Growing a cell wall by driven dislocations

Dislocation-mediate growth of bacterial cell walls
A. Amir and D.R. Nelson, Proc. Natl. Acad. Sci. **109**, 9833-9838 (2012).

Recommended with a commentary by Alex J. Levine, UCLA

Bacteria are generally under large osmotic pressures, typically called *turgor pressure*. To prevent rupture with internal pressures of five atmospheres or more, they have a rigid wall made up of peptidoglycans, long chains of sugars that are cross-linked by specialized peptides. This structure has been described as a fairly rigid wicker basket that contains the fluid inner membrane of the bacterium. There is typically an outer lipid membrane as well, but the peptidoglycan layer bears the brunt of maintaining the mechanical integrity of the pressurized cell. Of course, the existence of rigid pressure vessels is not rare in the macroscopic world – examples abound from tanks of liquid nitrogen to propane tanks for outdoor barbecues. But cells need to grow while maintaining that pressure difference.

In a recent paper A. Amir and D.R. Nelson explore the physical implications associated with nature's solution to the problem of maintaining a rigid pressure-bearing structure that can simultaneously grow with the cell [1]. They propose that one may understand the growth of a pressurized cylindrical wall by a theory of the actively driven motion of dislocations, topological defects in the periodic structure of the lattice of peptidogylcan molecules. These driven defects essentially insert step-by-step new circumferential rings of molecules into the rigid cylindrical walls in a manner that allows the cylindrical bacterium to elongate while simultaneously supporting its internal pressure. In doing so, they define a new type of active matter – a material driven into a nonequilibrium steady-state via continuous energy input. Such materials have collective mechanical properties that are controlled by a combination of their microstructure and details of their dynamical state. Other examples include active fluids composed of swimming particles, and molecular-motor-driven polymer gels, like the cytoskeleton. This system provides another example: a stressed two-dimensional crystal with a novel active growth mechanism.

The story of defects in crystals is an old one. In fact, their study forms the basis for understanding the plastic deformation of metals and other crystalline materials. A nice introduction to the subject can be found in the *Theory of Elasticity* by L.D. Landau and E.M. Lifshitz [2], and there are many other options for the interested reader. In short, the defect in question is a dislocation – a point in the periodic array of particles where a line of particles (atoms in an atomic solid, but here peptidogylcan molecules – for brevity I will call them atoms hereafter) begins or ends. If one were to make a circuit counting equal numbers of lattice steps around such a dislocation, he would not return to his starting point, because on one side of the dislocation, he would have encountered the extra partial line of atoms, but not on the return trip taking place on the other side of the dislocation. The "missing step" representing the failure of the path of equal numbers of steps in the up/down and left/right directions defines a vector – the Burgers vector – characterizing

the particular dislocation. For the long cylindrical bacterium, these dislocations take the form of incomplete circumferential lines of atoms around the cylinder; their Burgers vectors point along the long axis of the cylinder.

The presence of a dislocation in the regular array of atoms introduces a long-range elastic distortion of the material. And distant dislocations interact elastically through their distortion fields. Moreover, elastic stresses applied to the material exert forces on the dislocations, causing them to move. These *Peach-Koehler* forces, which are similar to the Magnus force on a spinning curveball, act on the dislocations in the pressurized bacterium. As you might imagine, the tension in the bacterial wall along the direction of the long axis generates a force that attempts to move the dislocation in a direction so as to elongate a partial line of atoms and thus grow the cylinder. This force, however, is not alone sufficient to make the dislocations move in the bacterial cell wall. Instead, there are active processes mediated by bacterial proteins, which after attaching to the dislocation, catalyze the growth of partial lines of atoms. Thus, we must distinguish between active dislocations and inactive ones, which do not have such attached proteins.

The growth of the bacterial cylinder can now be understood in terms of active and passive dislocation dynamics. These include: dislocation pair creation, or the insertion of a new line of atoms; the attachment/detactment of bacterial proteins that cause the dislocations to actively move (climb in the language of elasticity theory) so that the partial lines of atoms grow around the cylinder; and the annihilation of pairs of dislocations having oppositely directed Burgers vectors. The latter process corresponds to the closing of a new circumferential ring of atoms and the successful elongation of our bacterium by one lattice constant. It should be noted that the motion of an active dislocation takes place in a complex energy landscape defined by the elastic distortion field due to all of the other (active and inactive) dislocations. This is a hard problem!

Based on the above ideas, the authors develop a set of coupled first order equations describing the time dependence of the number of active and inactive dislocations. From these predictions regarding the overall growth rate of the bacterium can be derived, although they depend upon a number of biological parameters controlling the rates of the various fundamental processes underlying the nonequilibrium dynamics. I leave it to the reader study the paper for the further details. And with the end of summer, I hope the attentive reader noted references above to barbecue, baseball, and (with some orthographic laxity) peach cobbler.

References

[1] A. Amir and D.R. Nelson, *Dislocation-mediate growth of bacterial cell walls*, Proc. Natl. Acad. Sci. **109**, 9833-9838 (2012).

[2] L.D. Landau and E.M. Lifshitz, *Theory of Elasticity*, (Elsevier Butterworth-Heinemann, Oxford, 1970).