fewest zeros possible[8,9].

Jorge *et al.* investigated this idea by studying the patterns of motorized synthetic particles, called Quincke rollers, as they moved through a large honeycomb network of channels. The authors observed the formation of steady flow patterns consisting of an intricate mix of self-avoiding loops that circled clockwise or anticlockwise. But unlike the deterministic flow patterns that form in normal fluids, Jorge and colleagues' flows displayed a different, disordered flow pattern each time the authors repeated an identical experiment. Even more intriguingly, they found that solving the sudoku-like optimization problem did not account for the flow-field statistics in their experiments. Instead, the authors observed that varying the channel's aspect ratio had an impact on the emerging flow fields: wide channels gave rise to segregated loops, whereas loops were more often nested in networks of narrow channels (Fig. 1b).

The authors determined that the reason for this lies in how an active fluid circulates in a channel that is constrained geometrically to have zero net flow. Wide channels can have only one circulating vortex, whereas narrow channels have two vortices circulating in opposite directions. In both cases, the circulating flow meets neighbouring directed flows at the nodes on either end of the zero-flow channel and dictates the direction of these flows through a gear-like mechanism (Fig. 1c). For a single vortex, directed flows that are separated by a zero-flow channel are antiparallel; for two vortices, the flows are parallel, and this triggers nested flow loops. Together with network topology and channel geometry, these interactions at nodes determine the whole flow pattern.

Research on active fluids in networks is dominated largely by theory and numerical simulations, so Jorge and co-workers' experiments are an exciting addition to the field. Their results show that the active nature of self-propelled fluids induces interactions between neighbouring flows in networks. Such interactions are expected for networks of regular fluids, in which flows split at every network node[1], but the interactions for active fluids reported by the authors were not anticipated. And these interactions are non-local, in that they correlate flows through channels that don't actually meet — a property that is essential for the emergent complexity that Jorge *et al.* observed.

It is always surprising — and gratifying — when an out-of-equilibrium process, such as an active fluid moving through a network, can be explained by the physics of systems in equilibrium. It also makes technological applications easier to design: Jorge and co-workers' quantitative description of active-flow patterns could enable the development of microfluidic devices that can transport self-propelled particles (for drug delivery, for example) in a controlled manner. The authors' rules could even be used to build active analogues of fluid-logic circuits[9] (devices that use fluids to perform computer-logic operations) for biocompatible computing. Jorge and colleagues' mechanistic insight into how non-local interactions emerge in active systems might also guide research into the motility of living cells and organisms in complex environments.

Mathieu Le Verge-Serandour and **Karen Alim** are in the School of Natural Sciences, Technical University of Munich, 85748 Garching, Germany.
e-mails: mathieu.le-verge-serandour@tum.de; k.alim@tum.de

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Animal behaviour

An innovative way for whales to sing

Joy S. Reidenberg

Mammals make sounds when air flow causes paired tissue folds in their voice box to oscillate. However, such air flow in the baleen group of whales takes an unusual path, enabling them to make sounds in a previously unknown way. **See p.123**

Baleen whales — a group that includes blue whales (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) — are known for their ability to sing under water. Songs are produced by an organ located in the animal's throat called the larynx, or voice box. However, the anatomical basis of the mechanism that generates sound is not fully understood. On page 123, Elemans *et al.*[1] report the discovery of a previously unknown method of sound production that originates from an unusual site for vibrations. This research is a game-changer for understanding how biological sounds are generated.

Until now, whales were thought to produce sound only by pushing air between paired folds of tissue, causing them to vibrate. But Elemans and colleagues reveal a unique airflow pathway in the larynx of baleen whales, in which air is squeezed between a fold of tissue and a cushion of fatty material above it, causing the fold to vibrate and generate sound.

Society has long been fascinated by baleen whale songs. Early sailors documented hearing eerie sounds below deck that reverberated through the ship's hull. These haunting melodies were attributed to ghosts, mythical sea creatures or simply the imagination of drunken sailors. The sea was otherwise considered to be a silent world.

It wasn't until the invention of in-water microphones, called hydrophones, that underwater sounds could finally be documented. The first hydrophones were used to locate icebergs as a safety check after the ocean liner *Titanic* sank in 1912. Hydrophones were modified during the First World War to detect submarines. During the Second World War and the cold war, arrays of these devices were used to track submarine movements on the basis of engine or propeller noise, but these recordings also included a variety of natural underwater sounds. The soundtracks were military secrets until marine biologists were given access and found that many of the sounds were produced by whales[2,3].

Scientists have searched for decades to discover the method that whales use to produce sound. Publications before the 1960s describe the anatomy of whales using specimens dissected after the animals had become stranded on a beach or examined at commercial whaling stations. These studies included depictions of the whale larynx, but they did not associate it with sound production or identify its internal structures as vocal cords. This is because whales were considered not to have the ability to make sounds, and several papers[4] suggested that whales lacked vocal cords (or in more-scientific terminology, vocal folds).

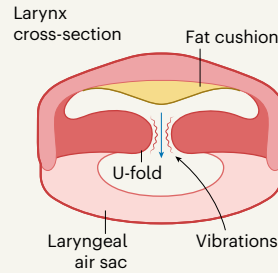But anatomical studies have now established that a U-shaped structure in the whale's larynx
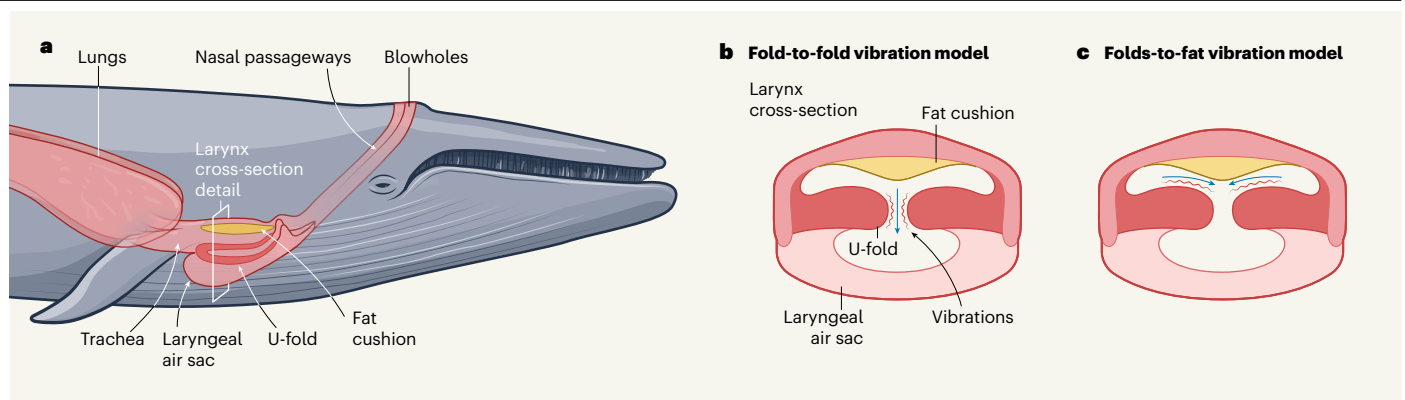
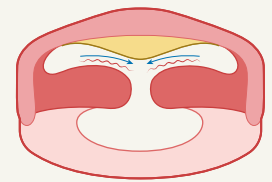**Figure 1 | A surprising method for sound generation in whales.**
a, Baleen whales, which include blue whales (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*), use their larynx (also known as the voice box) to sing. During breathing, air enters through the animal's paired blowholes (nostrils) and travels down the nasal passageways to the larynx, trachea (windpipe) and lungs. During singing, air flows from the lungs to the larynx, where it passes under a fat cushion and through a gap surrounded by the U-fold to enter the laryngeal air sac. When the laryngeal air sac contracts, air is recycled back to the lungs for use in the next vocalization. **b**, The conventional model of sound production in the larynx involves fold-to-fold vibration. Air (blue arrow) passes under the fat cushion and down through the narrow gap between the U-fold arms, generating vibrations on the opposing inner surfaces of the U-fold. This model reflects the vocalization mechanism of land mammals, in which opposing paired vocal folds are moved by airflow to generate sound. **c**, Elemans *et al.*[1] suggest sound is produced through a different mechanism, by folds-to-fat vibration. The authors propose that the flow of air in the narrow space between each U-fold arm and the fat cushion generates vibrations on the folds' top surfaces that face the fat cushion. They suggest that most baleen whales use only this folds-to-fat vibration method to produce sound, although humpback and bowhead whales (*Balaena mysticetus*) might use both fold-to-fold and folds-to-fat vibration methods.

is equivalent to a land mammal's paired vocal folds and their supporting cartilages[4–6]. It is called a U-fold because it resembles the letter U when viewed from above. Baleen whales inherited this laryngeal anatomy from their land-mammal ancestors, but it became modified during the process of evolution into marine mammals. Unlike typical vocal folds in other mammals, the U-fold of whales is rotated 90 degrees to lie parallel to the trachea (windpipe), and the gap between the 'arms' of the U-fold leads into a laryngeal air sac (Fig. 1a).

Although some similarities remain between the larynges of whales and those of land mammals, the source of the whale's song and the mechanism whales use to make sounds are difficult to identify. Because of the large size of baleen whales, the anatomy and function of their vocal structures cannot be tested in captivity or examined using modern visualization methods, such as endoscopy, or imaging techniques (including computed tomography or magnetic resonance imaging). Small whales, such as dolphins, that can be studied more easily in captivity are poor models because they vocalize in a different frequency from large baleen whales and use nasal structures instead of folds[7,8].

Assumptions about how baleen whales vocalize are therefore usually based on comparative anatomy dissections. Baleen whales are thought to produce sounds in a similar manner to land mammals. Air is brought in through the blowholes (nostrils) and fills the respiratory tract (nasal passageways, larynx, trachea and lungs). It is then pushed from the lungs back to the larynx for sound production.

This model suggests that as air flows through the gap between the arms of the U-fold, the surface tissues move (fold-to-fold vibration, Fig. 1b) and generate sound[9]. The laryngeal air sac located below this gap is thought to capture and recycle air back to the lungs for reuse, enabling continuous singing during long periods of breath holding[10,11]. When the whale is not vocalizing, the gap is proposed to be sealed for protection by a fat cushion attached to the top of the larynx[5,6].

Mathematical acoustic modelling further supports an air-driven mechanism for sound production and the U-fold arms as its source[12–14]. However, the assumption remains that there is only one airflow path, located between the facing tissues of the U-fold arms. This proposed fold-to-fold vibration method of sound production has not been observed directly in live whales.

A second question also remains to be addressed. Recordings of baleen whales indicate that a single whale can make at least two different sounds simultaneously[15,16]. This is puzzling. How can whales do that with only one vocal organ?

Several studies have proposed that sound is generated in two separate locations[12,14,17]. These sites involve fold-to-fold vibration of the U-fold as described previously, plus contributions from other oscillating flaps of tissue at the front of the larynx. Elemans and colleagues, however, describe a unique location for sound generation in the whale larynx that uses a different method of tissue contact.

The authors did experiments that involved blowing air through three larynges removed from the carcasses of baleen whales and visualizing the vibrating tissue surfaces inside these structures. Strikingly, they found that vibrations occur on the soft-tissue portion of each arm of the U-fold that faces the fat cushion at the top of the larynx (folds-to-fat vibration, Fig. 1c), rather than on the surfaces of the U-fold arms that face each other (fold-to-fold vibration, Fig. 1b). This result indicates that air flows through an alternative pathway that goes from the side to the middle of the larynx, rather than from the top to the bottom, as previously suggested. Sound generation by folds-to-fat vibration can happen on both sides of the larynx because the U-fold has two arms. Having two sites where vibration can occur increases the vocal abilities of whales, and I wonder whether this might enable them to generate two distinct sounds simultaneously.

The airflow speed and pressures used in the authors' experiment lie within the physiological ranges of these animals' tissues. The sounds produced are within the frequency span recorded for these whales, thus confirming folds-to-fat vibration as a probable method for sound generation. Vibrations in this model are thought to occur in one direction only − through air flowing outwards from the lungs. This suggests that song pauses allow air to be recycled from the laryngeal air sac back to the lungs for use in another vocalization.

However, this folds-to-fat vibration model for sound production has physiological limits that affect the frequencies and air pressures at which sounds can be produced. Furthermore, the volume of air necessary to generate sound places a time constraint on vocalization. Although this mechanism might explain the unique features of whale songs, it nevertheless means that whales would have challenges in terms of the distance at which a song can be heard, the depth at which it can be made, and its duration.

Elemans and colleagues' work also provides

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insights into the evolution of the folds-to-fat vocalization method. A U-fold opposite a fat cushion has been found in the larynges of all whales examined until now[6], prompting Elemans and colleagues to suggest that this sound-production method was probably present in the ancestors of modern whales. Thickened U-folds were found only in humpback and bowhead whales (*Balaena mysticetus*), indicating that this characteristic was acquired later during whale evolution. Thicker U-folds are more mobile than the thinner ones of other whales and they can meet to seal the gap between them, allowing them to function as vocal folds. This indicates that whales have either independently acquired or regained the fold-to-fold vocalization method used by land mammals, in addition to the folds-to-fat vocalization method.

In land mammals, vibrations of the vocal folds produce sound (pressure waves) in the air. However, given that whales vocalize underwater, how does the sound get transferred to the water? Future work should address this step of sound generation.

The main limitation of Elemans and colleagues' work is that the authors could test only isolated larynges, removed from the whales' bodies, that were then artificially suspended in air. The natural path of sound production by the vibrating whale larynx therefore remains unknown. Modelling the surrounding tissues in a more 'fleshed-out' experimental design might uncover the full sound-production pathway of whales.

The evolutionary picture will not be complete until we understand how an air-driven system, which generates sound in air and transfers it to the mouth of land mammals, became adapted to work under water for whales. This, in turn, might help us to decipher how baleen whales generate unusual sounds, such as the 'Star Wars' or 'boing' sounds of minke whales and the 'gunshot' sounds of right whales[18–20].

Joy S. Reidenberg is at the Center for Anatomy and Functional Morphology, Icahn School of Medicine at Mount Sinai, New York, New York 10029, USA.
e-mail: joy.reidenberg@mssm.edu

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Electrochemistry

Solvent trick boosts battery performance

Chong Yan & Jia-Qi Huang

Small solvent molecules have been found to enable a previously unknown ion-transport mechanism in battery electrolytes, speeding up charging and increasing performance at low temperatures. **See p.101**

Two issues that limit the further development of lithium batteries are the lengthy charging times and the poor performance of these batteries at low temperatures[1]. One of the most effective solutions to these problems is to upgrade the electrolyte[2,3] — the material that acts as the 'blood' of the battery by enabling the flow of lithium ions between the electrodes. On page 101, Lu *et al.*[4] report that organic solvents consisting of small molecules can greatly improve ion mobility in lithium-ion-battery electrolytes, enabling fast charging and impressive battery performance at temperatures as low as −80 °C.

Most electrolytes of lithium-ion batteries consist of one or more lithium salts dissolved in an organic solvent. An ultraconcentrated aqueous solution of a lithium salt — referred to as a water-in-salt electrolyte — is now emerging as a useful alternative[5]. When an electrolyte is injected into the porous electrodes of a lithium-ion battery, it rapidly fills the pores. The result is a medium that allows lithium ions to pass from one electrode to the other but does not conduct electrons.

When lithium salts dissolve in a solvent, their crystalline structure fully disintegrates. This process is driven partly by entropy, a measure of disorder: the second law of thermodynamics favours increases in entropy, and the ions in a salt become much more disordered when they are liberated from an ordered crystal lattice. A bigger driver of dissolution comes from enthalpy, a measure of the total energy of a system. Strong electrical interactions between lithium ions and the solvent molecules result in the formation of solvation structures, in which a central lithium ion is surrounded by bound solvent molecules. This is a thermodynamically favourable process, because it lowers the enthalpy of the system.

The solvent molecules in solvation structures can adopt various arrangements that depend, for example, on the concentration of the electrolyte solution[6–8]. When there is strong binding between a lithium ion and its primary solvation sheath (the first layer of molecules and ions around the lithium ion), the whole solvation structure moves with the lithium ion during its translational motion. This is known as vehicular transport (Fig. 1a).

It might be assumed that the speed of lithium-ion transport in battery electrolytes is strongly associated with the arrangement of molecules and ions in solvation structures, which, in turn, is governed by the solvent properties and the concentration of the lithium salt. Such a model would suggest that lithium ions with smaller solvation structures move faster through the electrolyte. This is indeed true in the case of vehicular transport, especially for small solvent molecules and when the number of molecules in the primary solvation sheath is low[9].

Sometimes, however, this mechanism alone cannot account for exceptionally high ion mobilities, such as those observed for the transport of protons (hydrogen ions, H^+) in aqueous electrolytes. Protons associate with water molecules in aqueous solutions to form hydronium ions (H_3O^+), and this allows protons to be passed between neighbouring water molecules like batons in a relay race. This relay mechanism is termed structural transport (Fig. 1b), because it depends on a particular solvation structure that enables ions to 'hop' between molecules. Structural transport boosts the ionic conductivity of aqueous