

# Pressure is not a state function for generic active fluids

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**Pressure is the mechanical force per unit area that a confined system exerts on its container. In thermal equilibrium, it depends only on bulk properties—such as density and temperature—through an equation of state. Here we show that in a wide class of active systems the pressure depends on the precise interactions between the active particles and the confining walls. In general, therefore, active fluids have no equation of state. Their mechanical pressure exhibits anomalous properties that defy the familiar thermodynamic reasoning that holds in equilibrium. The pressure remains a function of state, however, in some specific and well-studied active models that tacitly restrict the character of the particle-wall and/or particle-particle interactions.**

For fluids in thermal equilibrium, the concept of pressure,  $P$ , is familiar as the force per unit area exerted by the fluid on its containing vessel. This primary, mechanical definition of pressure seems to require knowledge of the interactions between the fluid's constituent particles and its confining walls. But we learn from statistical mechanics that  $P$  can also be expressed thermodynamically, as the derivative of a free energy with respect to volume. The pressure therefore obeys an equation of state, which involves only bulk properties of the fluid (temperature  $T$ , number density  $\rho$ , and so on). Hydrodynamics provides a third definition of  $P$ , as the trace of the bulk thermodynamic stress tensor, whose microscopic definition in terms of momentum fluxes is again well known<sup>1</sup>. In thermal equilibrium, all these definitions of pressure coincide. The corresponding physical insight is that the fluid may be divided into blocks that are in mechanical equilibrium with each other and with any confining walls, so bulk and wall-based pressure definitions must agree.

Purely thermodynamic concepts, such as temperature, are well known to be ill defined in systems far from equilibrium<sup>2</sup>. However, one could hope that mechanical properties, such as pressure, are less problematic. Here we investigate this question for active fluids, in which energy dissipation at the microscopic level drives the motion of each particle to give strong non-equilibrium effects<sup>3</sup>. Assemblies of self-propelled particles (SPPs) have been proposed as simplified models for systems ranging from bacteria<sup>4,5</sup> and active colloidal 'surfers'<sup>6–8</sup>, to shaken grains<sup>9–11</sup> and bird flocks<sup>12</sup>. We define the mechanical pressure  $P$  of an active fluid as the mean force per area exerted by its constituent particles on a confining wall. This was studied numerically for a number of active systems, showing some surprising effects for finite-size, strongly confined fluids<sup>13–19</sup>. Alternatively, when describing the dynamics of such active fluids at larger scales, some authors have introduced a bulk stress tensor and defined pressure as its trace<sup>3,17–19</sup>, leading to recent experimental measurements<sup>20</sup>. As we are far from equilibrium, an equivalence between these different definitions, as seen numerically in refs 13, 17, 18, requires explanation.

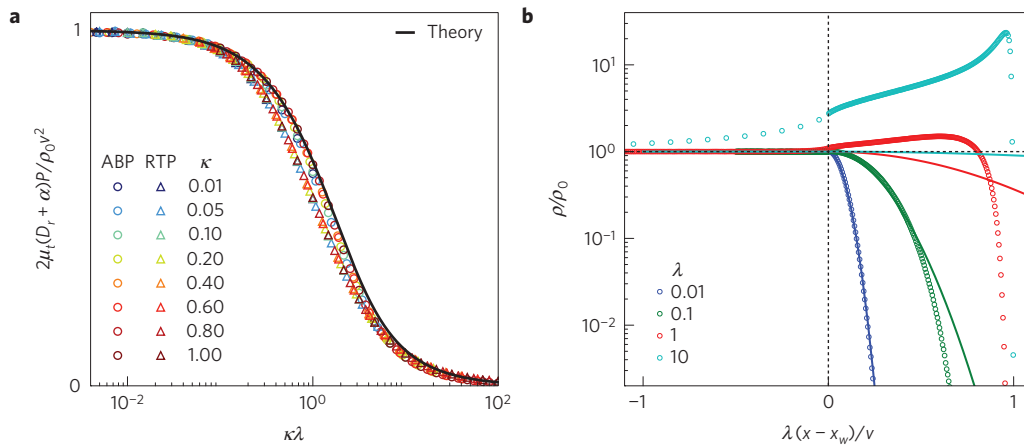
In this article, we show analytically and numerically that the pressure  $P$  exerted on a wall by generic active fluids depends

directly on the microscopic interactions between the fluid and the wall. Unless these interactions, as well as the interactions between the fluid particles, obey strict and exceptional criteria, there is no equation of state relating the mechanical pressure to bulk properties of the fluid. Therefore, all connections to thermodynamics and to the bulk stress tensor are lost. Nevertheless, we provide analytical formulae to compute the wall-dependent pressure for some of the most-studied classes of active systems. Exceptional models for which an equation of state is recovered include the strictly spherical SPPs considered in refs 13, 17, 18. Below we find that such simplified models are structurally unstable: small orientation-dependent interactions (whether wall-particle or particle-particle) immediately destroy the equation of state. Such interactions are present in every experimental system we know of.

A clear distinction exists between the present work and that of ref. 21. The latter includes an explicit proof that pressure is, after all, well defined within a narrow class of models: spherical SPPs with torque-free wall interactions and torque-free pairwise interparticle forces. Because this class has been a major focus of theory and simulation studies, that finding is important, creating in those cases a direct link between pressure and correlation functions that can be exploited in future theoretical advances. However, in general terms it is even more important to know that an equation of state for the pressure is the exception, rather than the rule, in active matter systems. This we establish here.

To appreciate the remarkable consequences of the generic absence of an equation of state, consider the quasi-static compression of an active fluid by a piston. As the mechanical pressure depends on the piston, compressing with a very soft wall—into which particles bump gently—or with a very hard wall requires different forces and hence different amounts of work to reach the same final density. This is not the only way our thermodynamic intuition can fail for active systems. We will show both that pressure can be anisotropic, and that active particles admit flux-free steady states in which the pressure is inhomogeneous. Finally, in the models we consider (which best describe, for example, crawling bacteria<sup>4</sup> or colloidal surfers or rollers near a supporting surface<sup>22,23</sup>) there are situations in which the confinement forces at the edges

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**Figure 1 | Non-interacting self-propelled ellipses.** **a**, Normalized pressure as the particle anisotropy  $\kappa$  and the wall stiffness  $\lambda$  are varied for ABPs and RTPs. The theoretical prediction for ABPs corresponds to equation (5). **b**, Density profiles for spherical ABPs for four different wall stiffness values, all yielding a pressure equal to  $\rho k T_{\text{eff}}$ . The solid lines are Boltzmann distributions at  $k T_{\text{eff}}$ , showing that the pressure is given by the effective temperature far outside the Boltzmann regime  $\lambda \ll D_r$ .  $v=1, D_t=0, D_r=1$  for ABPs and  $\alpha=1$  for RTPs, with box size  $L_x \times L_y = 10 \times 1$ .

of a sample do not sum to zero. We show how this unbalanced force is compensated by momentum transfer to the support. The issue of whether an equation of state exists in so-called ‘wet’ active matter<sup>3</sup>—in which full momentum conservation applies throughout the interior of the system—remains open.

### Non-interacting particles

We consider a standard class of models for SPPs in which the independent Brownian motion of each particle (diffusivity  $D_t$ ) is supplemented by self-propulsion at speed  $v$  in direction  $\mathbf{u}$ ,

$$\frac{d\mathbf{r}}{dt} = v\mathbf{u} + \sqrt{2D_t}\boldsymbol{\eta}(t) \quad (1)$$

with  $\boldsymbol{\eta}(t)$  a Gaussian white noise of unit variance. The reorientation of the direction of motion  $\mathbf{u}$  then occurs with a system-specific mechanism: active Brownian particles (ABPs) undergo rotational diffusion, whereas run-and-tumble particles (RTPs) randomly undergo complete reorientations (‘tumbles’) at a certain rate. These well-established models have been used<sup>5,7,24–28</sup> to describe respectively active colloids<sup>6,8,22,23</sup>, or bacterial motion<sup>4,28</sup> and cell migration<sup>29</sup>. Such models neglect any coupling to a momentum-conserving solvent, and are thus best suited to describe particles whose locomotion exploits the presence of a gel matrix or supporting surface as a momentum sink. This is true of many active systems, such as crawling cells<sup>30</sup>, vibrated disks or grains<sup>9–11</sup>, and colloidal rollers<sup>23</sup> or sliders<sup>22</sup>.

We address a system of SPPs with spatial coordinates  $\mathbf{r}=(x, y)$  in two dimensions; we assume periodic boundary conditions, and hence translational invariance, in the  $\hat{y}$  direction. The system is confined along  $\hat{x}$  by two walls at specified positions, which exert forces  $-\nabla V(x)$  on particles at  $x$ ; these forces have finite range and thus vanish in the bulk of the system. The propulsion direction of a particle is  $\mathbf{u}=(\cos\theta, \sin\theta)$ , with  $\theta=0$  along the  $\hat{x}$  direction. In the absence of interactions between the particles, the master equation for the probability  $\mathcal{P}(\mathbf{r}, \theta, t)$  of finding a particle at position  $\mathbf{r}$  at time  $t$  pointing along the  $\theta$  direction reads

$$\begin{aligned} \partial_t \mathcal{P} = & -\nabla \cdot [(v - \mu_t \nabla V(x))\mathcal{P} - D_t \nabla \mathcal{P}] \\ & - \partial_\theta [\mu_r \Gamma(x, \theta)\mathcal{P} - D_r \partial_\theta \mathcal{P}] - \alpha \mathcal{P} + \frac{\alpha}{2\pi} \int \mathcal{P} d\theta' \end{aligned} \quad (2)$$

Here  $\mu_t$  and  $D_t$  are the translational mobility and diffusivity; likewise  $\mu_r$  and  $D_r$  for rotations. The propulsive velocity is  $\mathbf{v}=v\mathbf{u}(\theta)$ ,

and  $\alpha$  is the tumble rate. ABPs correspond to  $\alpha=0$  and RTPs to  $D_r=0$ . Here we allow all intermediate combinations, to test the generality of our results. In addition to the external force  $-\nabla V(x)$ , we include an external torque  $\Gamma(x, \theta)$ , which may, for example, describe the well-documented alignment of bacteria along walls<sup>31</sup>. Generically, just as in passive fluids, a wall-torque will arise whenever the particles are not spherical, and its absence is thus strictly exceptional. Obviously, the asphericity of (say) water molecules does not violate the thermodynamical precepts of pressure; remarkably, we show below that, for active particles, it does so.

As our set-up is invariant along the  $\hat{y}$  direction, the mechanical pressure can be computed directly from the force exerted by the system on a wall (which we place at  $x=x_w \gg 0$ ), as

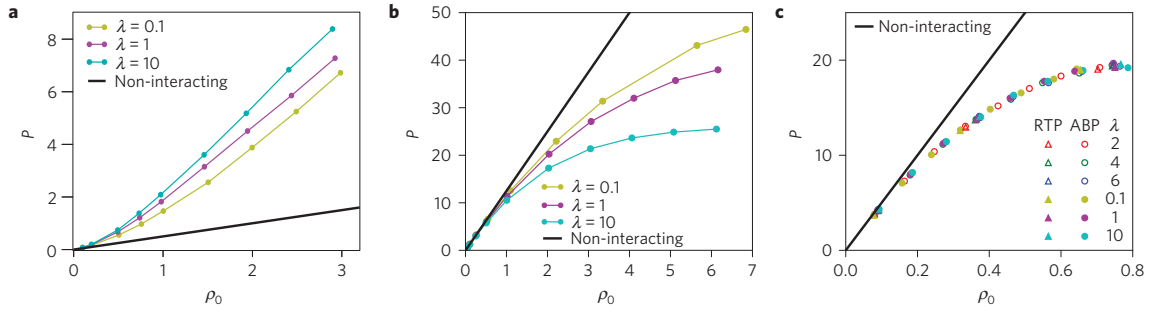
$$P = \int_0^\infty \rho(x) \partial_x V(x) dx \quad (3)$$

Here an origin  $x=0$  is taken in the bulk, and  $\rho(x) = \int_0^{2\pi} \mathcal{P}(x, \theta) d\theta$  is the steady-state density of particles at  $x$ . As stated previously, for a passive equilibrium system ( $v=0$ ) with the same geometry, the mechanical definition (3) of pressure is equivalent to the thermodynamic definition, as proved for completeness in the Supplementary Information. Note that equation (3) still applies in the presence of other particles, such as solvent molecules, so long as those particles do not themselves exert any direct force on the wall (which is thus semipermeable). Under such conditions  $P$  is, by definition, an osmotic pressure; the results below will still apply to it, whenever equation (2) remains valid.

As described in the Supplementary Information, the pressure can be computed analytically from equation (2) as:

$$\begin{aligned} P = & \left[ \frac{v^2}{2\mu_t(D_r + \alpha)} + \frac{D_t}{\mu_t} \right] \rho_0 \\ & - \frac{v\mu_r}{\mu_t(D_r + \alpha)} \int_0^\infty dx \int_0^{2\pi} \Gamma(x, \theta) \sin\theta \mathcal{P}(x, \theta) d\theta \end{aligned} \quad (4)$$

This is a central result, and exact for all systems obeying equation (2). Clearly,  $\Gamma(x, \theta)$  in general depends on the wall–particle interactions, as does  $\mathcal{P}(x, \theta)$ , which is sensitive to both  $\Gamma(x, \theta)$  and  $V(x)$ . Thus the mechanical pressure  $P$  obeying equation (4) is likewise sensitive to these details: it follows that no equation of state exists for active particle systems in the general case.



**Figure 2 | Interacting self-propelled spheres. a–c,** Pressure versus density  $P(\rho_0)$  for interacting particles ( $L_x \times L_y = 200 \times 50$ ). **a,** Aligning ABPs. The torque exerted by particle  $j$  on particle  $i$  is  $F(\theta_j - \theta_i, \mathbf{r}_i, \mathbf{r}_j) = (\gamma/N(\mathbf{r}_i)) \sin(\theta_j - \theta_i)$  if  $|\mathbf{r}_j - \mathbf{r}_i| < R$  and 0 otherwise, where  $N(\mathbf{r}_i)$  is the number of particles interacting with particle  $i$ .  $v=1$ ,  $D_r=1$ ,  $D_t=0$ ,  $R=1$  and  $\gamma=2$ . **b,** ‘Quorum sensing’ interactions  $v(\bar{\rho}) = v_0(1 - \bar{\rho}/\rho_m) + v_1$  with  $v_0=10$ ,  $v_1=1$ ,  $\rho_m=5$ ,  $D_r=D_t=1$ . **c,** The pressure of particles interacting with repulsive WCA potentials is independent of the wall potential. Triangles and circles represent RTPs and ABPs, respectively, with  $v=10$ ,  $D_r=1$ ,  $\alpha=1$  and  $D_t=0$ . Open and filled symbols correspond to linear and harmonic wall potentials, respectively. (See Supplementary Information for numerical details.)

To illustrate this effect and show that (4) can indeed be used to compute the pressure, we study a model of ABPs with elliptical shape (see Supplementary Information for details). We choose a harmonic confining potential,  $V(x) = (\lambda/2)(x - x_w)^2$  for  $x > x_w$ , with  $V=0$  otherwise, accompanied by a torque  $\Gamma = \lambda\kappa \sin 2\theta$  (again, for  $x > x_w$  and zero otherwise). With  $\kappa = (a^2 - b^2)/8$ , this is the torque felt by an elliptical particle of axial dimensions  $a, b$  and unit area  $\pi ab$ , subject to the linear force field  $-\nabla V(x)$  distributed across its body. Assuming the steady-state distribution  $\mathcal{P}(x, \theta)$  to relax to its bulk value outside the range of the wall potential,  $\mathcal{P}(x_w, \theta) = \rho_0/2\pi$ , the pressure in such an ABP fluid (for  $D_t=0$ ) is given by

$$P = \frac{\rho_0 v^2}{2\lambda\mu_t\mu_r\kappa} \left[ 1 - \exp\left(-\frac{\lambda\mu_r\kappa}{D_r}\right) \right] \quad (5)$$

For  $\kappa > 0$ , the torque reduces the pressure by orienting the ABPs parallel to the wall. Equation (5) shows explicitly how walls with different spring constants  $\lambda$  experience different pressures, in sharp contrast with thermodynamics. We checked this prediction by direct numerical simulations of ABPs and found good agreement (see Fig. 1). We also found similar behaviour numerically for (likewise elliptical) RTPs, confirming that the failure of thermodynamics is generic.

For passive particles in thermal equilibrium,  $v=0$  and equation (4) reduces to the ideal gas law,  $P = \rho_0 k_B T$ , on use of the Einstein relation ( $D_t/\mu_t = k_B T$ ). Another case where an equation of state is recovered is for torque-free (for example, spherical) particles, with  $\Gamma=0$ . In that case equation (4) reduces to the same ideal gas law, but with an effective temperature

$$\frac{P}{\rho_0} = k_B T_{\text{eff}} = \frac{v^2}{2\mu_t(D_r + \alpha)} + \frac{D_t}{\mu_t} \quad (6)$$

This explains why previous numerical studies of torque-free, non-interacting active particle fluids gave consistent pressure measurements between impenetrable<sup>14,15</sup> or harmonically soft walls<sup>13</sup>. Related expressions for the pressure of such fluids were found by computing the mean kinetic energy<sup>13</sup>, or the stress tensor<sup>17–19</sup>, possibly encouraging a belief that all reasonable definitions of pressure in active systems are equivalent. However, equation (4) shows that these approaches cannot yield consistent results beyond the simplest, torque-free case.

The ‘effective gas law’ of equation (6) for the torque-free case is itself remarkable. For ABPs or RTPs in an external potential  $V(x)$ , the effective temperature concept predicts a steady-state density  $\rho(x) \propto \exp[-V(x)/k_B T_{\text{eff}}]$  that is accurate only for weak force fields<sup>32,33</sup>. Yet equation (6) holds even with hard-core walls, for which the opposite applies and the steady-state density profile

is far from a Boltzmann distribution (see the simulation results of Fig. 1 and the analytical results for one-dimensional RTPs in the Supplementary Information). In fact the result stems directly from the exact computation of  $\int_0^\infty \rho(x) \partial_x V(x) dx$ , which can be done at the level of the master equation and leads to equation (4), so that no broader validity of the  $T_{\text{eff}}$  concept is required, or implied.

### Interacting active particles

Equation (4) gives the pressure of non-interacting active particles and we now address the extent to which our conclusions apply to interacting SPPs. Clearly, interactions will not restore the existence of an equation of state in the presence of wall torques, and we thus focus on ‘torque-free’ walls.

Interparticle alignment is probably the most-studied interaction in active matter<sup>3</sup>. To measure its impact on pressure, we consider  $N$  ABPs whose positions  $\mathbf{r}_i$  and orientations  $\theta_i$  evolve according to (1) and

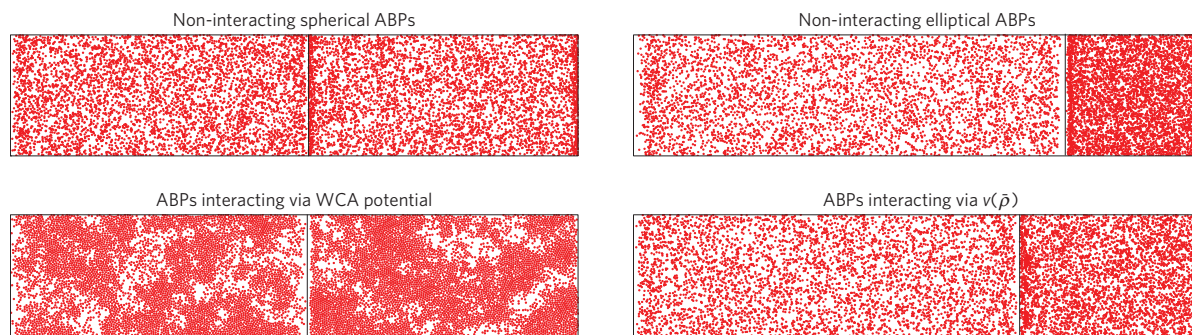
$$\frac{d\theta_i}{dt} = \mu_r \sum_{j=1}^N F(\theta_j - \theta_i, \mathbf{r}_i, \mathbf{r}_j) + \sqrt{2D_r} \xi_i(t) \quad (7)$$

where  $F$  is an aligning torque between the particles. As shown in the Supplementary Information, the pressure can be computed analytically to give

$$P = \left[ \frac{v^2}{2\mu_t D_r} + \frac{D_t}{\mu_t} \right] \rho_0 - \frac{v\mu_r}{\mu_t D_r} \int_0^\infty dx \int_{-\infty}^\infty dy \int_0^{2\pi} d\theta \times \int d\mathbf{r}' \int_0^{2\pi} d\theta' F(\theta' - \theta, \mathbf{r}, \mathbf{r}') \sin \theta \langle \mathcal{P}(\mathbf{r}, \theta) \mathcal{P}(\mathbf{r}', \theta') \rangle \quad (8)$$

where the integral over  $\mathbf{r}'$  is over the whole space. As the distribution  $\mathcal{P}(\mathbf{r}, \theta) = \sum_{i=1}^N \delta(\mathbf{r} - \mathbf{r}_i) \delta(\theta - \theta_i)$  depends (for  $x > 0$ ) on the wall potential, so does the pressure. Therefore, even in the absence of wall torques, alignment interactions between particles destroy any equation of state. Simulation results of ABPs evolving according to equations (1) and (7) are shown in Fig. 2a, with a particular choice of interparticle torque  $F$ : the measured pressure indeed depends on the wall potential and agrees with equation (8).

In active matter, more general interactions than pairwise torques often have to be considered. For example, in bacteria with ‘quorum sensing’ (a form of chemical communication), particles at position  $\mathbf{r}$  can adapt their dynamics in response to changes in the local coarse-grained particle density  $\bar{\rho}(\mathbf{r})$  (ref. 34). Also shown in Fig. 2b are simulations for the case  $v(\bar{\rho}) = v_0(1 - \bar{\rho}/\rho_m) + v_1$ , reflecting a pairwise speed reduction (see Supplementary Information for details). This is an example where even completely torque-free



**Figure 3 | Simple test for the existence of an equation of state.** Four snapshots of the steady state of 10,000 ABPs in a  $200 \times 50$  cavity split in two by a mobile asymmetric harmonic wall ( $\lambda=1$  on the left and  $\lambda=4$  on the right,  $v=10$ ,  $D_r=1$ ,  $D_t=0$ ) for: non-interacting spherical ABPs (top left), non-interacting elliptical ABPs with  $\mu_r=\kappa=1$  (top right), ABPs interacting via the WCA potential (bottom left) and via  $v(\bar{p})$  (bottom right) with  $v_0=10$ ,  $v_1=1$ ,  $\rho_m=4.8$ . A spontaneous compression of the right half of the system is the signature of the lack of an equation of state.

particles have no equation of state. Again, we show in the Supplementary Information how an explicit formula for the pressure can be computed from first principles.

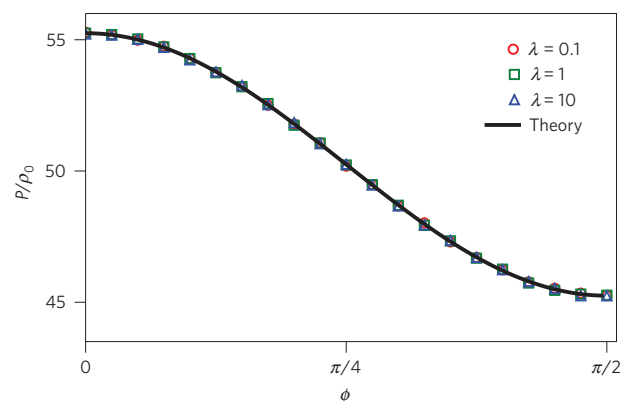
The case of torque-free ABPs with short-range repulsive interactions<sup>24,25,35,36</sup> was recently considered in refs 17,18. The mechanical force exerted on a wall was found to coincide with a pressure computed from the bulk stress tensor, suggesting that in this case an equation of state does exist. To check this, we choose a Weeks–Chandler–Andersen (WCA) potential:  $U(r)=4[(\sigma/r)^{12}-(\sigma/r)^6]+1$  if  $r < 2^{1/6}\sigma$  and  $U=0$  otherwise, where  $r$  is the interparticle distance and  $\sigma$  the particle diameter. Using simulations we determined  $P$  as a function of bulk density  $\rho_0$  for various harmonic and linear wall potentials. As shown in Fig. 2c, all our data collapse onto a wall-independent equation of state  $P(\rho_0)$ . An analytical expression for  $P(\rho)$  in this rather exceptional case is derived and studied in ref. 21 in the context of phase equilibria.

The cases explored above show that there is generically no equation of state in an active fluid, one exception being when wall-particle and particle–particle torques are both negligible and the self-propulsion speed is constant. Given this outcome, a simple test for the presence or absence of an equation of state, in simulations or experiments, would be welcome. If the pressure is set by bulk properties of the fluid, when an asymmetrically interacting partition is used to separate the system into two parts, no force acts on the partition and it does not move. Conversely, if the partition does move, there is no equation of state. To check this, we simulated a large box of homogeneous active fluid, introduced at its centre a mobile wall with asymmetric potentials on its two sides, and let the system reach steady state. In the cases shown above to have an equation of state, the wall remains at the centre of the box so that the densities on its two sides stay equal. In the other cases, however, the partition moves to equalize the two wall-dependent pressures, resulting in a flux-free steady state with unequal densities in the two chambers (Fig. 3).

### Anomalous attributes of the pressure

A defining property of equilibrium fluids is that they cannot statically support an anisotropic stress. Put differently, the normal force per unit area on any part of the boundary is independent of its orientation. This applies even to oriented fluids (without positional order), such as nematic liquid crystals<sup>37</sup>, but breaks down for active nematics<sup>3</sup>.

We next show that it can also break down for active fluids with isotropic particle orientations, as long as the propulsion speed is anisotropic, that is,  $v=v(\theta)$ . This could stem from an anisotropic mobility  $\mu_t(\theta)$ , as might arise for cells crawling on a corrugated surface. We suppose  $v(\theta)=v(\theta+\pi)$  so that oppositely oriented particles have the same speed; equation (2) then shows that the



**Figure 4 | Anisotropic pressure.** RTPs with anisotropic speed  $v(\theta)=v_0+v_1\cos(2\theta)$ , with  $v_0=10$ ,  $v_1=1$ ,  $D_t=0$ . The pressure depends on the angle,  $\phi$ , between the wall and the axis  $\hat{y}$ , but not on the stiffness of the potential.

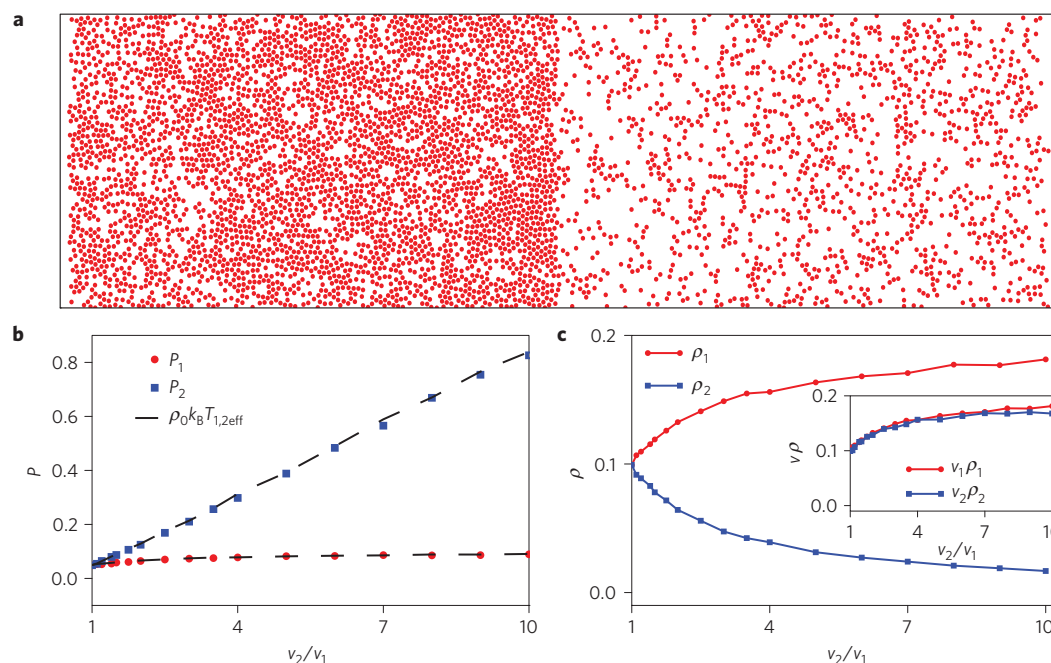
bulk steady-state particle distribution  $\mathcal{P}(\mathbf{r},\theta)$  remains isotropic. In addition, as shown in Supplementary Information, the pressure  $P(\phi)$  acting on a wall whose normal is at angle  $\phi$  to the  $\hat{x}$  axis remains independent of the wall interactions, but is  $\phi$ -dependent; for RTPs ( $D_r=0$ ) it obeys

$$P(\phi) = \frac{\rho_0 D_t}{\mu_t} + \frac{\rho_0}{2\pi\mu_t\alpha} \int_0^{2\pi} v^2(\theta) \cos^2(\theta - \phi) d\theta \quad (9)$$

To verify that the pressure is indeed anisotropic we performed numerical simulations for  $v(\theta)=v_0+v_1\cos(2\theta)$  which show perfect agreement with equation (9) (see Fig. 4).

For passive fluids without external forces, mechanical equilibrium requires that the pressure is not only isotropic, but also uniform. This follows from the Navier–Stokes equation for momentum transport<sup>37</sup>, but also holds in (say) Brownian dynamics simulations which do not conserve momentum<sup>1</sup>.

We now show that  $P$  need not be uniform in active fluids, even when an equation of state exists. Consider non-interacting spherical ABPs in a closed container with different propulsion speeds in different regions, say  $v=v_1$  for  $x < 0$  and  $v=v_2$  for  $x > 0$ . This is a realizable laboratory experiment in active colloids whose propulsion is light-induced<sup>8,22</sup>. From equation (2), the flux-free steady state has  $\rho \propto 1/v$  throughout<sup>26,27,38</sup>, so that the pressures  $P_{1,2} \propto \rho v^2$  are unequal. Although different, the pressures in the two compartments are well defined, uniform within each bulk, and independent of the wall–particle interactions. They remain different when interparticle interactions are added (see Fig. 5). Indeed, if for  $v_1 \neq v_2$  equality of



**Figure 5 | Inhomogeneous pressure.** Spherical ABPs interacting with a WCA potential, with speeds  $v_1$  for  $x < 0$  and  $v_2$  for  $x > 0$ . **a**, Snapshot of the cavity in steady state ( $v_1 = 1$ ,  $v_2 = 5$ ). **b**, Pressures  $P_1$  and  $P_2$  as  $v_2/v_1$  is varied. **c**, As  $v_2/v_1$  varies, the densities evolve to equalize  $\rho v$  rather than  $P \sim \rho v^2$ .  $D_r = 1$ ,  $D_t = 0$ ,  $\lambda = 1$ ,  $L_x \times L_y = 200 \times 50$ .

the ideal pressure is restored by setting  $D_r \propto v$ , the effect of such interactions is to reinstate a pressure imbalance. Non-uniformity of  $P$  is thus fully generic for non-uniform  $v$ .

The above example implies a remarkable result, that also holds for systems with no equation of state enclosed by spatially heterogeneous walls. In both cases the net force acting across the system boundary is generically non-zero. Were momentum conserved, this would require the system as a whole to be accelerating. Recall, however, that equation (2) describes particles moving on, or through, a medium that absorbs momentum, and this net force is exactly cancelled by the momentum exchange with the support. The latter vanishes on average in the isotropic bulk, but is non-zero in a layer of finite polarization ( $m_1 \neq 0$ ) close to each wall.

## Discussion

Our work shows that in active fluids the concept of pressure defies many suppositions based on concepts from thermal equilibrium. The generic absence of an equation of state is the most striking instance of this. Despite its absence, we have shown how to compute the mechanical pressure for a large class of active particle systems. Clearly, the concept of pressure is even more powerful in the exceptional cases where an equation of state does exist. This excludes any chemically mediated variation in propulsion speed, and also requires wall-particle and interparticle torques both to be negligible. Because it can easily be achieved on a computer, although not in a laboratory, the torque-free case of spherical active Brownian particles without bulk momentum conservation has played a pivotal role in recent theoretical studies of active matter<sup>13,17,18</sup>. The proof<sup>21</sup> that an equation of state does exist for this system is all the more remarkable because, as we have seen, such an outcome is the exception and not the rule.

It is interesting to inquire how our results would change for systems with full momentum conservation in the bulk. As mentioned previously, if equation (2) still applies, our exact results for  $P$  remain valid so long as this is taken as an osmotic pressure. For dilute systems equation (2) should indeed hold in bulk, even though particles now propel by exerting force multipoles on the

surrounding solvent. (As the walls of the system are semipermeable, the solvent can carry momentum across them, and effectively becomes a momentum sink for the active particles.) However, even for spherical swimmers, hydrodynamic interactions can now cause torques, both between the particles and near the wall<sup>39</sup>, making an equation of state less likely. Its absence would then manifest as a non-zero net force on a semipermeable partition between two identical samples of (say) a swimming bacterial fluid. We predict this outcome whenever the two faces of the partition have different interactions with the swimming particles.

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## Author contributions

All authors participated in designing the project and performing the research. A.P.S. and Y.F. performed the numerical simulations. All authors participated in writing the paper.

## Additional information

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## Competing financial interests

The authors declare no competing financial interests.