A. Subjects

For frequencies below 32 Hz, the 15-in. woofer was oriented toward one corner of the chamber while the subject was placed in the opposite corner where standing waves occurred. This was done to obtain intensities to over 100 dB SPL as attempting to produce such high intensities by increasing the gain of the amplifier resulted in measurable distortion of the signal. Although this situation was not a free field (i.e., the sound was coming from more than one direction), it was still possible to accurately calibrate the sound field as the sound-measuring microphones are omnidirectional at these very low frequencies and no correction for the orientation of the microphone to the sound sources is needed. That the orientation of the microphone to the direction of the sound was not critical was demonstrated by showing that the

TABLE I. Free-field pure-tone thresholds of three Japanese macaques in decibels with respect to 20 μPa.

Frequency (in kHz)	Monkey 286	Monkey 605	Monkey 638	Average
0.008	>85	>85	83	⋯
0.0125	81	77	76	78
0.016	71	73	72	72
0.025	63	66	60	63
0.032	56	57	57	57
0.063	37	35	37	36
0.125	18	19	19	19
0.250	13	15	17	15
0.500	7	2	10	6
1.0	4	5	3	4
2.0	7	0	9	5
4.0	4	−2	1	1
8.0	8	0	6	5
16.0	9	1	0	3
32.0	41	37	38	39
36.0	77	64	72	71
40.0	92	85	89	89

II. RESULTS

The three monkeys used in this study had been previously trained using the conditioned avoidance procedure and had prior experience on a variety of auditory tasks including sound localization and the discrimination of Japanese macaque vocalizations. Thus, the animals already knew how to perform the avoidance task and were experienced auditory observers.

The individual and average thresholds for the three Japanese macaques are given in Table I. Only one of the animals (monkey C) was able to hear 8 Hz at an intensity of 85 dB or less, the highest intensity that could be used without producing overtones in the acoustic signal that could be detected with the spectrum analyzer. However, all three animals were able to hear 12.5 Hz with an average threshold of 78 dB SPL with sensitivity improving as frequency was increased. The animals showed a broad range of good sensitivity extending from 125 Hz to 16 kHz with their best threshold of 1 dB at 4 kHz. Above 16 kHz their sensitivity decreased rapidly, with the monkeys able to hear 40 kHz with an average threshold of 89 dB. At an intensity of 60 dB, the average hearing range for the three monkeys extended from 28 Hz to 37 kHz, a range of over 10 octaves.

The individual and average thresholds for the seven human subjects are given in Table II. All of the subjects were able to hear down to 4 Hz, with an average threshold of 101 dB. The audiograms showed a broad range of good sensitivity extending from 125 Hz to 8 kHz, with a best average threshold of -10 dB at 2 and 4 kHz. Above 8 kHz, sensitivity decreased rapidly, with only three of the six subjects tested able to hear 20 kHz at a level of 91 dB (subject JM's performance on 20 kHz at 91 dB was slightly below 0.50 resulting in an extrapolated threshold of 92 dB). None of the human subjects were able to hear 22.4 kHz at a level of 91 dB. At an intensity of 60 dB, the average hearing range for the human subjects extended from 31 Hz to 17.6 kHz.

TABLE II. Free-field pure-tone thresholds of seven humans in decibels with respect to 20 μPa.

Frequency (in kHz)	Subject CC	HH	JM	LH	PH	RH	SM	Average
0.004	101	100	101	101	100	100	101	101
0.008	95	92	95	95	95	92	92	94
0.016	88	78	83	87	87	86	68	82
0.032	63	58	62	65	62	56	42	58
0.063	38	39	39	34	38	29	34	36
0.125	20	12	17	⋯	21	12	21	17
0.250	14	13	7	⋯	11	7	8	10
0.500	11	14	8	⋯	10	10	7	10
1.0	−11	−8	−2	⋯	−4	1	2	−4
2.0	−10	−14	9	⋯	−14	−20	−10	−10
4.0	−11	−2	−4	⋯	−13	−12	−19	−10
8.0	14	17	4	⋯	2	4	13	9
16.0	14	41	28	⋯	17	49	4	26
18.0	67	81	77	⋯	66	85	51	71
20.0	91	>91	92	⋯	>91	>91	91	91+
22.4	>91	>91	>91	⋯	>91	>91	>91	>91

III. DISCUSSION

A. Japanese macaque and human free-field audiograms

Figure 2 compares the Japanese macaque and human audiograms generated by this study with the International Organization for Standardization free-field audiogram (ISO, 1961). In comparing these audiograms, three points can be made.

First, the human free-field audiogram obtained here is in good agreement with the ISO free-field audiogram especially at low frequencies (500 Hz and below), where the greatest difference is 3 dB. Similar close agreement is also found at high frequencies (above 4 kHz). Interestingly, the two audiograms differ most in the midrange where they reach a maximum difference of 12 dB at 2 kHz. Although this difference suggests that individual audiograms may vary most in the region of best sensitivity, and, indeed, our subjects varied by up to 29 dB at 2 kHz, we also had large variation at 32 Hz and 16 kHz, frequencies at which our average audiogram

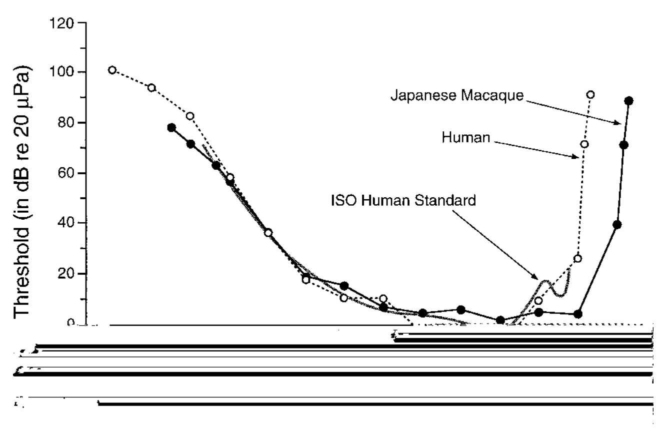

FIG. 2. Average free-field audiogram of three Japanese macaques and seven humans compared with the ISO free-field threshold curve (ISO, 1961). Note the similarity in low-frequency hearing between humans and Japanese macaques.

agreed well with the ISO standard (Table II and Fig. 1). However, it is the low- and high-frequency portions of mammalian audiograms that are of particular theoretical interest and the close agreement of the two human audiograms at these frequencies suggests that there was nothing unusual about either our sound field or our acoustic measurements that would affect our estimates of low- and high-frequency hearing.

Second, the free-field audiograms of both humans and Japanese macaques show very good low-frequency hearing, and the audiograms are virtually identical for frequencies below 1 kHz. Indeed, the similarity between the low-frequency hearing of humans and Japanese macaques has been noted in audiograms obtained using headphones (cf. Owren *et al.*, 1988). However, good low-frequency hearing is not universal as many mammals, such as the Norway rat, are not sensitive to low frequencies (H. Heffner *et al.*, 1994; R. Heffner *et al.*, 1994).

Finally, Japanese macaques have better high-frequency hearing than humans: We found the highest frequency audible to humans at a level of 60 dB SPL to be 17.6 kHz whereas the Japanese macaque can hear 37 kHz at that level. Because humans and macaques have similar low-frequency hearing, it is tempting to conclude that the human audiogram is truncated at the high-frequency end, perhaps as part of a specialization for the reception of speech. However, when viewed from the larger perspective of mammalian hearing as a whole, neither the low-frequency, nor the high-frequency portion of the human audiogram is unusual.

With regard to high-frequency hearing, mammals with small heads and pinnae need to hear higher frequencies than larger mammals in order to make adequate use of binaural spectral differences and pinna cues to localize sound. As illustrated in Fig. 3(a), there is a robust correlation between head size and high-frequency hearing such that small mammals hear higher frequencies than larger mammals (e.g., Koay *et al.*, 1997; Masterton *et al.*, 1969). Thus, the difference in high-frequency hearing between humans and macaques is explained by the difference in head size and, indeed, animals with larger heads, such as the Indian eland Olszyk, 1997). Our free-field audiogram is in good agreement with the headphone audiograms at the mid and high frequencies. For example, the highest frequency audible at 60 dB SPL in the study by Owren *et al.* is 41.5 kHz, which is within 0.20 octaves of the 37-kHz 60-dB limit of our free-field audiogram. Such a difference is minor in a comparative analysis of mammals as their high-frequency hearing spans a range of more than 4 octaves (Koay *et al.*, 1997, 1998).

In contrast, at frequencies below 1 kHz, our free-field audiogram shows the hearing of Japanese macaques to be more sensitive than either of the two headphone audiograms. For example, the lowest frequency audible at 60 dB SPL in these two audiograms is approximately 80 Hz, which is 1.5 octaves higher than the 28-Hz limit of the free-field audiogram. Even though mammalian low-frequency hearing varies by more than 9 octaves (Koay *et al.*, 1997), this difference is too large to be ignored.

The difference between the headphone and free-field audiograms is most likely due to the difficulty in calibrating headphones. Whereas a free field is calibrated by placing a microphone in the sound field and pointing it at the loudspeaker, there is more than one way to calibrate headphones. One method is to insert a probe microphone underneath the cushion of a headphone or into the tube of an insertion earphone. Another way is to place the headphone or earphone on a coupler or artificial ear that simulates the volume of the ear canal. However, as Phingst and his colleagues have pointed out, these calibration procedures can result in estimates of threshold that vary by up to 20 dB, especially at low frequencies (Pfingst *et al.*, 1975). This uncertainty in calibration may account for not only the difference between the headphone and free-field audiograms, but also for the observation that audiograms conducted on the same species in different laboratories may show large differences when headphones are used (cf. the low-frequency portion of the two headphone audiograms shown in Fig. 4).

Although headphones are appropriate for studies involving pre- and post-treatment tests on the same animals, especially when the ears must be tested independently, carefully conducted free-field audiograms are known to result in audiograms that can be replicated across time and laboratories (cf. H. Heffner *et al.*, 1994; Kelly and Masterton, 1977). This reliability is essential when making cross-species comparisons in order to ensure that any differences between species are true species differences and not the result of procedural differences, acoustic or otherwise. An additional advantage is that the free-field audiogram tests the ability of the whole animal. That is, by placing an animal into a calibrated sound field, the resulting audiogram also reflects the effects of the animal's head and pinnae on its sensitivity to sound. However, should it be of interest to determine the sensitivity of the ear alone, it is possible to place a sedated animal into a calibrated sound field and then measure the intensity of the sound at the eardrum.

C. Hearing in macaques

Audiograms are available for three other species of macaques: the rhesus macaque *M. mulatta* (Pfingst *et al.*, 1978), Philippine or crab-eating macaque, *M. irus*, and pigtail macaque *M. nemistrina* (Stebbins *et al.*, 1966), all of which were determined using headphones. As can be seen in Fig. 4, the audiograms of these three species are quite similar to the Japanese macaque audiograms at the mid and high frequencies. At low frequencies, they more closely resemble the Japanese macaque free-field audiogram, even though they were determined with headphones themselves. Because all four species of macaques are closely related and are of similar size, it might be expected that their audiograms would likewise be quite similar. Thus, the differences between the audiograms at low frequencies may be due more to uncertainties inherent in calibrating headphones than to species differences.

ACKNOWLEDGMENTS

We thank G. Koay for his help with the illustrations and his comments on the manuscript. This work was supported by NIH Grant No. NS 30539 to H.E.H. and NIH postdoctoral fellowship DC 00305 to L.L.J.

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