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Otoacoustic Estimates of Cochlear Tuning: Testing Predictions in Macaque

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Abstract

Otoacoustic estimates of cochlear frequency selectivity suggest substantially sharper tuning in humans. However, the logic and methodology underlying these estimates remain untested by direct measurements in primates. We report measurements of frequency tuning in macaque monkeys, Old-World primates phylogenetically closer to humans than the small laboratory animals often taken as models of human hearing (e.g., cats, guinea pigs, and chinchillas). We find that measurements of tuning obtained directly from individual nerve fibers and indirectly using otoacoustic emissions both indicate that peripheral frequency selectivity in macaques is significantly sharper than in small laboratory animals, matching that inferred for humans at high frequencies. Our results validate the use of otoacoustic emissions for noninvasive measurement of cochlear tuning and corroborate the finding of sharper tuning in humans.

Keywords

cochlea; frequency tuning; auditory nerve; otoacoustic emissions

INTRODUCTION

Mechanical frequency tuning underlies the fundamental capacity of the cochlea to separate sounds into different frequency components. Although direct measurements of frequency tuning are not available in humans—or in other animals for which the necessary mechanical or neural recordings are difficult, undesirable, or prohibited—otoacoustic emissions enable the noninvasive assessment of cochlear tuning. One promising procedure exploits the observation that the latencies of stimulus-frequency otoacoustic emissions (SFOAEs) appear well correlated with the sharpness of neural tuning across a variety of laboratory animals [11, 12]. The observed correlations are consistent both with models of emission generation [1, 13, 15] and with relationships between tuning and delay expected from filter theory [2].

The working assumption that the empirical correlations between SFOAE delay and neural tuning evident in laboratory animals extend to other mammals allows the quantitative estimation of cochlear tuning from otoacoustic measurements [11, 12]. 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 [7]. However, because the procedures remain untested in primates—and because they indicate that human cochlear tuning is substantially sharper than that of common laboratory animals—the reliability of the otoacoustic and behavioral estimates have been questioned [8, 14]. Here we test the otoacoustic method by measuring both

otoacoustic emissions and auditory-nerve responses in macaque monkeys. As Old-World primates, macaques are more closely related to humans than the small laboratory animals commonly employed in studies that stress the similarity of tuning and delay across species [8, 9].

METHODS

We performed the otoacoustic and neural recordings using separate populations of macaque monkeys in laboratories at the Massachusetts Institute of Technology and the University of Leuven, respectively. All procedures were approved by the corresponding animal care and ethics committees.

Otoacoustic emissions

The measurement of SFOAEs and the analysis of their phase gradients used procedures well established in humans and other animals [10]. We measured otoacoustic emissions in 21 healthy, adult rhesus macaques (*Macaca mulatta*) while they were anesthetized for routine veterinary care. SFOAEs were obtained using the suppression method [5] implemented on the Mimosa Acoustics measurement system, which employs Etymotic Research ER10c transducers. Probe and suppressor levels were 40 and 55 dB SPL, respectively. System distortion limited the measurements to probe frequencies less than about 7 kHz. Although behavioral audiograms are not available for the monkeys, their emission levels are comparable to those measured in other mammals with normal hearing, including humans. SFOAE phases were corrected for the approximate acoustic delay due to round-trip propagation between the microphone and tympanic membrane, and acoustic calibrations removed delays introduced by the measurement system. Measurement frequency resolution was sufficient to resolve ambiguities due to phase unwrapping. Phase-gradient delays were computed from the slope of the unwrapped phase using centered differences [10]. Only data at least 10 dB above the noise floor were included in subsequent analyses.

Auditory-nerve recording

We obtained auditory-nerve recordings from 753 single fibers in 16 macaque monkeys (10 *M. fascicularis*, 6 *M. mulatta*) using methods routinely applied for similar recordings in cats at our laboratory at the University of Leuven [4, 6]. Recordings were made in a double-walled sound-attenuating booth with the animals under deep barbiturate anesthesia. Sounds were delivered with a dynamic speaker and compensated digitally for the acoustic transfer function measured in the ear canal with a probe microphone. Threshold tuning curves were measured using a two-down one-up tracking paradigm. We obtained complete data sets from 496 different fibers. The lower envelope of the neural threshold data was consistent with behavioral threshold measurements for pure tones [3]. To quantify the sharpness of tuning, we derived the equivalent rectangular bandwidth (ERB) and the corresponding dimensionless quality factor ($Q_{\text{ERB}} = \text{CF}/\text{ERB}$) from each neural tuning curve. Only the most sensitive fibers—those with CF thresholds within 30 dB of the dashed curve—were used in subsequent analyses.

RESULTS

Otoacoustic delays

Figure 1 shows SFOAE delays in the dimensionless form, N_{SFOAE} , representing the delay in periods of the stimulus frequency. SFOAE delays in macaques appear intermediate between those in cats and humans. Although closer to delays measured in small laboratory animals at frequencies below 1 kHz, N_{SFOAE} values in the macaque begin to approach the longer human values at higher frequencies (note the logarithmic ordinate). If SFOAE delays reflect

the bandwidths of frequency filtering within the cochlea, as previously suggested [11, 12], the otoacoustic measurements indicate that the sharpness of tuning in macaques is broader than in humans at low frequencies but more similar at high frequencies.

Otoacoustic prediction of cochlear tuning

We make these qualitative comments more precise by using the otoacoustic data to derive quantitative predictions for the sharpness of cochlear tuning in macaque. According to the procedure, approximate trend values of Q_{ERB} in macaques can be obtained from measurements of SFOAE delay using the formula [12]

$$Q_{\text{ERB}}(\text{CF}) \cong r \left(\text{CF} / \text{CF}_{\text{alb}} \right) N_{\text{SFOAE}}(f) \big|_{f=\text{CF}} \quad (1)$$

In this equation, r is the tuning ratio and CF_{alb} is the apical-basal transition CF, an empirically determined, species-dependent parameter that divides the cochlea of a given species into two parts: a high-frequency region of apparently “basal-like” behavior ($\text{CF} > \text{CF}_{\text{alb}}$) and a low-frequency region of more “apical-like” behavior ($\text{CF} < \text{CF}_{\text{alb}}$). The value of CF_{alb} can be estimated from the location of the bend in the N_{SFOAE} curve (Fig. 1). Previous work has shown that tuning ratios $r(\text{CF}/\text{CF}_{\text{alb}})$ in cats, guinea pigs, and chinchillas can be well approximated by a single, common curve [12], and the procedure applied here assumes that this approximate species-invariance of r extends to macaques. For the invariant tuning ratio, r , we used the average of the tuning ratios reported for cats, guinea pigs, and chinchillas [12]. The parameter CF_{alb} for macaques was taken as 1.7 kHz, intermediate between the transition CFs previously estimated for cats (in the range 3–4 kHz) and humans (1–1.5 kHz). Our estimate of CF_{alb} is not critical; varying its value by half an octave in either direction has relatively minor effects on the results. Figure 2 shows the estimated values of Q_{ERB} (dashed black line) computed from Eq. (1) using the N_{SFOAE} measurements from Fig. 1.

Testing the otoacoustic prediction with neural data

Figure 3 tests the otoacoustic predictions for macaque tuning by comparing the estimates of Q_{ERB} with direct measurements obtained from single auditory-nerve fibers (ANFs). The figure shows the neural Q_{ERB} values (gray dots) and their trend with CF (black line) together with the otoacoustic estimates from Fig. 2. The agreement between the otoacoustic estimates and the neural measurements of Q_{ERB} is excellent. The otoacoustic method evidently yields reliable values of the Q_{ERB} trend over the full range for which predicted values can be compared with the neural recordings.

DISCUSSION

Our data establish enhanced frequency selectivity in the primate inner ear using two independent methods: direct neural recordings and noninvasive measurements of otoacoustic delay. Although the two methods are conceptually and methodologically distinct, they yield results that are mutually and *quantitatively* consistent with one another (see Fig. 3). Together, the two data sets validate the otoacoustic method and corroborate revised psychophysical procedures [7] as reliable means to assess the sharpness of cochlear tuning noninvasively.

By themselves, the neural data demonstrate that the two species of macaques examined here have sharper cochlear tuning, especially in the basal high-frequency region of the cochlea, than the small laboratory animals for which frequency tuning has been most extensively studied (cats, guinea pigs, and chinchillas). By demonstrating significantly sharper tuning in macaques, the data provide an important counterexample to the claim that the sharpness of

cochlear tuning is essentially the same in all mammalian species [8]. Although the human estimates previously appeared exceptional, the neural data from macaque indicate that at CFs above 4–5 kHz cochlear tuning in Old-World monkeys can be just as sharp as the values previously derived for humans.

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FIGURE 1.

Stimulus-frequency otoacoustic emission delays in macaques compared to other species. Gray dots and trend (black line with flanking dots delimiting 95% confidence intervals in the central tendency) show macaque phase-gradient (group) delays, N_{SFOAE} , in periods of the stimulus frequency. Blue and red lines show published species trends in cats and humans [10] obtained from SFOAE data measured at the same stimulus level (40 dB SPL).

FIGURE 2.

Predicted sharpness of tuning in macaque. The black dashed line gives the macaque Q_{ERB} trend predicted from Eq. (1) using the values of N_{SFOAE} in Fig. 1. For comparison, the blue line shows the neural trend in cats (ensemble data from the Leuven lab and those of M.C. Liberman and B. Delgutte). The red dashed line gives the human trend previously derived from SFOAE delay [11, 12]; the red squares and standard errors show revised behavioral values [7].

FIGURE 3.

Sharpness of tuning in macaques and other species. Gray dots and trend (black line with flanking dots delimiting 95% confidence intervals for the trend) show macaque Q_{ERB} values derived from auditory-nerve tuning curves with qualifying thresholds ($n = 385$). For comparison with the otoacoustic predictions, the neural data have been superposed on Fig. 2.