

Figure 1. Mollicutes. *Mycoplasma mobile* (left, from M. Miyata) and *Spiroplasma melliferum* (right) represent the range of size, polarity and shape of the mollicutes. (Scale ~1 μm .)

in their length can quantitatively explain the dynamic range of all helical and non-helical cell geometries. The purified, detergent insoluble cytoskeleton complex from spiroplasmas contains over ten proteins, the main one being a 59 kDa product of the *fib* gene with no known prokaryotic or eukaryotic homologs. Infectivity in spiroplasmas is governed by an unusual lipoprotein, spiralin, which constitutes ~30% of the membrane mass and resides on the cell's outer surface.

In mycoplasmas, the cytoskeleton (or triton-shell) seems more complex, yet its components and their functions are better defined. The role of the cytoskeleton in motility is unclear; its role in cytodherence and pathogenicity is steadily being unravelled. The mycoplasmal cytoskeleton consists of a dense, banded or spiral, rod-like 'attachment organelle' with a wider 'terminal button' at the front end and an array of fibrils emanating from its rear end. About nine well-defined proteins form the attachment organelle, their spatial and temporal order of assembly determining the organelle's functions in pathogenicity and colonization. Cell division in mycoplasmas is linked to duplication of the attachment organelle. There is also evidence that, in mycoplasmas, a translational elongation factor (EF-TU) forms a spatial network with a cytoskeletal function.

How do mollicutes move?

Mollicutes lack external appendages such as the flagella and pili responsible for motility of cell-walled bacteria.

Spiroplasmas are active swimmers and respond

chemotactically. They swim by propagating a slight deformation or segment with switched handedness along the helical cell body. Swimming direction is changed by flexing. The cell movements are driven by the cytoskeleton acting as a linear motor.

Motile mycoplasmas glide on solid or semi-solid surfaces. In *M. mobile*, a fast glider, unique proteins located in the area between the cell's neck and body are thought to attach the cell to the surface and facilitate movement. The process is energized very likely by ATP hydrolysis.

Where can I find out more?

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Primer

Echolocation

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Because we rely largely on vision to perceive the world, we find it difficult to comprehend the challenges faced by organisms that use other senses for perception. Such challenges are especially acute for our understanding of echolocation — the production of sound by animals and the subsequent determination of the position (and other features) of objects from information encoded in acoustic reflections.

The philosopher Thomas Nagel chose the bat as an example of an organism using a very different form of perception from ours in his famous essay about understanding the experiences of others. In 'What is it like to be a bat?' Nagel states that "anyone who has been in a confined space with an excited bat knows what it is like to encounter a fundamentally alien form of life!". Despite these differences in perception, we have achieved much in understanding how echolocation works in animals, and how signal design is shaped by acoustic challenges in the environment.

Echolocation: what it is and how it works

Echolocation, or biosonar, is an active process, used by the species that have it for sensing the environment when vision is ineffective, for example at night or in turbid water. It involves the production of sound, and the reception of echoes that return from objects. By comparing the outgoing pulse with the returning echoes — which are modified versions of the outgoing pulse — the brain can produce images of the surroundings.

The location of a target in three dimensions can be determined from its range and direction. Echolocating animals can determine how far away objects are — their range — by



Figure 1. Natural selection shapes the faces of echolocating bats into bizarre forms.

The ears of echolocating bats are enlarged for the detection of faint echoes, and the noses of species that send sounds through their nostrils may become surrounded by elaborate noseleaves that focus the sound. These features are illustrated in bats from China, from left to right: *Aselliscus stoliczkanus*, *Rhinolophus paradoxolophus* and *Tadarida teniotis*.

measuring the time delays between call production and reception. Sound travels at 340 metres per second in air, and travels to the object and back again, so a delay of 2 milliseconds corresponds to a range of 34 centimetres.

Object direction can be determined in the vertical and horizontal planes. Many bats determine the vertical angle (elevation) of targets by interpreting interference patterns caused by sounds reflecting from the tragus, a flap of skin in the external ear. Horseshoe bats move their ears up and down independently, and may calculate elevation from intensity differences received at each ear. Bats determine the horizontal angle, or azimuth, of targets from differences in the intensity of sound received at each ear. Echo strength can give cues about target size, and surface texture may be determined from peaks and troughs in the frequency spectrum of the echo. Overall then, echolocation can provide rich detail about the environment.

Echolocation has evolved to its greatest sophistication in bats (Figure 1) and toothed whales (dolphins and their relatives), though simple forms of echolocation are also used by cave swiftlets and oilbirds, and by small nocturnal mammals such as shrews and rats. The main function of echolocation is orientation — calculating one's own position relative to the surroundings — although many bats and dolphins also use

echolocation for detecting, localising and even classifying prey.

Although echolocation can give bats and dolphins sophisticated information about their surroundings, in certain situations it becomes of little use. For example, mouse-eared bats use echolocation to detect airborne prey, but almost 'switch off' echolocation when detecting prey under leaf litter. Echoes from leaves mask echoes from prey, and in these situations the bats must rely on rustling sounds made by the insects as they move through the leaf litter for successful prey detection.

The discovery of echolocation

Echolocation is such a remarkable process that its discovery involved several incidences of disbelief. In 1793, the Italian scientist Lazzaro Spallanzani discovered that blinded bats were still able to negotiate obstacle courses. The Swiss naturalist Charles Jurine reported in 1794 that bats use hearing in orientation, as they collided with wires when their ear canals were closed with wax. An influential doubter of these results was the palaeobiologist Georges Cuvier, who dismissed Spallanzani's and Jurine's experiments as flawed, and concluded that bats use "the organs of touch" for orientation. Cuvier's influence did much to hinder further research on bat orientation for over a century.

Most bat echolocation calls are ultrasonic (>20 kHz), and hence

inaudible to human ears. High frequencies have short wavelengths, and therefore reflect strongly from very small targets such as insects. Because people cannot hear bat sounds, how bats use their hearing to detect obstacles remained difficult to fathom.

In 1938, Harvard student Donald Griffin became fascinated by the ability of bats to fly adeptly in darkness. Griffin made contact with the physicist G.W. Pierce, who had developed piezoelectric crystals that could transform ultrasound into frequencies audible to humans. Griffin and Pierce were able for the first time to listen to the ultrasonic echolocation calls of bats. Griffin coined the term 'echolocation', described how bats change their call design as they approach targets, and began to uncover the great diversity in bat echolocation signals (Figure 2).

In collaboration with auditory physiologist Robert Galambos, Griffin established the auditory basis for echolocation. Such was the incredulity that greeted their discovery, that Galambos was held by his lapels at a scientific meeting by a scientist who thought that the suggested mechanism of echolocation was crazy! Now we know that some of the echolocation signals produced by bats may exceed 130 decibels in intensity at 10 centimetres from the bats' mouths, making them some of the most intense airborne animal signals yet recorded.

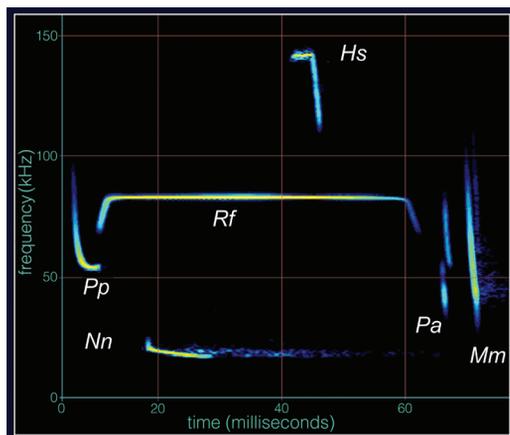


Figure 2. Echolocation calls from a selection of bat species.

A spectrogram plotting frequency against time, with signal amplitude coded in colour (higher amplitudes are yellow or red, lower amplitudes more blue). The noctule *Nyctalus noctula* (*Nn*) produces calls that are relatively low in frequency, long in duration, and narrowband. These calls are well suited for the detection of distant targets, and the noctule hunts in open habitats. The brown long-eared bat *Plecotus auritus* (*Pa*) and the whiskered bat

Myotis mystacinus (*Mm*) emit brief broadband signals adapted to localizing targets in cluttered habitats such as woodland where these bats hunt. The soprano pipistrelle *Pipistrellus pygmaeus* (*Pp*) uses calls starting with a broadband sweep and terminating in a narrowband tail: it hunts for insects along treelines. The greater horseshoe bat *Rhinolophus ferrumequinum* (*Rf*) produces long constant frequency calls that allow powerful potential for detecting and classifying insect prey in clutter. The bat adds broadband sweeps at the start and end of the calls, and the terminal sweep functions in localization. The greater horseshoe bat uses Doppler shift compensation, and separates pulse and echo in frequency when flying. Schneider's leaf-nosed bat *Hipposideros speoris* (*Hs*) uses a shorter version of the horseshoe bat-type signal, and compensates for Doppler shifts partially when flying. Time-expanded versions of these calls can be heard at www.biosonar.bris.ac.uk

In 1947, Arthur McBride speculated that dolphins used echolocation. Kellogg and Kohler found in 1952 that dolphins have ultrasonic hearing, and went on to show that they can discriminate different objects without using vision. Around the same time Forrest Wood recorded the first ultrasonic echolocation signals from dolphins, and in 1961 Ken Norris confirmed their use of echolocation by blindfolding dolphins while they swam through obstacle courses. Sounds that probably function in echolocation have now been recorded from almost all species of toothed whales (suborder Odontoceti) studied to date.

The diversity of echolocation signals

Echolocation call design has been used to illustrate 'good design' through evolution by natural selection by Richard Dawkins in '*The Blind Watchmaker*'. Acoustical theory allows us to predict the costs and benefits of different signal designs in bats, and we can then determine whether bats indeed use signals that are well adapted

for the ecological situations that they face in the field.

Uli Schnitzler and colleagues have categorised three major tasks in echolocation, and have identified the best signal design for each task. Narrowband signals span a narrow range of frequencies, and are relatively long in duration. They allow ranging of distant targets, and are well adapted for the *detection* of acoustic glints from flying insects. Broadband calls span a wide range of frequencies and are typically short — often <5 milliseconds — in duration. They are well adapted for *localization*.

Detection and localization performance are traded off against one another, so a signal that is well designed for detection is poor for localizing targets. A noctule bat hunting insects will switch from using narrowband signals to broadband ones once the target has been detected and needs to be localized for capture. The broadband signals are emitted at an increasingly rapid rate as the bat approaches the prey, resulting in a so-called 'feeding buzz'.

Arguably the most sophisticated type of echolocation calls is used by horseshoe bats in the Old World, and was evolved independently by Parnell's moustached bat *Pteronotus parnellii* in the New World. These bats emit signals with a long constant frequency component that allows efficient detection, and also allows the bats to *classify* targets; for example, they can distinguish a mosquito beating its wings rapidly from a beetle with slower wing beats. The bats also achieve excellent localization performance by using broadband sweeps at the end of the calls.

Horseshoe bats and *Pteronotus parnellii* show a behaviour called Doppler shift compensation. At rest, their hearing is tuned sharply to a frequency close to that of the emitted signal, typically about 83 kHz in a greater horseshoe bat. In flight, the bats experience Doppler shifts caused by their own movement — the faster the flight speed, the greater the Doppler shift. The bats therefore reduce the frequency of the call more as their flight speed increases, so that the echo also returns at their frequency of best hearing.

Bats that use such Doppler shift compensation therefore emit a call and receive its echoes at different frequencies when flying, so that they do not deafen themselves with their intense emissions. Most other bats have to adjust the duration of the outgoing signal so they receive echoes after they have finished calling — call and echo are separated in time, and this is important because the bats' middle ear muscles contract during calling so the bat does not deafen itself.

So tight are the acoustic constraints shaping bat signals that we can reliably predict some aspects of the lifestyle of a bat from its calls, even if we were unable to identify the bat to species. For example, the noctule calls at a low frequency: low frequencies suffer reduced attenuation and travel relatively far. The signals are long in

duration — about 20 milliseconds — so that the bat is probably anticipating echoes from distant targets that will arrive after it finishes calling. The listening intervals between calls are long, again characteristic of a bat echolocating at distant targets. The narrowband signals are well adapted for detection. All these features are characteristic of a relatively large bat that is flying in open space, clear of obstacles, and is searching for prey items at some distance (Figure 2).

Dolphin echolocation differs from bat echolocation in several respects. The click-like vocalizations produced by echolocating cetaceans are typically much shorter in duration than the tonal airborne calls of bats. Cetaceans may be forced to produce short calls to obtain good temporal resolution in water, where sound travels almost five times faster than in air. With the exception of the Old World fruit bat *Rousettus*, bats probably need to produce longer duration signals because the energy content of brief clicks may be insufficient for effective echolocation in air. The high speed of sound in water probably makes it impossible for cetaceans to exploit Doppler-shift information.

The acoustic images perceived by dolphins may differ substantially from those perceived by bats. Most objects in the bat's surroundings will produce echoes. Water, however, has a greater density and is less compressible than air, giving it greater acoustic impedance. The skeleton and swim bladder of fish may stand out to an echolocating dolphin, because their impedance mismatches that of water, and dolphins can even detect prey under sediment.

In general, signal structure in cetaceans is not as diverse as in bats. Sperm whales, however, produce rapid pulse trains or 'creaks' when they dive to great depths, and creaks are associated with sudden body movements suggestive of the pursuit of prey. The rapid increase in calling rate during prey capture is similar to the

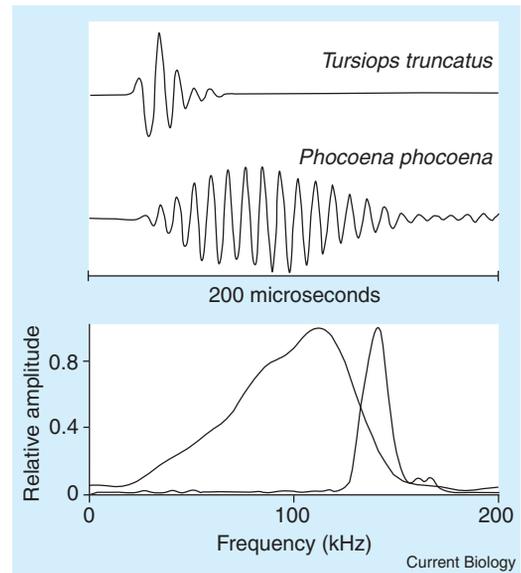
Figure 3. Typical sonar signals produced by echolocating cetaceans.

Brief broadband clicks are produced by the bottlenose dolphin *Tursiops truncatus*. Longer, more narrowband signals are emitted by the harbour porpoise *Phocoena phocoena*. The upper plots are waveforms. The bottom section of the figure shows power spectra, plotting frequency versus amplitude, with the more broadband spectrum of *Tursiops* shown on the left. The signals of dolphins are usually depicted as waveforms and power spectra because their short duration renders them unsuitable for spectrographic analysis. Modified from an illustration in Au, W.W. L. (2004) In *Echolocation in Bats and Dolphins* (eds. Thomas, J.A., Moss, C.F. and Vater, M.).

'feeding buzzes' produced by bats that capture insects in the air, providing the signaller with more information as it homes in on the prey item.

Mechanisms for the production, transmission and reception of sound are also very different between bats and dolphins. Bats produce sounds in the larynx, direct the pulses through their mouths or nostrils, and receive echoes at their large pinnae. Dolphins produce sound from within phonic lips in the nasal passages, transmit sound through a waxy melon on the forehead to remove the impedance mismatch with water, and receive echoes via their lower jaws.

Dolphin signals tend to be of two major types. Bottlenose dolphins *Tursiops truncatus* are among species that produce signals that are broadband and short in duration (<100 microseconds). Species such as the harbour porpoise *Phocoena phocoena* often produce signals that are longer in duration (>125 microseconds), and more narrowband than the higher-intensity shorter signals used by a bottlenose dolphin (Figure 3). Although many cetacean echolocation signals are ultrasonic, those produced by



sperm whales are dominated by frequencies within the range of human hearing.

Ultrasonic hearing in prey and predator detection

Bats and dolphins have both evolved sophisticated sonar systems that allow them to detect and localize prey in conditions where vision is ineffective. But prey have evolved ears as ultrasound detectors in both terrestrial and aquatic environments. Insect ears typically use tympanic membranes (eardrums) for sound detection, and sensitivity to ultrasound has evolved in at least six orders of insects. Some moths fly away from low amplitude ultrasound, because low amplitudes may imply that the bat is distant and the moth can escape simply by leaving the area. After hearing high intensity ultrasound, however, the same moth may begin unpredictable power dives as a last ditch response to evade a bat that is probably nearby. Some species of tiger moths (Arctiidae) produce ultrasonic signals soon after hearing bat calls, and these may function to signal the moth's distastefulness, to startle the predator, or even to interfere with echo processing by the bat.

Only recently have researchers discovered that certain fish are also sensitive to ultrasound. Cod may be able to detect echolocating odontocetes at 10–30 metres, and shad may detect their main predators, dolphins, at a range of 180 metres. Blueback herring swim away from echosounders used to survey them, raising the possibility that fish may exhibit negative phonotactic behaviour in the way that moths do. Some clupeid fish even show movements interpreted as escape manoeuvres when subjected to ultrasound.

Applications

Echolocation is obviously a remarkable way of sensing the world: bats may be able to detect differences in target range that require time difference discriminations of 10–12 nanoseconds, an ability that some physiologists refuse to believe is possible. Can humans learn anything from biosonar? There are remarkable similarities between bat calls and signals developed by engineers working in the fields of sonar and radar. Doppler shifts are exploited in radar speed-traps to measure velocity, and broadband echolocation calls have certain parallels with signals used in chirp radar.

Dean Waters, a scientist working on bat echolocation at the University of Leeds, recently helped to develop a walking stick which emits ultrasonic signals through four sensors. A small computer calculates the direction and relative range of an object, and sends information to four vibrating buttons on the handle. The walking stick is now marketed as an 'ultracane', and has received excellent reviews from visually impaired users.

Challenges

Recent advances in portable devices that can record ultrasound in the field, combined with imaging methods such as multiflash photography have permitted great advances in understanding how bats use echolocation in natural

conditions over the past 15 years or so. Until recently, our understanding of cetacean echolocation was largely restricted to studies on trained laboratory animals.

This imbalance is now changing because archival tags that monitor sound, depth and acceleration can be fitted to diving cetaceans. In the same way that simultaneous multiflash photography and the recording of echolocation calls allowed a better understanding of prey capture behaviour in bats, it is now possible to understand how foraging cetaceans are moving through the ocean in relation to the sounds they produce.

Field studies on interactions between tympanate insects and echolocating bats have revealed some remarkable sensory battles between predator and prey, and the potential for similar studies in fish–dolphin interactions is exciting indeed. Although ultrasound is well suited for the detection of small targets such as insects at night, it attenuates rapidly in air and is limited in its range of operation. Bats use echolocation for orientation very effectively, though how they navigate over longer distances is still unclear, and research into further sensory abilities — such as magnetoreception — should be illuminating.

Further reading

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Early visual deprivation induces structural plasticity in gray and white matter

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Early onset blindness allows one to investigate how the human brain adapts to sensory experience in infancy and early childhood. Here we report that, relative to the sighted, early blind (< 2 years) subjects exhibit gray and white matter decreases in early visual areas and the optic radiation. We observe equally significant white matter increases in the sensory-motor system. This may reflect compensatory experience-dependent plasticity in the spared modalities. Importantly, white matter changes are strongly predicted by the onset age of blindness. This suggests sensory experience shapes structural brain organisation during critical early periods in neurodevelopment.

How do early sensory experiences shape brain structure? Early onset blindness provides a unique opportunity to investigate the effects of visual experience on the organisation and structure of the brain during development. Visual deprivation might induce plastic changes, not only in the visual system, but also in the remaining intact sensory-motor system, secondary to altered experience in these spared modalities [1]. Previous neuroimaging studies have focused on functional reorganisation following blindness. Blind subjects recruit occipital, usually visual, areas compared to sighted subjects when they process tactile [2] and auditory signals [3] or when working on higher cognitive tasks [4,5]. This recruitment of regions