INTRODUCTION

Active materials, bacteria, molecular motors, and self-propelled colloids, continuously transform chemical energy from the environment to mechanical work. Dense active matter, from layers of cells to flocks of birds, self-assembles into intricate patterns. Nature's engines are complex and efficient, and we would like to exploit her ideas to fabricate nano-machines.

Nature's Engines: Active Matter

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Active particles operate out of thermodynamic equilibrium. They take energy from their environment and use it to move or to do work [1,2]. Familiar biological examples are swimming bacteria and crawling cells. Perhaps less familiar are the motor proteins, for example myosin and kinesin, which are the engines of the cell (Box 1). Moreover many inanimate active systems can now be engineered. These are often colloids, which can be driven by light and by local concentration gradients. Active matter is of interest to physicists because it is *meant* to exist out of thermodynamic equilibrium. Therefore it provides a platform for motivating and testing theories of non-equilibrium statistical physics. Moreover active systems have evolved to be very efficient tiny engines. Understanding how they self assemble and then operate may suggest novel energy technologies.

What happens to all the energy when active particles move together? A common behaviour is clustering. Dilute colloids undergo Brownian motion and do not order. However when they become active, so that there is a ballistic as well as a Brownian component to their velocity, they aggregate in dynamic groups (Fig. 1a). This can be partially explained by theories that assume that the active particles' velocity decreases with their density [3]. Flocking, exemplified by the beautiful swirling patterns of starling flocks coming in to roost, is another collective behaviour characteristic of active systems; one that is still not well understood (Fig. 1e).

Bacteria are a few microns in length and the Reynolds number governing their flow is tiny, typically $\sim 10^{-4}$. This is far into the viscous regime where flows are expected to be linear and time reversible, and mixing difficult. Therefore it was a surprise when Dombrowski *et al.* showed that in a dense, two-dimensional layer of bacteria the velocity field of the cells appears turbulent [4]. Flow vortices, swirls and jets form on length scales ~5-10 times that of an individual bacterium (Fig. 2a,b).

Active turbulence has now been observed in active systems over a range of length scales [5]. An example is a suspension of microtubules and two headed, kinesin motor proteins (Box 1). The molecular motors bridge pairs of microtubules, holding them together to form microtubule bundles. These motors are directed; they move in a particular sense along their tracks. This means that motors bridging oppositely aligned pairs of microtubules will push them past each other as they walk, extending the filament bundles. The bundles then buckle and drive turbulent flows. Dense layers of cells, for example epithelial cells that line body cavities and organ surfaces, are also active. The activity is due to both cell motion and cell division. There is increasing evidence that these confluent cell layers can also show the vorticity which characterises active turbulence (Fig. 1c).

Active turbulence shares similarities across the diverse systems and length scales, most obviously the highly vortical and unsteady nature of the flow. Details remain to be worked out, but we understand why active turbulence occurs. The reason can be traced right back to Newton's laws of motion. Active particles swim by exerting forces on the surrounding fluid. They are moving autonomously, with no external driving, and therefore at any time forces or torques must be balanced in equal and opposite pairs. Fig. 3c shows that the same is true for the kinesin motors: they exert equal and opposite forces on neighbouring microtubules. Such force dipoles have nematic (head-tail) symmetry which is well known in liquid crystals (Box 2). Therefore the far flow field produced by the microswimmers or motors also has nematic symmetry.

The symmetry properties of the active flow mean that passive liquid crystals in the nematic state provide a useful starting point to understand dense active systems, which are often termed *active nematics*. In particular continuum equations of motion rely primarily on symmetry. Therefore the equations describing how active nematics flow are very similar to those for passive nematic liquid crystals. Just one addition is needed to introduce the activity; an extra term in the stress tensor. Because the active term contributes to the stress it appears under a derivative. This implies that any changes in the direction or magnitude of the nematic order contribute to stresses that drive flows.

An important consequence of this extra, active stress term is that it destroys the nematic ordering [6]. Any small fluctuations from perfect nematic alignment cause shear flows that enhance the fluctuations. This drives the ordered nematic state unstable,which results in active turbulence. Fig. 2c shows simulations of the nematic director field (the swimmer or microtubule directions) in the active turbulent state. The nematic ordering is strongly deformed and the resulting stresses drive the turbulent-like velocity field characterised by flow jets and flow vortices.

Topological defects are a defining feature of passive liquid crystals (Box 2). They lead to distinctive and beautiful images if liquid crystals are placed between crossed polarisers, but are usually a nuisance in applications, reducing the efficiency of liquid crystal displays. Topological defects are energetically unfavourable and anneal out in passive nematics. In active systems, however, they make an important contribution to the energy balance.

In regions of high nematic distortion, the elastic energy and the active flow are able to overcome the energy barrier to creating pairs of topological defects. The defect pairs can escape their mutual attraction because they are mobile: the distortions in the nematic field around a defect drive flows. For a +1/2, comet-like, defect these are unbalanced and the defect moves away from its -1/2 twin until it meets a different -1/2 defect and annihilates with it. Thus, in the steady state, topological defects are created in pairs, unbind, and annihilate in (generally) different pairs. As they move apart they restore regions of nematic order. These are again unstable to shear flows set up by fluctuations, and the dynamic steady state of active turbulence is established.

Fig. 4c shows a pair of defects forming and moving apart in a microtubule - molecular motor suspension. An observation, which is still lacking an explanation, is that for thin active layers the +1/2 topological defects are themselves aligned nematically: the vectors joining the comet head and tail are predominantly parallel or antiparallel [7].

Nature's engines, bacteria, cells and molecular motors, are miracles of engineering. Understanding and mimicking their design principles is becoming a feasible scientific endeavour. To compare: the motor that turns the bacterial flagellum is about 35 nm in diameter and is made up of a complex self-assembled array of proteins. It uses a proton current across the cell membrane to turn a flagellum of length ~10 μm at up to 1,000 rpm. Examples of state-of-the-art, man-made nanomotors are magnetic helices of width 100 nm and length 400 nm, driven by a magnetic field at similar frequencies [8].

Very recently ways have been proposed to harness the energy in active turbulence [9,10,11]. If bacteria are confined to a channel or circular well, which is about the same size as the velocity vortices, the turbulence is replaced by steady flow which could be used to drive micro-propellers. Turbulence in the microtubule - kinesin systems can be controlled by putting a layer of the active fluid next to a passive liquid crystal. Ordering in the passive liquid crystal exerts an anisotropic frictional force on the active suspension and this constrains it to flow in a preferred direction. Simulations have shown that active matter can be used to drive arrays of microscopic gears (Fig. 2e) – the bacterial wind-farms of the future perhaps?

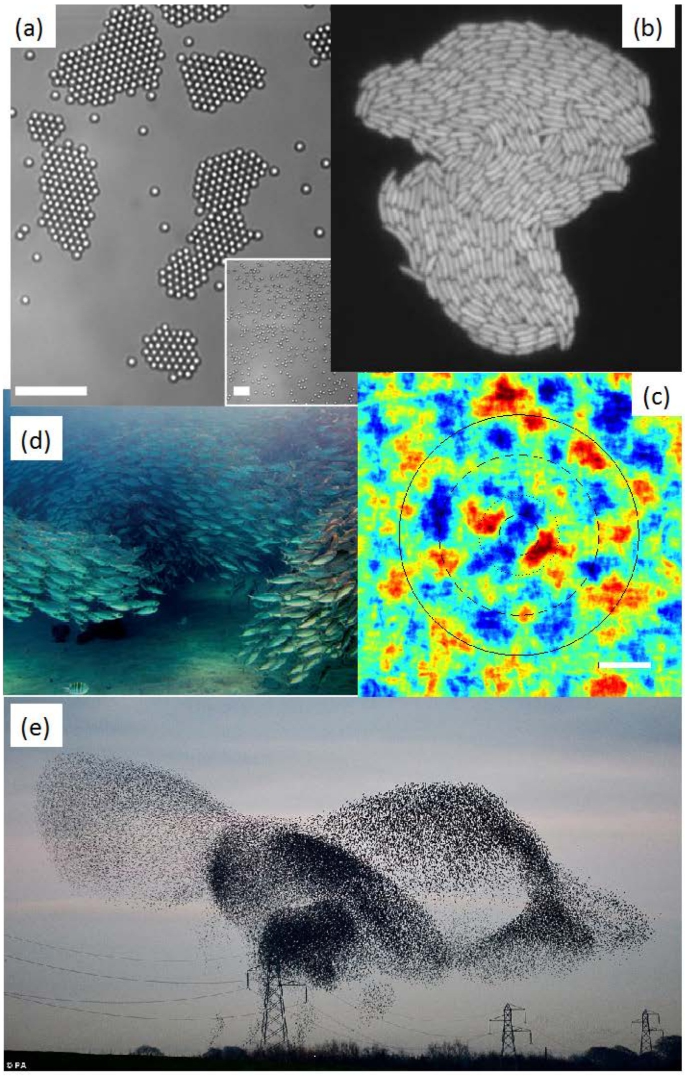
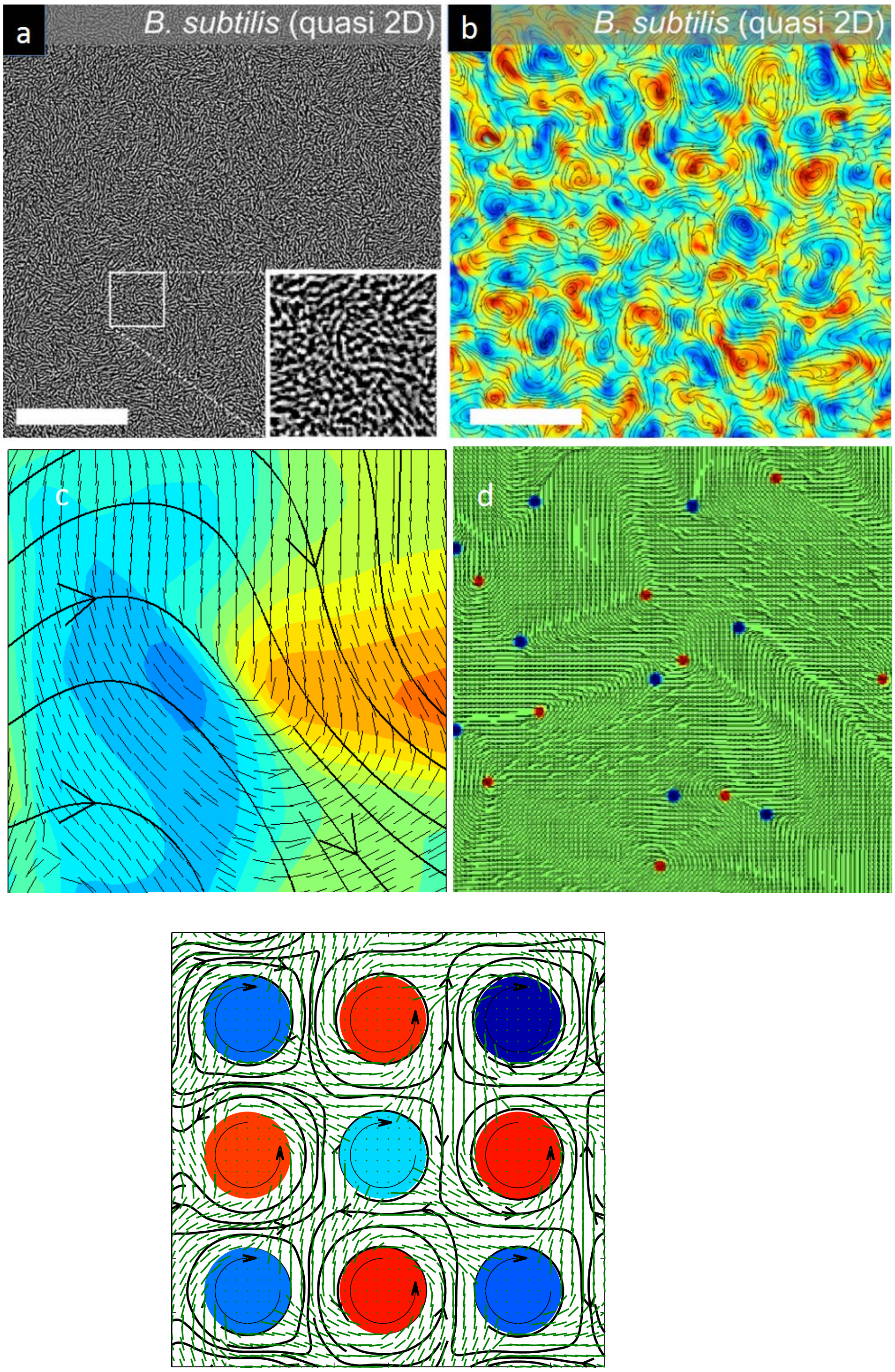


Fig 1: **Active matter**: (a) Colloids, activated by light, cluster when the light is on but disperse when it is turned off (bottom right), after [13]; (b) growing E-coli colony; (c) flow field around a dividing epithelial cell, the colours represent vorticity: clockwise (blue) and anticlockwise (red), after [14]; (d) fish shoaling; (e) starlings flocking.



(e)

Fig 2: Active turbulence: Experiments: (a) a dense suspension of swimming bacteria; (b) the associated vorticity field. Red (blue) regions correspond to high positive (negative) vorticity, after [15]; Simulations: (c) Active turbulence at a smaller length scale. Deformations in the nematic director field drive a velocity jet (black flow lines, with arrows); (d) +1/2 (red) and -1/2 (blue) topological defects, after [5]; (e) The turbulent vortices can be captured by discs which are then rotated by the activity. Here discs are coloured according to their angular velocity as shown in the colourbar (red, anti-clockwise; blue, clockwise), after [11].

Box 1

Motor proteins

Animals like machines need engines. Molecular motors, for example myosin and kinesin, are the engines of the cell. They are responsible for mechanical biological processes as diverse as muscle contraction, turning the bacterial flagellum, cell crawling, transcribing RNA from DNA and moving large molecules around.

The motors proteins are tens of nanometres in size, yet have to operate in the strongly fluctuating crowded cellular environment. To cope with moving in a microscopic gale, motor proteins responsible for intra-cellular transport, such as kinesin, are attached to microtubules, long polymers of tubulin. The tubulin can self-assemble and disassemble as required, creating an evolving network of railway tracks. The motors move along the microtubule tracks in a gait that resembles walking. The back head unbinds, driven by ATP, and tends to move past the front head and reattach. These tiny motors drag around vesicles, membrane sacks, containing proteins and they are responsible for arranging chromosomes ready for cell division.

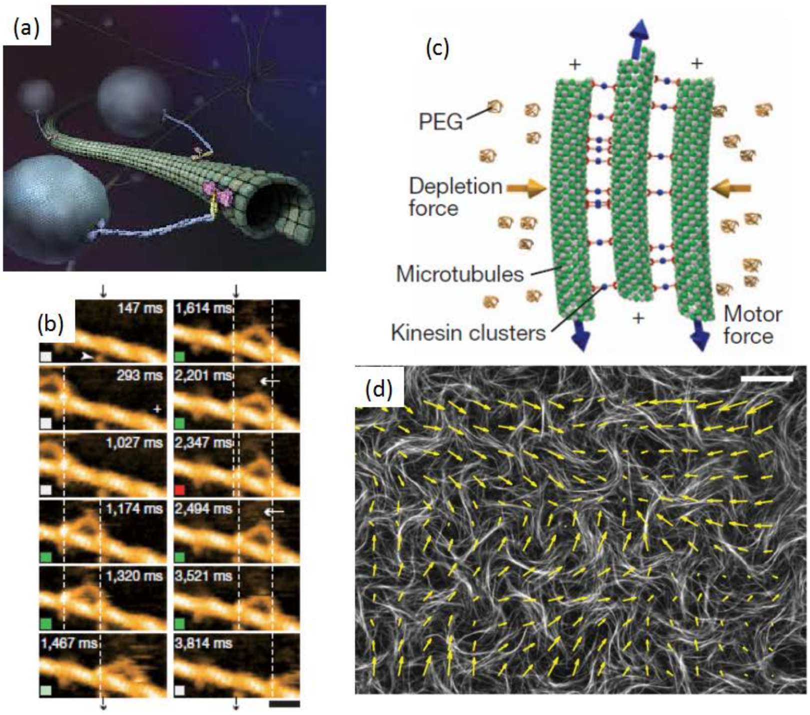


Fig 3: **Motor proteins:** (a) Graphical representation of kinesin motors walking along microtubules. See Youtube: *Inner life of a cell* for an animated version; (b) High speed atomic force microscopy images; successive snapshots show myosin heads moving along an actin filament, after [16]; (c) Microtubules bridged by two-headed kinesin motors; (d) microtubule bundles (white) driven by the motors. The yellow arrows show the velocity field, after [17].

Box 2

Nematic liquid crystals and topological defects

Long, thin molecules or colloids can form a nematic phase which is characterised by long-range orientational order (Fig. 4a) [12]. On average the rods point in the same direction, described by an order parameter called the director. The director is a `headless' vector reflecting the head-tail symmetry of the nematic particles. The nematic is stabilised primarily by entropy as the rods have more room to move around if they lie parallel. Note that there is no long-range order in the rod positions, as would be the case in a crystal.

Nematic liquid crystals are elastic liquids. They flow, but also resist deformations that tend to destroy the alignment of the rods.

The nematic symmetry implies the possibility of topological defects, mistakes in the nematic ordering that cannot be corrected by local rearrangements of the director field. In two-dimensional nematics the most common topological defects, labelled m=+1/2 and m=-1/2, are shown in Fig. 4b. Single topological defects cannot exist in a perfect nematic as they have infinite energy. Defects pairs can form as a liquid crystal orders in the nematic state, between regions of different director orientation. +1/2 and -1/2 defects then attract each other, in a way similar to electric charges, and slowly anneal out.

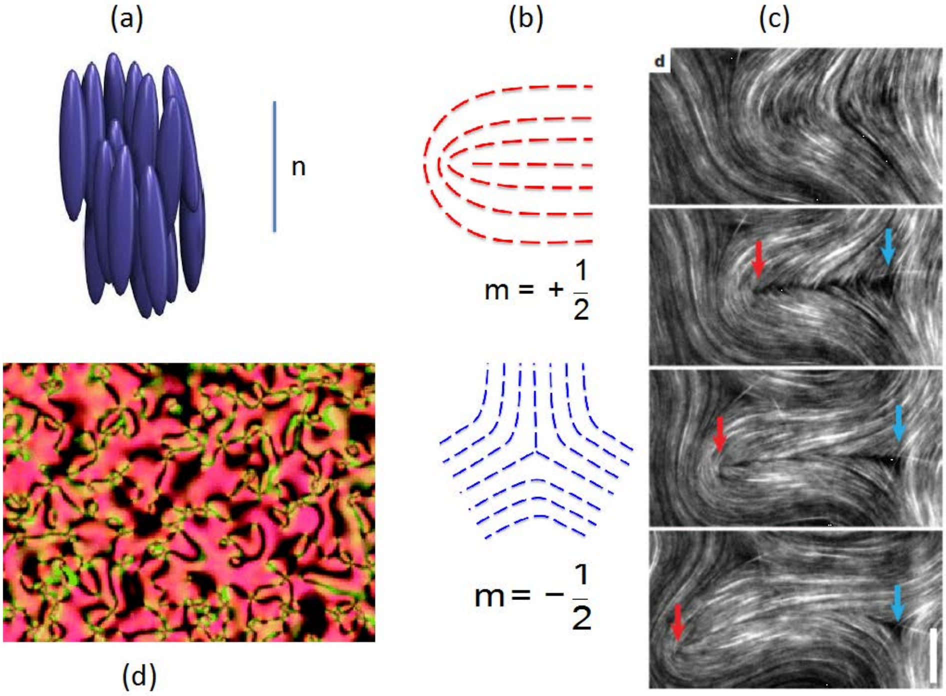


Fig. 4: **Topological defects:** (a) Nematic phase characterised by a director **n** indicating the average direction of the nematogens; (b) topological defects in the nematic field, characterised by topological charge m=+1/2 (red) and m=-1/2 (blue); (c) topological defects forming in an active suspension of microtubules and kinesin motors, after [17]; (d) a nematic liquid crystal between crossed polarisers: the pattern results from topological defects in the nematic ordering.

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BIO

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