ACTIVE MATTER

Playful topology

The combination of topological constraints and deformability in an active system of microtubules and molecular motors leads to rich dynamic behaviour.

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Animals, plants, bacteria and other active systems exist out of thermodynamic equilibrium. Inanimate systems — such as vibrated granular materials or sheared fluids — can also operate out of equilibrium and may be considered active, yet their energy source is external. Driven by advances in nanotechnology and imaging techniques, research in the collective behaviour of active matter has burgeoned, and has led to surprises that are challenging theories of non-equilibrium statistical physics. For example, a dense suspension of bacteria can behave akin to a turbulent fluid, with a velocity field that is continuously changing and with swirls and jets forming and decaying. Normally, turbulence is a consequence of inertia, which is usually negligible at micrometre and smaller length scales; hence, the ‘active turbulence’ seen in bacterial systems needs a different explanation. Moreover, similar flow fields have been seen in other active systems on widely varying length- and timescales, from suspensions of microtubules and molecular motors to agitated granular matter, schools of fish and flocks of birds, and the extent to which the properties of active turbulence are universal across length scales remains an open question. Reporting in Science, Andreas Bausch, Zvonimir Dogic, Cristina Marchetti and colleagues now show that in a confined active system, a dense suspension of microtubules and molecular motors on the surface of a lipid vesicle, unexpected behaviour such as cyclic oscillations between defect configurations or between vesicle shapes can arise when activity is combined with topological constraints and deformability.

Molecular motors — the active protein complexes responsible for intracellular transport, for contracting muscles and for lining up the machinery required for cell division — are a few nanometres in size (whereas bacteria are typically a few micrometres long), and walk on microtubules or actin filaments. For example, the molecular motor kinesin has two heads that alternately bind to, and are released from, the microtubule track (in a process mediated by the exchange of the fuel molecules ATP and ADP), and the particular catapult-like configuration of the tether connecting its two heads gives the directionality to the gait. Previously, Dogic and co-authors used kinesin clusters that bridge pairs of microtubules (Fig. 1c) to generate spontaneous motion. Because kinesin motors are directional, those walking in different directions along bridged microtubules cause the bundles of microtubules to extend, buckle, break-up and re-form. This drives active turbulence. The authors showed that when the active material is placed within drops of water-in-oil tens of micrometres in size the active suspension adsorbs at the oil/water interface to form a spherical shell, and that when the shell is placed in frictional contact with a hard surface it actively rolls around, driven by ATP.

Dogic and collaborators’ experiments and related theoretical work highlighted an unexpected player in the interpretation of the behaviour of dense active systems: topological defects. These are defects that cannot be removed by a local rearrangement; familiar examples are dislocations in crystals, point defects in two-dimensional liquid crystals and knots in closed loops. In the experiments of Bausch, Dogic and co-authors, the topological defects are local distortions in the directions of the microtubules (and can be formed or destroyed in pairs as the microtubules are stretched and bent by the kinesin clusters) that arise as a mechanism of strain removal (Fig. 1d). Such topological defects act as sources of vorticity (Fig. 1e), and help to drive active turbulence. As the topological defects are a consequence of motor activity, one expects that once all available ATP is used up the defects should eventually anneal away. This is what occurs on planar surfaces. On the surface of a spherical object such as a lipid vesicle, however, it is not possible to align microtubules without introducing intrinsic topological defects (similarly, the north and south poles on the Earth can be seen as defects in the alignment of longitude lines). A less obvious, yet often energetically

Figure 1 | Examples of active turbulence. a-e, Dense suspensions of fish (a), and of microtubules and molecular motors (b–e), continuously create energy, resulting in high-vorticity flow fields (e). Regions of clockwise (red) and anticlockwise (blue) flow are highlighted in the vorticity plot in e. Individual microtubules are bridged by kinesin clusters that move the microtubules in the direction shown by the blue arrows (c). PEG, polyethylene glycol. Topological defects (arrows in d) form as the microtubules bundle, stretch, buckle and bend. Figures reproduced with permission from: a, © Thalia Watmough/aliki image library/Alamy; b–d, ref. 5, Nature Publishing Group; e, ref. 3, © 2012 National Academy of Sciences.
more stable, configuration involves four topological defects positioned at the corners of a tetrahedron. Yet, what would happen to such a tetrahedral arrangement if the defects are active and generate velocity fields? On the lipid vesicles, Bausch and co-authors find four active defects that oscillate regularly between two symmetric tetrahedral defect states by way of a configuration where all four defects lie in a plane. The oscillations arise from the coupling between velocity fields and elastic defect–defect interactions, and the period of oscillation follows a pattern that is distorted but not destroyed by thermal fluctuations. More unexpectedly, when the authors changed the flexibility of the encapsulating vesicle by means of hypertonic stress, the vesicle became elliptical and fluctuated in tune with the defect oscillations. On a timescale of minutes, four filopodia-like protrusions stemmed from the defect sites, reaching tens of micrometres in size before the vesicle re-swelled and the protrusions disappeared (Fig. 2). Other vesicle radii gave microtubule spindles where two defects at the poles led to vesicle extension, buckling and folding. These are likely to be the first of a myriad of dynamical states that result from the interplay between activity-driven defect motion and the deformability of the supporting vesicle.

Bacteria have been used to rotate a tiny paddle wheel, as microscopic stirrers, or as shunt engines to self-assemble colloidal templates. Bausch and co-workers’ findings may push forward the design of systems that harness the ability of nanoscale active matter to transform chemical energy into mechanical work, and are a step towards the creation of a synthetic cell.

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References

Figure 2 | Shape changes of an active vesicle with four defects. a, Confocal images showing z projections of the shape of the vesicle as the flexibility of its membrane is increased by means of hypertonic stress. b, Three-dimensional reconstruction of the vesicle shapes in a, showing the dynamic protrusions that grow from the defect sites as the vesicle de-swells. Figure reproduced with permission from ref. 4, © 2014 The American Association for the Advancement of Science.