Convergent Evolution of Hearing

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Science **338**, 894 (2012);
DOI: 10.1126/science.1231169

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growth of nanotubes as long as 10 cm has recently been reported (*3*). Forests of 2-cm-long nanotubes have also been produced, and the quality is being improved by annealing (*4*). These recent results point to there being no physical barrier to growing long nanotubes, as was anticipated by Smalley (*5*).

Another issue is the role of defects in nanotubes; even a few defects can greatly reduce nanotube strength (i.e., weak links in a chain). Thermal annealing can substantially heal the defects to bring the nanotubes to near pristine condition (*6*). Finally, commercial applications of actuators might require use of different architectures. Thus, a practical area of improvement would be to expand the number of forms of nanotube materials that can meet this need. Fortunately, nanotube tubes, posts, braids, fabrics, tiles, and sheets (see the figure) are already under development (*4*). For example, braiding yarn increases energy storage (*7*), and fabrics and sheets allow two-dimensional actuation. Further work could study the mechanics and failure mechanisms of the muscle, including how elastic modulus changes with actuation and characterizing extrusion of the guest, and how, at higher stress, nanotubes slide in the yarn.

The artificial muscle developed by Lima *et al.* is also a step toward commercialized devices. Applications of nanotube-based actuators include sensors for the environment, aerospace materials, carbon machines (*1*–*4*), nanotextiles (*7*), and nanopropulsion (*8*). Artificial muscle also serves as a prime example of how changes in mechanics at the nanoscale can enable invention.

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Acknowledgment: The nanotube forms shown in the figure are being developed by A. Krishnaswamy, G. Li, S. Filakova, S. Yarmolenko, V. Shanov, M. Haase, W. Cho, N. Alvarez, W. Li, C. Jayasinghe, A. Song, B. Suberu, R. Malik, J. Sullivan, J. Head, J. T. Jones, and G. Conroy.

10.1126/science.1230428

EVOLUTION

Convergent Evolution of Hearing

The functional and anatomical aspects of hearing in a rainforest insect are remarkably similar to those in humans.

Ronald R. Hoy

How do human ears work? The textbook explanation starts by dividing the ear into three separate anatomical entities that have equally separate functions in converting airborne sound (pressure waves outside the ear) into fluid-borne traveling waves inside the ear, a conversion that makes long-distance hearing on dry land possible (*1*, *2*). On page 968 of this issue, Montealegre-Z. *et al.* (*3*) show that although the hearing organ of a rainforest insect looks very different from a human ear, it can be divided into the same three functional entities, providing evidence for convergent evolution.

In the first step of human hearing, airborne sound waves arriving at the outer ear cause the tympanal membranes/eardrums to vibrate. The eardrum is anatomically coupled to a trio of interlocked, delicate ear bones (hammer, anvil, and stirrup) that comprise the middle ear. These bones convert the airborne vibrations of the eardrum into fluid-borne vibrations in the cochlea, wherein our acoustic detector hair cells are bathed and reside. It is through these tiny ear bones that the extreme inefficiency of transferring the intensity of airborne waves through fluid is overcome through a process called impedance matching. In effect, the middle ear bones act as a lever that mechanically couples the eardrum to the cochlea (see the figure). This lever action converts

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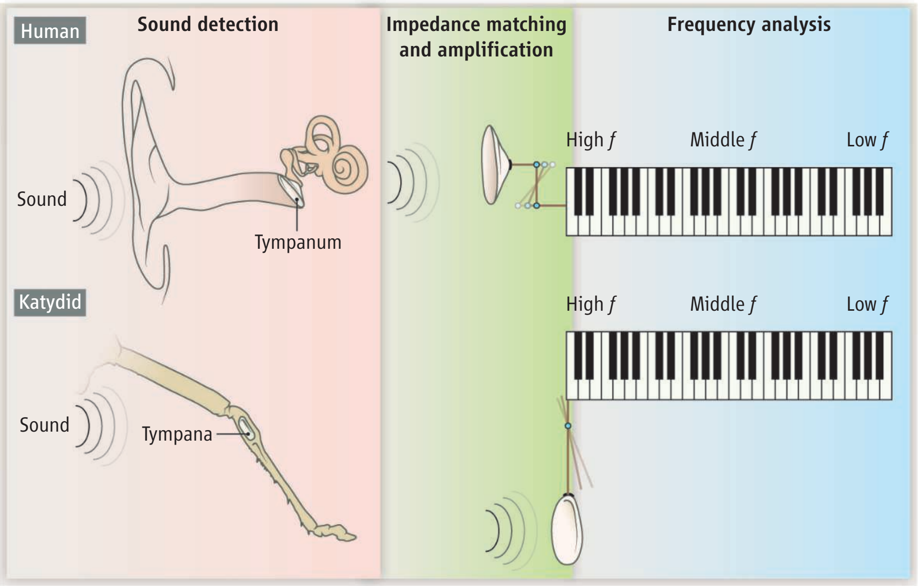

Convergent evolution of the hearing mechanism in humans and katydids. In the detection stage (pink panel), airborne sound stimulates the tympana, which drive an energy transfer mechanism (green panel). In both humans and katydids, this coupling mechanism efficiently transfers and amplifies vibrational energy from air to fluid, solving the problem of impedance mismatch. Montealegre-Z. *et al.* now show that an equivalent mechanism operates in katydidas. In both cases, it involves a system of mechanical levers (brown bars/blue circles = fulcrums/pivot points). The fluid-filled inner ear contains a linear array of auditory receptor cells, represented here by the keys of a keyboard; this is where frequency analysis is performed (blue panel). In humans, this auditory mechanism has been known for nearly a century and thought to be special to humans. Montealegre-Z. *et al.*'s discovery of a closely analogous mechanism in katydid ears is a triumph of the power of micromechanics and nano-optics technology applied to minute biological specimens.

and amplifies large-amplitude vibrations of the eardrum into smaller but more forceful vibrations that are conducted through the fluid of the cochlea as a traveling wave. Finally, the traveling waves are converted into bioelectric signals in auditory sense cells in the inner ear, leading to excitation of the auditory nerve itself. In the cochlea, the sensory hair cells are distributed as an orderly linear array along the length of the cochlear membranes. Each cell in the linear array of receptors responds to a specific pitch/frequency of a pure tone according to its location along the array, with low frequency cells at one end, high frequency cells at the other, and intermediate frequency cells between them (see the figure) (*4*); this is the principle of tonotopic organization (*1*, *2*).

Montealegre-Z. *et al*. now report that the functional and anatomical aspects of hearing in humans find extraordinary similarity in the ear of a rainforest katydid. They show that in the latter, outer-ear tympanal membranes are coupled to a stiff, leverlike middle ear–like structure, which is in turn coupled to an elongated, fluid-filled chamber of the inner ear that contains a linear array of sensory receptors (see the figure). The key finding is the impedance matching and amplification step by a leverlike, middle ear–like component, the tympanal plate (TP), which acts in concert with the tympanal membranes (TM) that heretofore had not been known to exist. This TM-TP "middle ear" efficiently transfers airborne vibrations into vibrations of the fluid-filled acoustic vesicle.

These findings were made possible by the use of an array of state-of-the-art technologies: x-ray microtomography, which allows high-resolution imaging of fresh animals or specimens, microscanning laser-Doppler vibrometry (DLV), which allows measurement of sound-induced tympanal and cuticular vibrations at high spatial resolution, and 3D reconstruction imaging software applied to the microtomography (micro-CT) data. The micro-CT permits imaging of a stationary live insect (or appendage) while the x-ray tube and detector rotate around it. It would have been extremely difficult to reveal the microscale anatomical features and measurement of their mechanical responses to sound using conventional microscopy.

The parallelism in anatomy and function is the result of convergent evolution between the ears of humans and katydids. It is as surprising as it is remarkable and has important implications for comparative auditory research. Katydids belong to a large suborder of acoustically active insects, the Ensifera, which includes the crickets (*5*). The tympanal mechanics (*6*) and even the linear tonotopic distribution of sensory cells (*7*) in these insects have been known for decades, but the manner in which tympanal mechanics generate linear tonotopy has been debated. The work of Montealegre-Z. *et al*. opens the way for re-examining previous results to see if a similar TM-TP mechanism occurs widely within the Ensifera.

Given the discovery of such an unexpected hearing anatomy in an insect, it may be valuable to revisit the phylogenetic spread of sensitive hearing and frequency tonotopy not only in insects but across all invertebrates. Insect ears are much more diverse than those of vertebrates, in location on the body as well as in form and function. The three compartment hearing organ in terrestrial vertebrates, including mammals, evolved out of the developmental imperatives surrounding the evolution of the vertebrate ear on the head (*8*). However, no such constraints apply to the hearing organs of insects (*9*). In fact, three-compartment hearing organs are likely to have evolved first in insects, and only much later in mammals. Moreover, all insect ears are miniscule organs, compared to those of vertebrates. The miniature ears of insects may provide valuable insights for developing the next-generation of auditory biosensors.

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10.1126/science.1231169

ARCHAEOLOGY

Mediterranean Island Voyages

Alan Simmons

Archaeological studies show that humans reached Mediterranean islands much earlier than previously thought.

Some of the classical world's most innovative cultures developed on Mediterranean islands, but their earlier human use is poorly known. The islands, particularly those further from the mainland such as Crete and Cyprus, were thought to have been first colonized about 9000 years ago by late Neolithic agriculturalists with domesticated resources. Until about 20 years ago, claims of earlier, pre-Neolithic occupations on any of the islands did not stand up to critical scrutiny (*1*), but current investigations are challenging these perceptions. Discoveries on Cyprus, Crete, and some Ionian islands suggest seafaring abilities by pre-Neolithic peoples, perhaps extending back to Neanderthals or even earlier hominins. In Cyprus, Neolithic sites have been documented that are nearly as early as those on the mainland.

Evidence for early seafaring by pre-Neolithic humans comes from several parts of the world. For example, pre-Neolithic people must have been able to cross substantial expanses of sea to reach Australia by at least 50,000 years ago (*2*). Additionally, findings from the Indonesian Wallacea islands suggest the presence of hominins as early as 1.1 million years ago on Flores Island (*3*). If correct, the latter suggests that *Homo erectus* had considerable seafaring and cognitive skills, because even at times of lower sea levels, these areas were separated from the mainland by substantial amounts of open sea.

In the Mediterranean, the early-seafaring debate has focused on three time periods (*4*). "Deep time" claims for Paleolithic occupations have been particularly controversial and not well documented because they involve hominins that potentially predate *Homo sapiens*. Evidence for occupation around 12,000 years ago, immediately before the Neolithic, was somewhat more convincing but was restricted to islands that were either close to the mainland or may have been con-

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