

Figure 2 Ion transport in the inner ear. The balance of activities of various ion channels and ion transporters (including Na^+ , K^+ -ATPase, NKCC1, KCNQ1, KCNE1 and the CIC-K channels) ensures that the concentration of K^+ ions is high inside the endolymph of the ear. This aids in the mechanism by which sensory cells convert sound waves to voltage signals for transmission to the brain.

the stria vascularis, thin and thick ascending limbs, and other kidney cells that are known to express Cl^- channels. Moreover, barttin is needed for these channels to function: injecting RNA that encodes CIC-Ka or CIC-Kb into frog eggs did not result in measurable Cl^- currents, but also injecting RNA that encodes barttin resulted in Cl^- currents characteristic of those in ear or kidney cells. In addition, Estévez *et al.* introduced into barttin specific mutations that are seen in patients with type IV Bartter's syndrome. The mutations reduced the ability of the protein to support the expression of CIC-K channels. The authors' proposal that barttin is an accessory subunit (a ' β -subunit') of CIC-K channels seems the most reasonable explanation of these findings.

Barttin is the first known β -subunit of a Cl^- channel. But it may be that such subunits are the norm and that most ion channels

rely on them. Indeed, accessory subunits have been found to affect the expression and properties of several other channels, including various K^+ , Na^+ and Ca^{2+} channels⁹. The addition of β -subunits to the ion-channel armoury adds yet another layer of flexibility and diversity to ion-channel function. ■

Malcolm Hunter is at the School of Biomedical Sciences, Worsley Medical and Dental Building, University of Leeds, Leeds LS2 9NQ, UK.
e-mail: m.hunter@leeds.ac.uk

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Materials science

A broader view of membranes

Roderic Lakes

Membranes that get fatter when they are stretched are considered counterintuitive, but may be more common than we think. They might even turn up in human tissue.

Stretch a rubber band and it becomes thinner; squeeze a rubber eraser and it becomes fatter. Most common, and not-so-common, materials share this property, even those that are so stiff you cannot see the deformation. The opposite effect — becoming fatter when stretched — is a property of some specially designed materials, notably foams with unusual structures, as well as certain single crystals. Writing in *Physical Review Letters*, Bowick and co-workers¹ show that a broad class of membrane structures also becomes fatter when

stretched. These structures include certain types of naturally occurring membranes, so if we look closely we may find that some biological cells deform in unexpected ways.

Elastic materials deform easily when under strain but return to their original dimensions when the force is removed — they resist changes to both shape and volume. Rubbery materials, which easily change shape but not volume, become notably thinner in cross-section when stretched. This is described by Poisson's ratio, the ratio of transverse contraction to longitudinal

extension during stretching. For rubber, Poisson's ratio is close to the theoretical upper limit of 0.5; for most other common materials it is between 0.25 and 0.35. Because all these materials become thinner when stretched, Poisson's ratio is always positive. The reason for the thinning is that interatomic bonds tend to align when deformed.

A negative Poisson's ratio, which requires a transverse expansion (thickening) on stretching, is considered counterintuitive; indeed such materials were once thought not to exist or even to be impossible. But materials with negative Poisson's ratio do occur², and have been called anti-rubber, auxetic or dilational. For example, two-dimensional honeycomb structures have been developed with 'inverted' cells^{3,4}, which unfold when stretched (Fig. 1, overleaf). (Regular honeycomb lattices, like most materials, have a positive Poisson's ratio.) Similarly, some foam materials with a three-dimensional microstructure of 'inwardly bulging' cells⁵ also get fatter when stretched. These foams and honeycombs have such unusual elastic behaviour because of non-uniform unfolding or deformation of the microstructure⁶. Such materials are usually tougher and more resilient than most conventional materials, and so would make good knee pads, seat cushions, biomaterials and air filters that are easily tuned or cleaned.

Bowick and co-workers¹ have shown that structures known as 'fixed connectivity' membranes have a negative Poisson's ratio. Such membranes are assumed to have fixed connections: their bonds do not break. They occur in some biological^{7,8} and synthetic⁹ systems, and are a two-dimensional counterpart to one-dimensional molecular chains of polymers¹⁰. Like polymers they have a fractal-like structure, but unlike polymers, which are always crumpled, polymerized membranes can undergo a phase transformation from a crumpled phase at high temperatures to a 'flat' but locally rough phase at low temperatures.

The negative Poisson's ratio in fixed-connectivity membranes¹¹ is due to changes in entropy⁸ (a measure of thermal disorder) that occur with deformation. Stretching the membrane tends to flatten out undulations arising from thermal fluctuations (Fig. 2, overleaf), producing expansion in two directions. This deformation, as with the honeycomb and foam, is non-uniform. But the honeycomb expands in the same plane as that in which its microstructure unfolds. By contrast, the thermally induced undulations of the polymerized membrane are perpendicular to the surface of the membrane. Some cubic single crystals¹² can also expand in one direction and constrict in another, although a polycrystalline version of the cubic material has 'normal' elasticity. In polycrystalline materials the elastic properties of the individual crystals are averaged,

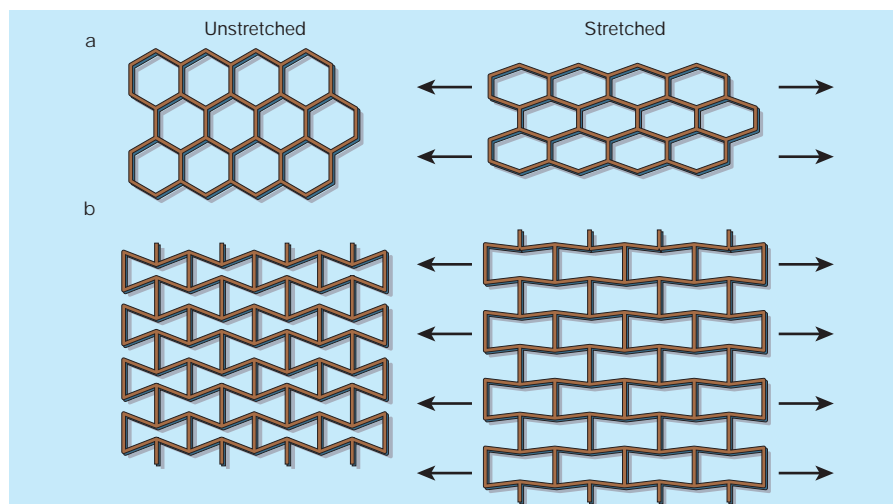


Figure 1 Positive and negative Poisson's ratios. Stretching these two-dimensional hexagonal structures horizontally reveals the physical origin of Poisson's ratio. **a**, The cells of regular honeycomb or hexagonal crystals elongate and narrow when stretched, causing lateral contraction and so a positive Poisson's ratio. **b**, In artificial honeycomb with inverted cells, the structural elements unfold, causing lateral expansion and a negative Poisson's ratio.

so the overall Poisson's ratio is almost always positive.

The elastic behaviour of the membranes studied by Bowick *et al.*¹ is said to be 'universal' because the authors require only a sparse set of assumptions to predict the Poisson's ratio. They start with a simple network of nodes, resembling a fishing net with fixed connections, which they model using a Monte Carlo simulation. Bowick *et al.* show that a negative Poisson's ratio is a universal property of such systems, whether the membrane is dominated by rigid bonds that resist bending or by 'self-avoiding' interatomic forces that prevent portions of the structure overlapping.

This unusual form of elasticity may also arise in biological processes because the membranes considered by Bowick *et al.* are similar to the protein skeletons⁸ of biological

membranes. The overall elasticity of a cell membrane results from both the protein skeleton and the high lipid content, but the relative contributions are not yet known. Even so, Bowick and colleagues' results are provocative. If our usual expectations about how things deform do not apply to biological membranes then we may need to reconsider the influence of membrane mechanics⁷ on the shape of cells, the formation of vesicles, and the deformation of cells during life processes. For example, red blood cells are routinely deformed when they pass through fine blood capillaries. As they deform, the membrane skeleton can unfold, which might help to transport large molecules or expose reactive chemical groups. Similar concepts may be used in the design of industrial membranes for responsive filtration or catalysis. Materials with specific Poisson's ratios are always useful — cork, for example, has a ratio of almost zero, making it ideal for sealing wine bottles. For membranes with a negative Poisson's ratio, the applications are sure to keep expanding. ■

Roderic Lakes is in the Department of Engineering Physics, Engineering Mechanics Program at the University of Wisconsin-Madison, 1500 Engineering Drive, Madison, Wisconsin 53706-1687, USA. e-mail: lakes@engr.wisc.edu

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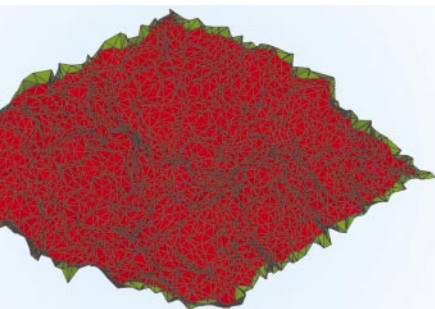


Figure 2 An artificial membrane with a negative Poisson's ratio. The local roughness of a 'flat' fixed-connectivity membrane is due to thermal fluctuations. Stretching the membrane flattens the roughness, causing lateral expansion in the plane of the membrane. In their simulation, Bowick *et al.*¹ find that all fixed-connectivity membranes, possibly including some biological ones, share this property. (After M. Bowick, with permission.)

Daedalus

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