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How Hearing Happens

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HOW HEARING HAPPENS^a

Senses and Sensitivity: The Neuroscience of Perception

In addition to possessing the classical senses of vision, hearing, touch, smell, and taste, humans respond to a variety of other stimuli. For example, the vestibular apparatus of the internal ear provides continuous feedback about linear and angular accelerations and allows us to maintain an upright posture. Pressure receptors in our vascular systems and osmoreceptors in our brains help maintain a constant blood volume. Other species employ still more exotic sensory modalities. Many migratory species, especially birds, can orient themselves by reference to the earth's magnetic field. Pit vipers and boas use thermal imaging to strike warm mammalian prey; bats and cetaceans employ sonar to locate respectively insects and fishes.

Despite the wide variety of physical stimuli to which various senses are responsive, there are consistent principles in their operation. A sensory response commences with an antenna, an apparatus for accumulating sensory energy and concentrating it at the receptor cells. In the key step of sensory transduction, the physical stimulus engenders an electrical response that represents the magnitude, duration, and other properties of the input. Most responses are then amplified to assure that their sizes exceed those of any noise sources. Many sensory systems use tuning to enhance responsiveness to stimuli at behaviorally important frequencies and to suppress those at less significant frequencies. In some instances, a sensory receptor bears an axon along which information flows into the central nervous system; in other cases the receptor must forward information across a chemical synapse to excite the nerve fiber. In either event the final step in a peripheral sensory response is the encoding of relevant information in the firing pattern of an afferent nerve fiber.

How the Ear's Works Work: The Operation of Cochlear Hair Cells

Human hearing is extraordinary in its technical specifications. We can perceive frequencies as great as 20 kHz and discriminate between different tones with a precision of 0.2%. At the acoustical threshold, the inner ear responds to vibrations of only ± 0.3 nm, an atomic dimension. Finally, our auditory system can register sound-pressure levels from 0 dB to 120 dB, representing a millionfold range in amplitude and a trillionfold range in power.

The defining feature of a hair cell is its mechanoreceptive organelle, the hair bundle. Extending less than 1 μm to more than 100 μm from the flattened apical surface, the bundle comprises from a dozen to over 300 cylindrical protrusions

a. Albert James Hudspeth a été invité par l'Assemblée des professeurs, sur proposition du Pr Christine Petit. Les conférences ont eu lieu les 1er, 8, 15 et 22 octobre 2013. Les supports de cours et les enregistrements audio sont disponibles sur le site internet du Collège de France : <http://www.college-de-france.fr/site/christine-petit/guestlecturer-2013-10-01-11h00.htm> [NdÉ].

called stereocilia. Each stereocilium consists of a core of parallel actin filaments that are cross-linked into a rigid fascicle. The stereocilia are not of equal size, but display a monotonic decrease in length from one edge to another so that the bundle's top edge is beveled like a hypodermic needle. When the top of a hair bundle is displaced during stimulation, the adjacent stereocilia shear with respect to one another. This movement is communicated to a tip link, a fine filament comprising four cadherin molecules that extends from the tip of each short stereocilium to the side of the longest adjacent one. Each tip link probably contacts a pair of mechanically sensitive ion channels whose opening initiates the hair cell's electrical response.

Making an Effort to Listen: The Active Process of the Cochlea

Uniquely among sensory receptors the hair cell is not a passive recipient of stimuli, but instead uses an active process to enhance its inputs. The active process amplifies mechanical stimuli by as much as a thousandfold, thus greatly increasing our sensitivity to weak sounds. When this process fails, we become hard of hearing. Amplification is accompanied by frequency tuning, which restricts each hair cell's response to a narrow frequency band. If the active process deteriorates, we grow less sensitive to subtle differences in frequency and therefore suffer a diminished ability to discriminate sound sources. Finally, the active process produces a compressive nonlinearity that renders the ear sensitive to sounds over an astonishing trillionfold range in power. By enhancing weak stimuli and suppressing strong ones, this feature allows us to enjoy an instrumental soloist as comfortably as a full orchestra one hundred times as loud.

Two mechanisms cooperate in the active process of the mammalian cochlea. First, hair bundles serve not only as transducers but also as amplifiers. For sounds of relatively low frequency, myosin-1c motors attached at the upper insertions of tip links provide the motive force that enhances hair-bundle motion in response to weak stimuli. The other motile phenomenon involves changes in the length of a hair cell's entire soma. The plasmalemma of each outer hair cell is studded with millions of copies of the protein prestin. Changes in voltage alter the membrane area occupied by these molecules: depolarization causes a hair cell to shorten whereas hyperpolarization provokes elongation. These periodic changes in length pump energy into the basilar membrane's oscillation. The three cardinal features of the active process – amplification, frequency tuning, and compressive nonlinearity – emerge together because this dynamical system operates near an instability called the Hopf bifurcation.

Getting in Tune: Tuning, Transmission, and Turnover in the Ear

Our ability to identify different sound sources – to distinguish predators from prey, for example – rests upon the ear's ability to decompose complex sounds into their frequency components. Although the cochlear traveling wave initiates this process, individual hair cells are also tuned to specific frequencies both through hair-bundle mechanics and sometimes by electrical resonance. Not only the active process of hair cells, but even their synaptic transmission has been found to be frequency-selective.

Afferent axons of the eighth cranial nerve carry information from the cochlea into the auditory nuclei of the brainstem. These nerve fibers are excited by a neurotransmitter, glutamate, released by hair cells at specialized ribbon synapses. Unlike ordinary synapses, which respond to transient action potentials about 100 mV in amplitude, a ribbon synapse can release transmitter continuously and signal threshold stimuli only one thousandth as large. In addition, the ability of these synapses to encode phase information at frequencies up to 4 kHz helps us to localize sound sources in space by comparing the arrival times of signals at the two ears.

Hearing deficiency is widespread in industrialized countries, in which about 10% of the population is affected. Genetic deafness is relatively common, with at least 200 forms of syndromal hearing impairment and 100 non-syndromal types. Hearing can be damaged by loud sounds, for example in an industrial or military setting; by ototoxic drugs, including common antibiotics and anti-cancer agents; and by infections. Finally, in the phenomenon of presbycusis, hearing deteriorates with age. In all of these cases, the dominant problem is the loss of hair cells. An important focus of contemporary research is therefore the potential restoration of human hearing through the reprogramming of progenitor cells in the ear.

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ENTRE « CRÉATION » ET « COMMENCEMENT » : GEORGES LEMAÎTRE
ET LES DÉBATS PHILOSOPHICO-THÉOLOGIQUES AUTOUR DU BIG BANG^a

Questions posées par l'itinéraire intellectuel et spirituel de Georges Lemaître

Premier moment de son itinéraire

Marqué par une phase de concordisme, Lemaître cherche à faire se rejoindre sur un même plan la physique et sa lecture de l'Écriture marquée par une fidélité à des injonctions exégétiques discutables, données par la Commission biblique pontificale au début du XX^e siècle, dans un contexte de réaction au courant moderniste.

Ce concordisme de jeunesse est bien entendu une erreur épistémologique, et Lemaître l'abandonnera résolument, à partir des années 1929, suite aux interactions

a. Dominique Lambert a été invité par l'Assemblée des professeurs, sur proposition du Pr Thomas Römer. Les conférences, données les 28 février et 7 mars 2014, sont disponibles en audio sur le site internet du Collège de France : <http://www.college-de-france.fr/site/thomas-romer/guestlecturer-2014-02-28-14h30.htm> [NdÉ].