MSD) at steady state: $\Delta r^2(\Delta t) = \langle |\bar{r}_i(\Delta t) - \bar{r}_i(0)|^2 \rangle$, see Fig. 3(a). In the flowing phase ($a > a_c$), the system becomes diffusive at long times $\Delta r^2(\Delta t \rightarrow \infty) \approx 4D\Delta t$, which defines the diffusion constant D . In the arrested phase instead, the MSD saturates to a small, finite value at long times, demonstrating particle localisation in this

regime. As a result, we find that $D > 0$ above a_c and $D = 0$ below, with an abrupt change at a_c , as shown in Fig. 3(c). This sharp change in the long-time dynamics is also detected using the intermediate scattering function: $F_s(q, \Delta t) = \langle e^{i\vec{q} \cdot [\vec{r}_i(\Delta t) - \vec{r}_i(0)]} \rangle$, which decays from 1 to 0 when particles move on average a distance $2\pi/|\vec{q}|$. In Fig. 3(b), we show the time decay of $F_s(q, \Delta t)$ for $q = 2\pi$, which corresponds to particles diffusing over a distance comparable to their diameter. Above a_c , $F_s(q, \Delta t)$ decays to 0 relatively rapidly. We extract a relaxation time τ as $F_s(q, \tau) = 1/e$, with again a discontinuous change between the two phases. We extract a relaxation time τ as $F_s(q, \tau) = 1/e$, and so $\tau = \infty$ below a_c .

In Fig. 3(c) we report D^{-1} and τ as a function of activity a . Both measures of long-time dynamics increase modestly by about 1 decade as $a \rightarrow a_c^+$, and they do not diverge. In addition, just below a_c , we find that the flowing phase can be ‘metastable’ for a long time of order 30τ before suddenly evolving towards the arrested phase. Within this metastability window, long-time dynamical properties can be measured and we plot D^{-1} and τ for this metastable liquid phase as isolated points in Fig. 3(c), which appear as the continuation of data at $a > a_c$. These observations confirm that both timescales do not diverge at a_c and illustrate the first-order nature of the phase transition at a_c .

Finally in Fig. 3(d) we plot two dynamic correlation lengthscales measured in the flowing phase which only increase modestly without divergence at a_c . These dynamic lengthscales are obtained from analysis of a 4-point dynamic structure (see [35] for details about this classic measure of spatially heterogeneous dynamics). In particular, we have studied dynamic correlations both over a delay time $\Delta t = 1$ to probe spatial correlations of the one-cycle displacement map (see Fig. 1(b)), which gives us the one-cycle correlation length ξ_1 . We also measured the dynamic lengthscale ξ_τ characterizing the long-time dynamics by setting $\Delta t = \tau$. Both lengthscales increase modestly as $a \rightarrow a_c^+$, revealing collective motion in the flowing phase in the absence of any criticality at the fluidisation transition.

In conclusion, we have introduced a microscopic model for active materials where local energy injection stems from active change of the particle sizes. This model is directly motivated by experimental observations of volume fluctuations of cells in epithelial tissues [16, 17]. Our model exhibits a discontinuous non-equilibrium phase transition from an arrested to a fluid phase as the amplitude of self-deformation is increased. This active fluidisation transition is strikingly different from observations in self-propelled particles [25–27] in which continuous slowing down of several decades can be observed, accompanied by growing dynamic lengthscales, reminiscent of glassy dynamics in dense fluids [24]. It also differs markedly from the static transition discovered in the vertex model, which is akin to a continuous rigidity tran-

sition [21]. We propose that a better analogy is with the yielding transition in soft amorphous solids, where irreversible rearrangements and particle diffusion result from applying a mechanical forcing above the yield stress. Evidence that yielding corresponds to a non-equilibrium dynamic first-order transition is mounting [33, 34, 36], the difference with our system being the scale at which the mechanical force is acting. Our model bears a strong resemblance to the fluid-like dynamics observed in biological tissues, where flow and diffusion also occur with finite correlation lengthscales and timescales [3, 9, 11]. We notice that the critical activity reported here is relatively small, $a_c \simeq 5\%$. For comparison, certain eukaryotic cells have been observed to undergo volume fluctuations of up to $\sim 20\%$ [16] due to the formation of various protrusions [17]. Such fluctuations could be large enough to fluidize dense suspensions of cells. Our results suggest that active volume fluctuations play an important role in the collective dynamics of epithelial tissues in addition to previously studied mechanisms, and provide a novel paradigm to interpret this dynamics in terms of an active yielding transition.

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