Free-field audiogram of the Japanese macaque (*Macaca fuscata*)

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The audiograms of three Japanese macaques and seven humans were determined in a free-field environment using loudspeakers. The monkeys and humans were tested using tones ranging from 8 Hz to 40 kHz and 4 Hz to 22.4 kHz, respectively. At a level of 60 dB sound pressure level the monkeys were able to hear tones extending from 28 Hz to 37 kHz with their best sensitivity of 1 dB occurring at 4 kHz. The human 60-dB hearing range extended from 31 Hz to 17.6 kHz with a best sensitivity of −10 dB at 2 and 4 kHz. These results indicate that the Japanese macaque has low-frequency hearing equal to that of humans and better than that indicated by previous audiograms obtained using headphones. © *1999 Acoustical Society of America.* [S0001-4966(99)06511-X]

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INTRODUCTION

The audiogram as a basic measure of hearing has proven useful to the comparative study of hearing. Specifically, comparison of the audiograms of various species has revealed the existence of important variation in the hearing abilities of animals, especially in their ability to hear high- and low-frequency sounds. In the case of mammals, analysis of these differences has yielded clues regarding the selective pressures involved in the evolution of hearing (e.g., Koay *et al.*, 1997; Masterton *et al.*, 1969).

In order for the audiograms of different species to be comparable, they must be obtained under similar conditions. One consideration is that the behavioral methods used to test the animals must be capable of eliciting the best performance of the animal under test. Fortunately, this problem has largely been solved by the development of techniques for training animals to respond to sound (see Klump *et al.*, 1995). Another important concern is that the sound be presented in such a way that it can be accurately measured; there are two ways of doing this.

The most common way of presenting sounds to behaving animals is to play them through a loudspeaker, which is usually located directly in front of the animal being tested. In this procedure, care is taken to minimize acoustic reflections so that the sound reaching the animal is coming from only one direction, thereby approximating a free-field sound field that can be accurately measured. Thus, by generating a uniform sound field and using behavioral procedures that keep an animal's head fixed within that field, it has been possible to produce reliable audiograms that can be replicated on different individuals of the same species in different laboratories and years apart (cf. H. Heffner *et al.*, 1994; Kelly and Masterton, 1977).

Another way to present tones is through headphones, a method that is generally practicable only on larger animals. This method is often used with monkeys, especially macaques, which can be restrained in primate chairs to allow careful placement of the headphones. In this case, the sound field is considered to be a closed system in which a tight seal is made between the transducer and the animal's ear. Because sound-measuring microphones can be calibrated for either free-field or closed systems, it has generally been considered that the only differences between free-field and headphone audiograms would be due to the effect of the head and pinnae on the sound reaching the eardrum in the free-field test. Thus, a free-field audiogram could be considered to measure the sensitivity of an animal, whereas a headphone audiogram measures the sensitivity of the animal's ear.

Recently, we have had the opportunity to determine the free-field audiogram of Japanese macaques (*Macaca fuscata*), an animal commonly used in auditory research. When we compared it with thresholds determined in other laboratories using headphones (Owren *et al.*, 1988; Smith and Olszyk, 1997), we found significant differences between the audiograms at the low frequencies that could not be explained by the effect of the animal's head and pinnae. Nor could these differences be accounted for in terms of individual variation. The purpose of this paper, then, is to present the free-field audiogram of the Japanese macaque and to suggest reasons for the discrepancy in thresholds between the free-field and headphone audiograms. For comparison, the audiogram of humans was determined in the same free-field environment.

I. METHOD

The monkeys were tested using a conditioned avoidance procedure with a water reward (Heffner and Heffner, 1995). This involved training the animals to maintain steady contact with a water spout in order to obtain water and to break contact whenever they detected a tone in order to avoid a mild shock delivered through the water spout. The animals were tested in a specially constructed cage designed to minimize sound reflection and their heads were fixed within the sound field by requiring them to maintain contact with the water spout.

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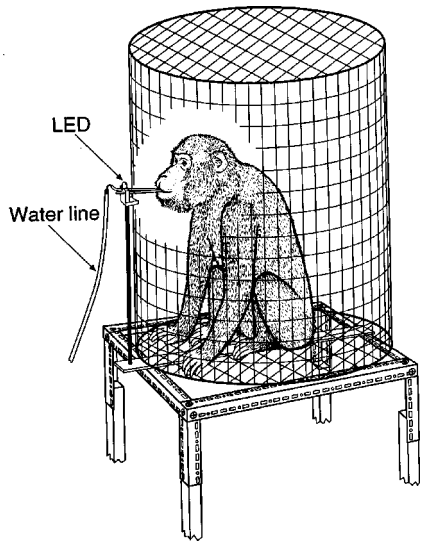

FIG. 1. Diagram illustrating the cage used in testing. The cage was specially constructed to minimize sound reflection.

A. Subjects

Three male Japanese Macaques (*Macaca fuscata*) were used in this study. Monkey 286 was 17 years old and monkeys 605 and 638 were 13 years old at the time of testing. The animals were housed individually in primate cages with free access to food. Water was used as a reward and was available only during testing, although additional water was given an animal in its home cage if needed. Each monkey's weight was checked daily to monitor its health and deprivational state.

Complete audiograms were obtained for six human subjects who had no known auditory disorders: CC (20-year-old male), HH (44-year-old male), JM (20-year-old female), PH (15-year-old male), RH (43-year-old female), and SM (23-year-old female). Low-frequency thresholds were obtained for an additional subject, LH (21-year-old female).

B. Behavioral apparatus

Testing was conducted in a double-walled acoustic chamber IAC model 1204 ($2.55\times2.75\times2.05$ m). The chamber floor was carpeted, and the walls and ceiling were lined with eggcrate foam to reduce sound reflections. The electronic equipment and microcomputer used for behavioral and stimulus control were located outside the chamber. The animals were monitored with two closed-circuit television systems. One camera was mounted on the wall in front of the animal and was directed toward the monkey's face; the second camera, mounted above and behind the animal, was directed at the back of the monkey's head. The cameras were used to verify that the monkey's head was facing directly toward the loudspeaker located in front of the cage.

The monkeys were tested in a cylindrical cage (66 cm diam, 76 cm high, mounted on 58-cm-high legs) constructed of 1×2-in. (2.54×5.08-cm) welded wire (Fig. 1). A double water spout was mounted horizontally on the front of the cage 42 cm above the cage floor (see Fig. 1), a height that allowed the animals to hold their heads in a normal posture while drinking. The spout consisted of two standard sipper tubes mounted parallel to each other and 1 cm apart to permit comfortable placement of a monkey's mouth on both sipper tubes. The degree to which the water spout protruded into the cage was adjusted so that the animals had to face the front of the cage and could not turn their heads sideways while drinking from the water spout; that they maintained a constant, frontal orientation was verified by daily observing the monkey's head positions on the closed-circuit monitors.

The two sipper tubes were electrically isolated from each other so that they could be attached to an electronic ''contact'' switch that detected when an animal had placed its mouth on them. A constant pressure water reservoir (a bottle with an air inlet tube that ended well below the water level, i.e., a Marriotte bottle) was connected to one spout via plastic tubing with an electrically operated water valve placed in line to control the flow of water. The water was trickled into the spout through a copper tube that fit loosely into the rear of one of the sipper tubes so that an animal could not increase water flow by sucking on the spout. The monkeys typically received 200–500 cc of water in a session lasting approximately 1 h.

A mild electric shock was provided by a constant-current shock generator (Grason-Stadler model 700) connected to the two spouts. Shock levels ranged from 1.6 mA at 350 V to 16 mA at 680 V. A light-emitting diode (LED) mounted just above the spout was turned on whenever the shock was on and turning the LED off signaled that the shock was over and that the animal could return to the spout.

The human subjects were tested by removing the cage and having them sit on a chair in the sound chamber in front of the loudspeaker. The sound field in the area occupied by a subject's head was carefully measured and the chair, which was small, did not protrude into the sound field. A subject was given a hand-held button and instructed to press it whenever he or she heard a tone.

C. Acoustical apparatus

Sine waves were generated by a signal generator (Krohn–Hite model 2400 AM/FM phase lock generator) that was calibrated daily with a frequency counter (Fluke 1900 A). The electrical signal was gated on and off with a rise/fall gate (Coulbourn S84-04), bandpass filtered at 1/3 octave above and below the test frequency (Krohn–Hite 3550 filter), attenuated (Hewlett–Packard 350D attenuator), amplified (Crown D75), and connected to a loudspeaker. The electrical signal to the loudspeaker was monitored with an oscilloscope for signs of distortion. In addition, the linearity of the attenuator was verified over the range of attenuation used for threshold testing at each frequency by measuring its output voltage and the resulting sound pressure level.

For frequencies 32 Hz and higher, a loudspeaker was placed approximately 1.0 m in front of the cage and oriented toward the position occupied by the animal's head when it was drinking from the water spout. The distance of the loudspeaker was varied by as much as 0.5 m as needed to achieve an even sound field of sufficient intensity around the monkey's head. The loudspeakers used were a 15-in. (38-cm) woofer for frequencies below 2000 Hz and a Foster ribbon tweeter for frequencies of 2000 Hz and higher.

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 same sound-level reading was obtained regardless of the orientation of the microphone. Thus, by taking advantage of the standing waves, it was possible to obtain undistorted tones at high intensities. However, because placement of the monkey cage was limited by its size, it was not always possible to place it in the most intense portion of the sound field as was the case with the human subjects.

Pure tone thresholds for monkeys and/or humans were obtained at octave intervals from 4 Hz to 32 000 Hz with additional thresholds at 12.5, 25, 18 000, 20 000, 22 400, 26 000, and 40 000 Hz. Tones were a 3.0-s pulse, gated on at zero crossing, with rise/fall times of 50 ms for 8 Hz–1 kHz, and 10 ms for 2 kHz–40 kHz.

The sound pressure level (SPL re 20 μPa) was measured daily with a Bruel & Kjaer (B&K) 1/4-in. (0.64-cm) microphone (B&K 4135), preamplifier (B&K 2618), microphone amplifier (B&K 2608), and filter (Krohn–Hite 3550) set to pass one octave above and below the test frequency. The measuring system was calibrated with a pistonphone (B&K 4230). Sound measurements were taken by placing the microphone in the position occupied by the animal's head and pointing it directly toward the loudspeaker (0° incidence). Care was taken to produce a homogeneous sound field (± 1 dB) in the area occupied by the animal's head and ears while it was drinking from the waterspout. As a precaution against transmission of low-frequency substrate vibrations to the animals through the floor, 8-cm-thick foam pads were placed under the 15-in. (38-cm) woofer used for low-frequency testing and under the legs of the animal's testing cage. Furthermore, each frequency was examined for the presence of overtones using a spectrum analyzer (Zonic 3535) connected to the output of the microphone amplifier during sound calibration with the microphone amplifier filter setting on linear (i.e., unfiltered signal). Care was taken to ensure that any overtones present were at least 40 dB below the fundamental frequency and at least 20 dB below an animal's threshold. This procedure was of particular importance when testing low frequencies at high intensities.

D. Psychophysical procedure

A thirsty animal entered the test cage and drank from the waterspout. Tones were presented for 3 s at random intervals and followed at their offset by mild electric shock delivered through the spout. The animal quickly learned to avoid the shock by breaking contact with the spout whenever it heard a tone. The shock was adjusted for each individual to the lowest level that would reliably produce an avoidance response. The mildness of the shock was attested by the fact that none of the animals developed a fear of the spout as they returned to it without hesitation after the shock had been delivered.

Test sessions were divided into 3.0-s trials separated by 2.0-s intertrial intervals. Each trial contained either a continuous tone (''warning'' signal) or silence (''safe'' signal) with 22% of the trials containing a tone. A response was recorded if an animal broke contact for more than half of the last 150 ms of a trial (as determined by the microcomputer). The response was classified as a ''hit'' if the trial contained a tone and as a ''false alarm'' if no tone had been presented. Both the hit and false alarm rates were determined for each block of 5–7 warning trials (which also included approximately 25 safe trials) for each stimulus condition. The hit rate was corrected for false alarms according to the formula: performance = hit rate − (false alarm rate × hit rate), with the hit and false alarm rate expressed as percentages. This measure proportionately reduces the hit rate by the false alarm rate observed under each stimulus condition and varies from 0 (no hits) to 1 (100% hit rate and 0% false alarm rate).

Three additional steps were taken to reward the animals for correct performance. First, the duration of the shock, which determined the time the animal had to pause before it could return to the spout after a warning trial, was 0.25 s following a hit (i.e., the animal correctly broke contact when a tone was presented), but was increased to 4.0 s following a miss (i.e., the animal failed to break contact when a tone was presented). Second, an extra amount of water was delivered to the spout when the animal returned to it following a hit in order to reward the animal for correctly breaking contact with the spout and to make up for the water it lost by responding. Finally, the water flow was shut off for 2 s following a false alarm (i.e., when the animal broke contact with the spout when no tone was present) to discourage false positives.

Absolute thresholds were determined by reducing the intensity of a tone in successive blocks of 5–7 warning trials until the animal no longer responded to the signal above the 0.01 chance level (binomial distribution). Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity in 5-dB increments extending from 10 dB below to at least 10 dB above the estimated threshold. Threshold was defined as the intensity corresponding to a performance of 0.50. Threshold testing for a particular frequency was considered complete when the thresholds obtained in at least two different sessions were within 3 dB of each other. Once a complete audiogram had been determined, each threshold was rechecked and further testing was given if the new threshold differed from the previous one by more than 3 dB.

Human subjects were tested by instructing them to hold down the button and release it whenever they heard a tone. Feedback was given on each tone trial by turning on a light at the end of each warning trial. Thus, the trials were presented in the same manner as with the monkeys except that shock was not used.

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

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

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.

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

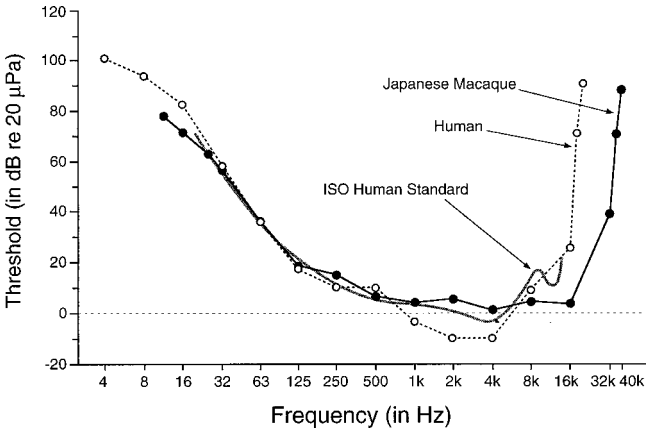

FIG. 2. Average free-field audiogram of three Japanese macaques and seven humans compared with the ISO free-field threshold curve (ISO, 1961). Note the similarity in low-frequency hearing between humans and Japanese macaques.

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 elephant, have even poorer high-frequency hearing than humans (Heffner and Heffner, 1982).

Low-frequency hearing, on the other hand, is correlated with high-frequency hearing such that animals with good high-frequency hearing usually have poor low-frequency hearing and vice versa [Fig. 3(b)]. However, there appears to be a floor effect such that the correlation differs between mammals depending on whether or not they hear well at low frequencies (e.g., Heffner and Heffner, 1985; Koay *et al.*, 1997, 1998). That is, among mammals with relatively poor low-frequency hearing (e.g., those that do not hear below 60 Hz), high- and low-frequency hearing are strongly correlated ($r=0.90, p<0.0001$) with low-frequency hearing shifting on average by 4.6 octaves for each octave change in high-frequency hearing. On the other hand, for mammals with good low-frequency hearing (e.g., those that do hear below 60 Hz), not only are high- and low-frequency hearing less strongly correlated ($r=0.67, p<0.0014$), but low-frequency hearing now shifts by only 0.44 octaves for each octave change in high-frequency hearing (see Koay *et al.*, 1997, 1998).

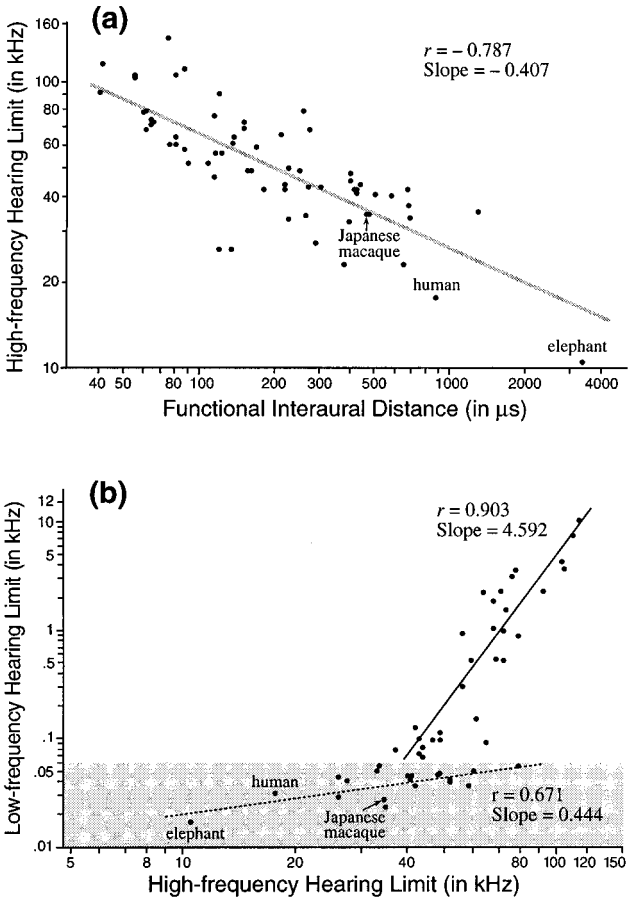

FIG. 3. (a) High-frequency hearing limit (highest frequency audible at 60 dB SPL) as a function of functional interaural distance (the number of microseconds required for a sound to travel from one auditory meatus to the other). This relationship is explained by the fact that mammals with small heads and pinnae require better high-frequency hearing than larger mammals in order to use binaural spectral and pinnae cues to localize sound. (b) Relation between the highest and lowest frequencies audible at 60 dB SPL. Although low-frequency hearing is highly correlated with high-frequency hearing, the slope of this relationship is much shallower among species with good low-frequency hearing, suggesting that there is a floor effect that limits improvement in low-frequency hearing. (Both figures modified from Koay *et al.*, 1998.)

Because both humans and Japanese macaques have good low-frequency hearing, they fall within the group for which changes in high-frequency hearing result in relatively small changes in low-frequency hearing. As a result, although their high-frequency limits are an octave apart, their predicted low-frequency limits are only 6 Hz apart—26 Hz for humans and 32 Hz for Japanese macaques. Moreover, the actual low-frequency limits of 31 Hz for humans and 28 Hz for the Japanese macaque are not significantly different from the predicted values. Thus, the human hearing range is not unusual when compared with those of other mammals.

B. Free-field versus headphone audiograms

The free-field audiogram of Japanese macaques is compared in Fig. 4 with two previous audiograms that were obtained using headphones, one using circumaural headphones (Owren *et al.*, 1988), the other using insert earphones (Smith

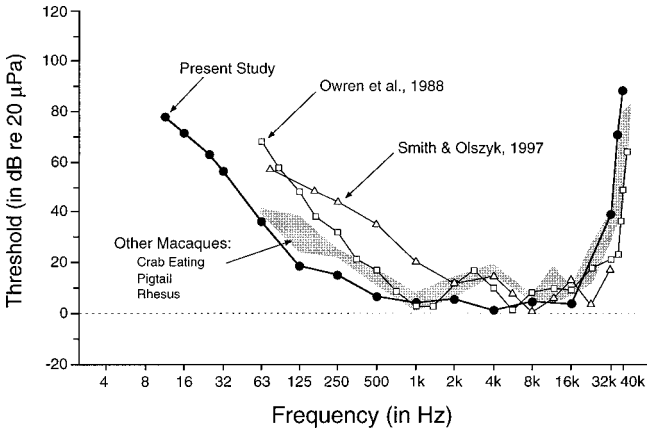

FIG. 4. Free-field audiogram of the Japanese macaque (present study) compared to previous Japanese macaque audiograms using headphones (Owren *et al.*, 1988, and Smith and Olszyk, 1997). Also shown is the range of thresholds for three other species of macaques (shaded area): rhesus macaque *M. mulatta* (Pfingst *et al.*, 1978), Philippine or crab-eating macaque, *M. irus*, and pigtail macaque, *M. nemistrina* (Stebbins *et al.*, 1966).

and 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.

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