Mammalian behavior and physiology converge to confirm sharper cochlear tuning in humans

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Ear has two primary functional purposes

- **sensitivity** (e.g., detect presence of sound)
- **selectivity** (e.g., discriminate between sounds)
Frequency selectivity

An Acoustic Prism

- High frequencies
- Mid frequencies
- Low frequencies

Zweig et al. (1976)

- How sharply tuned is human hearing?
  (surprisingly difficult-to-answer and controversial question!)

http://www.flickr.com/photos/athena/369037746/
Key Idea

Frequency “analysis” primarily arises at the periphery, not the CNS
Frequency selectivity in Old-World monkeys corroborates sharp cochlear tuning in humans

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Frequency selectivity in the inner ear is fundamental to hearing and is traditionally thought to be similar across mammals. Although direct measurements are not possible in humans, estimates of frequency tuning based on passive recordings of sound evoked from the cochlea (otoacoustic emissions) have suggested substantially sharper tuning in humans but remain controversial. We report measurements of frequency tuning in macaque monkeys, Old-World primates phylogenetically closer to humans than the laboratory animals often taken as models of human hearing (e.g., cats, guinea pigs, chinchillas). We find that measurements of tuning obtained directly from individual auditory-nerve fibers and indirectly using otoacoustic emissions both indicate that at characteristic frequencies above about 500 Hz, peripheral frequency selectivity in macaques is significantly sharper than in these common laboratory animals, matching that inferred for humans above 4–5 kHz. Compared with the macaque, the human otoacoustic estimates thus appear neither prohibitively sharp nor exceptional. Our results validate the use of otoacoustic emissions for noninvasive measurement of cochlear tuning and corroborate the finding of sharp tuning in humans. The results have important implications for understanding the mechanical and neural coding of sound in the human cochlea, and thus for developing strategies to compensate for the degradation of tuning in the hearing-impaired.

Auditory fibers: comparative hearing

Sound waveforms consist of pressure fluctuations in time and space. In the process of transducing mechanical vibrations into neural signals, the cochlea performs a mechanical frequency analysis that decomposes sounds into constituent frequencies (1, 2). The frequency tuning of the cochlear filters plays a critical role in the ability to distinguish and segregate different sounds perceptually. For example, sounds that radiate from different sources superpose in the air, and are thus “mixed up” before striking the eardrums. Based on the output of the cochlear filters, and by comparing responses from the two ears, the nervous system is capable of disentangling the various sounds, grouping related frequency components to identify auditory objects and localize their sources in space (3). The critical role of peripheral frequency selectivity is perhaps best illustrated by the consequences of damage to the inner ear, which typically leads to a degradation of the cochlear filters. The loss of sharp filtering results in an impaired ability to detect signals in noise and to separate different sounds (4). Frequency selectivity is therefore crucial to everyday human communication.

The study of the cochlea is hampered by its fragility and inaccessibility. Direct measurements of mechanical or neural frequency tuning in healthy cochlea are only possible in laboratory animals. To date, measurements of the mechanical vibration of the cochlea’s basilar membrane have been largely restricted to the basal high-frequency end of the cochlea, where surgical access is convenient (2). Recordings from individual auditory-nerve fibers (5–7) enable a detailed characterization of the frequency channels set up along the entire length of the cochlea (8–14), but they too are surgically invasive. Although direct measurements are not possible in humans, neural recordings indicate that cochlear tuning is generally similar across common laboratory animals (15); tuning in humans has therefore long been regarded as comparable.

A promising alternative procedure allows the objective noninvasive estimation of cochlear tuning, and can therefore be applied to humans (16, 17). As a byproduct of the tuned mechanical amplification responsible for the ear’s impressive sensitivity and dynamic range, the cochlea emits sound in response to sound (18). The delays (latencies) of the sounds evoked from the ear by pure tones, sounds known as stimulus-frequency otoacoustic emissions (SFOAEs), provide a measure of the mechanical delay within the cochlea (19, 20). Across a wide variety of animals ranging from mammals to birds, SFOAE delays appear well correlated with the sharpness of neural tuning (16, 17, 21), a correlation consistent both with models of emission generation (22–23) and with relationships between tuning and delay expected from filter theory (24). Consistent with the time-frequency uncertainty principle, filters with narrower bandwidths (i.e., more well-defined center frequencies) generally have longer group delays (i.e., impulse responses that are more spread out in time).

Interestingly, humans have the longest SFOAE delays of any species so far examined. Because filter theory associates longer delay with sharper tuning, human otoacoustic latencies have been interpreted as indicative of sharper tuning. An extension of this reasoning, based on the assumption that the relationship between SFOAE delay and neural tuning manifest in laboratory animals extends to other mammals, allows one to obtain quantitative estimates of neural tuning from otoacoustic measurements (16, 17). When applied to humans, the method yields tuning estimates that coincide with behavioral values obtained using revised psychophysical paradigms designed to mimic the measurement of neural tuning curves (25). Nevertheless, because they suggest that human cochlear tuning is substantially sharper than that of common laboratory animals, the reliability of the otoacoustic and behavioral estimates, as well as their apparent consequences for the exceptionality of the human cochlea, have been questioned and remain controversial (13, 20–26).

Results

We measured both otoacoustic emissions and auditory-nerve responses in two species of macaque monkeys. As Old-World primates, macaques are more closely related to humans than are the common laboratory animals generally used in studies of frequency selectivity. Our goal was thus to explore the apparent

How sharply tuned is human hearing?
Macaque auditory nerve fiber (ANF) tuning curves

Otoacoustic emission (OAE) delays
Otoacoustic emissions (OAEs)

- Much faster/easier than evoked potentials (i.e., ABR)

- OAEs used for newborn hearing screening (only healthy ears emit)

→ Non-invasive probe into cochlear physiology/function
Macaque auditory nerve fiber (ANF) tuning curves

Otoacoustic emission (OAE) delays

(2011 argument)
Combining OAE and ANF tuning measures in non-human primate confirms sharper tuning in humans

Joris et al. (PNAS 2011)
Yet controversy remained... (re psychophysics)

- Human psychophysical data still provided some ambiguity (e.g., tuning varied drastically for forward vs simultaneous notched-noise masking)

- Still no “gold standard” (i.e., ANF) for humans.....
Mammalian behavior and physiology converge to confirm sharper cochlear tuning in humans

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ANF: threshold tuning of auditory nerve fibers

OAE: phase gradient of otoacoustic emissions

PSY: psychophysical detection of tones in notched-noise masker

\[ \propto \frac{1}{\text{ERB}} \]

Sumner et al. (PNAS 2018)
Combining OAE, ANF, and PSY tuning measures in ferret confirms sharper tuning in humans

Sumner et al. (PNAS 2018)
Sound consists of a dynamic stream of energy at different frequencies. Auditory processing of sound frequency is critical in determining our ability to interact and communicate in a complex acoustic world, yet fundamental gaps remain in our understanding of how this is achieved. Indeed, the resolving power of the system, how best to measure it, and the mechanisms that underlie it are all still debated. Here we provide critical evidence demonstrating that humans can resolve the frequency components of competing sounds better than other commonly studied mammals. This finding raises important questions both for theories of auditory perception and for our understanding of the evolutionary relationships between the auditory system and acoustic communication, including speech.