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HEARING IN PRIMITIVE PRIMATES: SLOW LORIS (*NYCTICEBUS COUCANG*) AND POTTO (*PERODICTICUS POTTO*)[1]

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The behavioral audiograms of slow loris and potto were determined by the technique of conditioned suppression, and the auditory characteristics of Prosimians then estimated by combining the data with that of bushbaby. It is concluded that high-frequency hearing, low-frequency sensitivity, and total area of the audible field are well correlated with phyletic level, while lowest threshold and best frequency are not. Furthermore, the relation of high-frequency hearing to ecological demands for accurate sound localization is supported.

For almost a century it has been known that human hearing differs markedly from that of many other animals (e.g., Galton, 1883). But until recently, the nature and extent of this difference and the evolutionary transformation that brought it about have been mostly a matter of conjecture (cf. Masterton, Heffner, & Ravizza, 1969; von Békésy & Rosenblith, 1951). Due almost entirely to technical advances in behavioral testing, it has now become possible to determine the auditory capacity of a wide variety of mammals, including some that are known to be close approximations to the now-extinct animals in man's ancestral lineage. From these data it is possible to gain some idea of when, how, and in response to what selective pressures human auditory characteristics began to appear.

One of the pivotal stages in the mammalian segment of mankind's evolution occurred with the appearance of the first Primates. The Order of living (and fossil) Primates is usually subdivided into two suborders, Prosimians (lemurs, lorises, tarsiers) and Anthropoids (monkeys, apes, men; cf. Simpson, 1945). Since it is Prosimians which are the more primitive (Osman-Hill, 1953), extant members of this group provide the best approximation to the most ancient Primate ancestors of mankind. It follows that knowledge of their auditory characteristics is pertinent to questions concerning the evolution of anthropoid hearing in general, and human hearing in particular (Figure 1).

Of the three extant groups of Prosimians, two are impractical choices for psychological study: Lemurs are rarely available and tarsiers are too divergent to allow phylogenetic interpretation. For this reason, representatives of the lorises have been selected as subjects for these experiments.

The lorises themselves are composed of a single family, Lorisidea, of which there are two subfamilies, Galaginae and Lorisinae. Hearing in one of the two genera of Galaginae has already been described (*Galago senegalensis*, Heffner, Ravizza, & Masterton, 1969). This report describes the characteristics of two of the four genera in the remaining subfamily, Lorisinae: the slow loris and the potto.

Finally, due to the fact that many morphological and behavioral differences distinguish Lorisinae and Galaginae despite their close affinity, the combination of results from this report and the previous one provides a means for examining some popular explanations of the variation in mammalian hearing unconfounded by great differences in phylogeny. Therefore, this report has four goals: (*a*) to describe the auditory characteristics of the potto and slow loris; (*b*) to compare them with each other and deduce the characteristics of the

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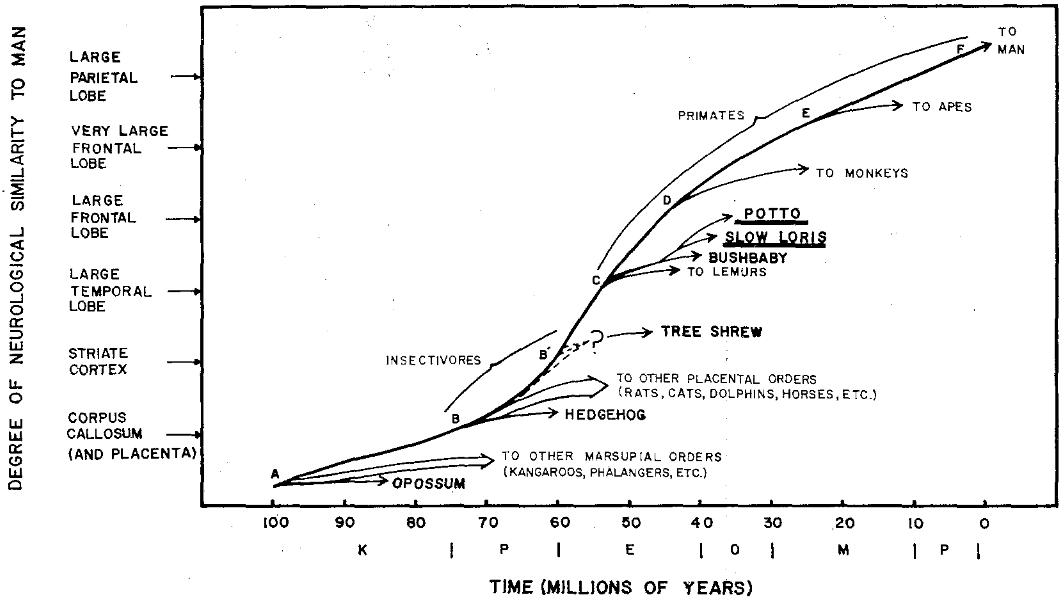

FIG. 1. Phylogenetic relationship between Prosimians and some other extant mammals. (Note that Man's common ancestry with Prosimians [Point C] is more remote in time than with higher Primates [Point D], but more recent than with any other living mammal [Points A, B, B']. K: Cretaceous; P: Paleocene; E: Eocene; O: Oligocene; M: Miocene; P: Pliocene [modified from Masterton et al., 1969].)

subfamily, Lorisinae; (*c*) to compare the Lorisinae with Galaginae and deduce the characteristics of the family, Lorisidea; and finally, (*d*) to compare the characteristics of Lorisidea to those of more primitive mammals, higher Primates, and Man.

METHOD

Details of the behavioral apparatus, the sound production, measuring, and monitoring equipment, and the procedures for training and testing primitive mammals are described below. Briefly, the animals were trained to lick a water spout in order to obtain a food reward. When the lick rate became stable, a pure tone was presented for 10 sec. and, at its offset, a mild shock was delivered to the animal's feet. After a few repetitions of the tone-shock pair, the animal would stop licking whenever an audible tone was presented. In test trials this stoppage or suppression of licking was used as evidence that the animal perceived a tone.

Subjects

Two wild-born pottos (*Perodicticus potto*), one male and one female, and two wild-born slow lorises (*Nycticebus coucang*), one male and one female, were used as subjects. Although it was not possible to determine their exact ages, they appeared to be young adults. Each subject received routine otological examinations during the course of behavioral testing.

Behavioral Apparatus

The animals were tested in an oval cage 36 × 18 × 24 in. with floors and walls made of $\frac{3}{16}$-in. brass rods and the ceiling made of screen mesh. A water spout connected to a water bottle was placed at one end of the cage along with a pellet dispenser that was capable of delivering food pellets into a cup on the cage floor beneath the water spout. To record the number of times an animal licked the water spout, a drinkometer (Grason-Stadler Model E4690A) was connected between the water spout and floor bars.

Training the animals to lick a water spout insured that the animals' heads were in a reasonably constant position relative to the speaker. This feature of the behavioral apparatus is an important one for establishing confidence in the results: It minimizes variations in sound-pressure level due to changes in the locus or attitude of the animals' ears.

The cage was mounted on 1-in.-thick fiberglass pads to minimize vibration transmission at low frequencies. A pan of pelleted cellulose (Pel-E-Cel) placed beneath the cage decreased sound reflections. The entire apparatus was placed in a burlap-draped acoustical chamber (IAC, Model 1202A).

A shock-generating apparatus was connected to the wall bars and floor bars of the cage. This apparatus was capable of delivering a brief (300 msec.) alternating constant-current shock to the animals' feet. During training shock levels were varied .50–1.75 ma. depending on the short-term performance of the subject. By this means reliable suppression of licking in the presence of a tone was quickly achieved.

Acoustic Stimulus Apparatus

To produce pure tones, sine waves from an oscillator (Hewlett-Packard, 200CD) were led first to an electronic switch (Grason-Stadler, Model 829E), then to an attenuator (Hewlett-Packard, 350D), and finally to a wide-range speaker (University 312). The speaker was mounted on a 1-in.-thick piece of fiberglass 7 in. directly in front of the water spout. This sound system proved to be capable of delivering undistorted tones from 30 Hz. to more than 70 kHz. at an intensity near 70-db. SPL.

The electrical signal was electronically keyed with a rise and decay time of 25 msec. for all frequencies except the very lowest ones. For frequencies less than 500 Hz., the rise time was set still slower (50, 100, or 250 msec.). By adjusting the rise and decay times to span at least 10 full cycles of the signal regardless of its frequency, onset and offset artifacts were successfully eliminated. In addition to these precautions the electrical signal to the speaker was continuously monitored with an oscilloscope for spurious signals.

The entire sound system was calibrated, and true sound-pressure levels were measured with a Bruel and Kjaer system consisting of a microphone amplifier (Model 2604), a ½-in. or ¼-in. condenser microphone (Models 4133 or 4136), and a band-pass filter (Model 1612). Calibration was accomplished by placing the microphone in the position where the animals' heads had been and pointing it directly at the speaker (zero-degree incidence). For most of the frequencies, the microphones were not sensitive enough to measure the intensity of the tone at threshold level so that it was necessary to measure a more intense tone and then extrapolate to the intensity at threshold. Zero-degree incidence, free-field correction curves provided by Bruel-Kjaer were used to convert the meter readings to db. SPL. Throughout this report sound intensities are scaled in decibels re 2×10^{-4} dynes/cm² SPL.

Psychophysical Procedure

Training. The training procedure consisted of two parts. First, the animal was trained to lick the water spout in order to receive food pellets (Noyes, 45 mg; "sucrose," "banana," "dog," "dextrose," in equal proportions). During training the rewarding pellets were delivered on a variable ratio (VR) schedule. This training provided a reliable rate of about three licks per sec. for most of each 1-hr. daily session.

In the second stage of training, after a steady rate of licking had been achieved at a low-reward schedule (e.g., VR 2%), the animal was presented with an obviously suprathreshold pure tone for 10 sec. At the offset of the tone, a shock was delivered through the bars of the floor. After several tone-shock pairings, the animal ceased licking at the onset of a suprathreshold tone and did not begin to lick again until the tone had been terminated and the shock had been received.

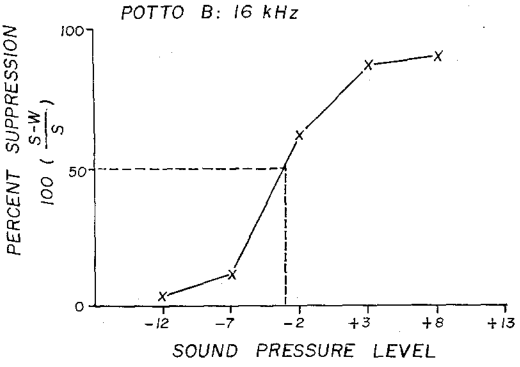

FIG. 2. Change in lick rate as a psychophysical function of intensity. (Performance axis is scaled so that perfect suppression [tone was invariably heard] yields a score of 100 and no suppression [tone was never heard] yields a score of 0. Dashed lines show threshold calculation.)

Threshold testing. At each frequency octave, threshold testing was conducted in two ways: First, the threshold was estimated by a method of limits, then a second and exhaustive determination was made by the method of constant stimuli.

In the first or exploratory stage of threshold testing, the intensity of the tone was gradually decreased in steps of 5-db. on each successive trial until an obvious failure to cease licking was observed. The intensity of the tone was then increased until an obvious cessation once more occurred. By repeating this procedure a number of times the threshold could be readily estimated.

In the second stage of testing, tones with intensity levels at 5 db. increments extending from at least 10 db. below to 10 db. above the previously estimated threshold were presented in random order. Because the animals were practiced listeners, a smooth psychophysical curve of performance as a function of intensity usually could be plotted after 10 presentations at each of the preselected levels (Figure 2). The data reported here are the results of tests of the second kind only; that is, the results of the constant-stimuli method.

To insure that an animal was not responding to artifacts in the sound system that might have escaped the keying and monitoring systems, sham trials were included in each session. The sham trials were identical to the test trials except that the signal generator was either entirely disconnected from the circuit, or the signal was attenuated at least 50 db. below the animal's estimated threshold, and the trial did not include a shock. Since significant suppression never occurred in these trials, the authors feel confident that the sound system was free of artifact. It should be emphasized, however, that all test trials included a shock, even at intensities which eventually proved to be subthreshold.

Analysis of Data

The technique of conditioned suppression, as it is used for the assessment of sensory thresholds, hinges on interpreting a change in the rate of response—in this case the rate of licking—as evidence that the subject has detected the stimulus. The many practical and theoretical questions surrounding the use of this technique have been treated at length elsewhere (e.g., Estes & Skinner, 1941; Hendricks, 1966; Kamin, 1967; Sidman, Ray, Sidman, & Klinger, 1966).

For convenience a unitless measure of performance has been chosen which is a joint function of the number of licks in the 10-sec. warning period in which the tone was presented—designated W—and the number of licks in the 10-sec. safe period immediately preceding the warning period—designated S—according to the formula:

Discriminatory performance

$$= 100\left(1 - \frac{W}{S}\right) = 100\left(\frac{S - W}{S}\right).$$

For a trained animal this measure varies from values near +100 to values near 0. A value of +100 signifies perfect suppression and is interpreted as indicating that the stimulus was heard by the subject whenever it was presented. A value of 0 signifies no change in the rate of licking upon presentation of the stimulus and is interpreted as indicating that the stimulus was not heard by the subject. Performance values between 0 and +100 are interpreted as indicating that the subject may have heard, or only occasionally heard, the stimulus. For the construction of audiograms, a performance value of +50 was (arbitrarily) chosen as threshold. Because the psychophysical functions show an abrupt change in performance with small changes in intensity, a less conservative definition of threshold, such as a performance value of +20, results in only a small (4-db.) reduction in the estimate of the threshold.

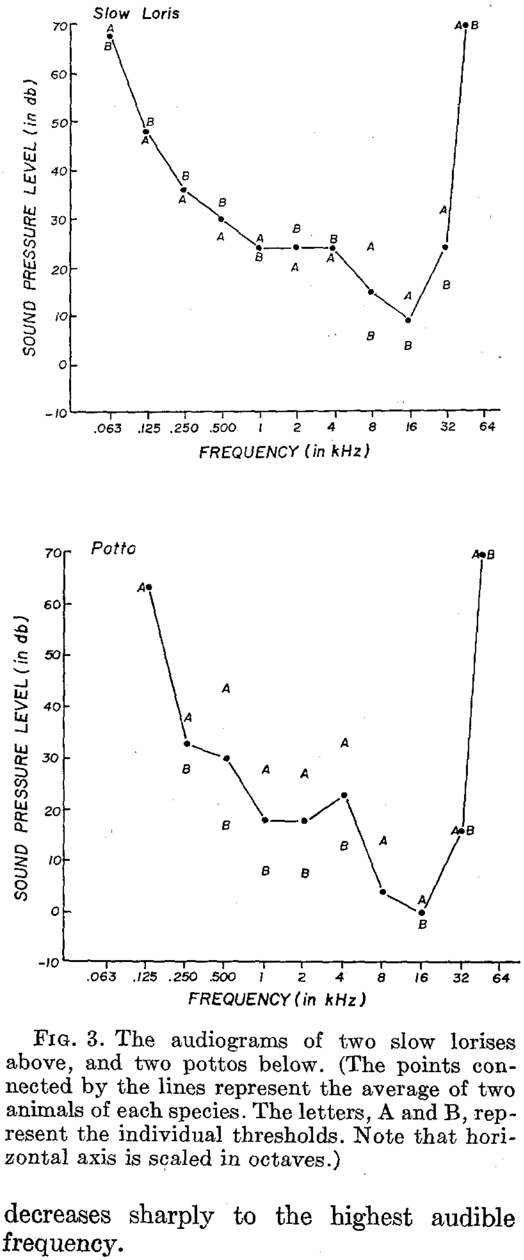

FIG. 3. The audiograms of two slow lorises above, and two pottos below. (The points connected by the lines represent the average of two animals of each species. The letters, A and B, represent the individual thresholds. Note that horizontal axis is scaled in octaves.)

RESULTS

Slow Loris and Potto

The audiograms of the two slow lorises and two pottos are shown in Figure 3. The audiograms exhibit the characteristic shape of audiograms of any animal. There is a gradual increase in sensitivity (decrease in threshold) as frequency increases from the lower ranges; it reaches a relatively broad range of "best" frequencies; and finally, decreases sharply to the highest audible frequency.

In the slow loris audiogram (top graph, Figure 3), it can be seen that the individual variation is quite small at low frequencies and increases at the higher frequencies. This increase in variation with increasing frequencies is a usual feature of audiograms. Individuals within every species (including humans) almost always vary more at high frequencies than at low ones. This variation at high frequencies is usually due to individual differences in the conducting apparatus in the middle ear or in the elasticity of the basilar membrane. Since both effects are closely correlated with age, and the age of the wild-born lorises was indeterminable, no further discussion of the variation seems appropriate.

However, Figure 3 (bottom graph) shows that the two pottos differ more at middle frequencies than at high frequencies. Since this type of variation is quite unusual, it deserves special comment.

To begin with, the variance between the two pottos is probably real, i.e., it is not a result of obvious measurement errors. This conclusion is supported by two facts. First, the forms of the psychophysical functions were quite comparable for each of the two animals at each frequency. The probability of spontaneous suppressions (false-positive responses) was negligible in each case. Second, attempts to make A's thresholds conform more closely to B's were without success. At the end of behavioral testing, it was tempting to consider Potto A as somehow intrinsically inferior to Potto B, possibly due to injury or disease, but careful otological examination of the ears failed to reveal any sign of infestation, infection, or deformity in either animal. Thus, there is no reason to believe that Potto A's insensitivity relative to Potto B was the result of disease, injury, or deformity to either the outer or middle ear.

In clinical assessment of human hearing, "deficits" confined to the lower and middle frequencies are usually interpreted as evidence of damage in the central auditory system, but again, we have no evidence to warrant such a conclusion in this case. Despite repeated observation for over a year, Potto A showed no neurological signs whatever and, at sacrifice, its brain was free from obvious lesion. Thus, there is no more reason to believe that Potto A is somehow anomalous by being "defective" than there is to believe that Potto B is anomalous by being somehow "superior." For the purposes of comparison at the present time, therefore, the differences between the two pottos shown in Figure 3 must be interpreted as representing the true variation of hearing in the natural population of pottos.

TABLE 1

AUDITORY CHARACTERISTICS OF LORISINAE COMPARED WITH MAMMALIA

Taxon	High-frequency cut-off	Threshold at 1 kHz.	Lowest threshold	Best frequency	Area of audible field
Loris	48	24	9	16	398
Potto	43	18	−2	12	430
Lorisinae	45	21	5	14	414
Mammalia[a]					
Average	52	3	−2	12	402
SD	10	22	9	10	180

[a] The mammalian averages and standard deviations are based on samples that are within 5% of the true distribution of mammalian genera per order, except for Primates (overweighted with eight genera instead of one) and Rodentia (underweighted with three genera instead of seven).

Auditory Characteristics of Lorisinae

Table 1 allows comparison of pottos with lorises on five arbitrary parameters extracted from the audiograms in Figure 3. The five parameters are (*a*) "high-frequency cut-off" (in kHz.)—defined as the highest frequency that can be heard at 70-db. SPL; (*b*) "low-frequency sensitivity" (in db.)—the threshold at 1 kHz.; (*c*) "lowest threshold" (in db.)—the intensity coordinate of the lowest point on the audiogram; (*d*) "best frequency" (in kHz.)—the frequency coordinate of the lowest point on the audiogram; and (*e*) "area of the audible field" (in db. per octave)—the area of the frequency-intensity plane bounded by the audiogram below and the 70-db. horizontal above. Details of the definitions of these parameters, the reasons for choosing them and the distribution of each parameter among mammals are given elsewhere (Masterton et al., 1969).

By comparing the first two rows of Table 1, it can be seen that the auditory characteristics of slow loris and potto are quite similar in spite of individual variation within the pottos. The slow loris has a slightly higher high-frequency cut-off, but the potto is a bit more sensitive throughout the rest of the frequency range. Furthermore, slow loris and potto are each within one standard deviation of the mammalian mean for every parameter except lowest threshold where slow loris is higher by slightly more than one standard deviation. Thus, neither slow loris nor potto, nor the two combined as Lorisinae, are particularly unusual mammals.

But the way that these animals differ from the mammalian mean is noteworthy. For example, the high-frequency cut-off is less than the mammalian mean. The authors have shown elsewhere that the best correlate of high-frequency cut-off among mammals is the inverse of the functional distance between the two ears (Masterton et al., 1969). That is, animals with wide-set ears have low high-frequency cut-offs while animals with close-set ears have high cut-offs due to the demand for accurate sound localization. Thus, it is interesting to note that the ear separation of the Lorisinae (71.9 mm.) is greater than the mean ear separation of mammals (65.3 mm.) which is exactly the direction that would be anticipated on the basis of the previous correlation (Masterton et al., 1969).

Finally, Table 1 shows that the Lorisinae are less sensitive at low frequencies than the mammalian mean. As will be seen below, part of this deviation is explainable by their "primitiveness" alone. However, another part of this deviation may be due to the bias in the mammalian average resulting from an underweighting of Rodentia in the sample from which it was estimated. Since by present estimates, rodents as a whole are likely to prove to be extremely insensitive to low frequencies, their absence results in a spuriously low estimate of the mammalian average for low-frequency threshold. Therefore, we place little weight on the apparently poor low-frequency sensitivity of Lorisinae relative to other mammals at the present time.

Auditory Characteristics of Lorisidea

The first two rows of Table 2 allow comparison of the auditory capacities of the Lorisinae (loris, potto) with the Galaginae (bushbaby; cf. Heffner et al., 1969). Together, the Lorisinae and Galaginae represent the two subfamilies of the family, Lorisidea. The characteristics of this higher level taxon are given in the third row of Table 2. Since Lorisidea is the only group of Prosimians on which audiograms are now available, the entries in the third row of Table 2 are also the best estimates of the auditory characteristics of Prosimian Primates.

TABLE 2

AUDITORY CHARACTERISTICS OF LORISIDEA COMPARED WITH PRIMATES AND MAMMALIA

Taxon	High-frequency cut-off	Threshold at 1 kHz.	Lowest threshold	Best frequency	Area of audible field
Lorisinae	45	21	5	14	414
Galaginae	65	30	3	8	447
Lorisidea	55	26	4	11	430
Primates[a]	40	9	−2	12	490
Mammalia[b]					
Average	52	3	−2	12	402
SD	10	22	9	10	180

[a] The averages for Primates are slightly biased by the inclusion of two many hominoids (two genera instead of none or one).

[b] See Footnote a in Table 1.

In a comparison of the Lorisinae with the Galaginae, four out of the five auditory parameters show no obviously significant difference between the two subfamilies at the present time. The only exceptional parameter is high-frequency cut-off. Though the Lorisinae appear to be superior at low frequencies (compare values for "Threshold at 1 kHz." in Table 2), the Galaginae are actually more sensitive at .500 kHz. and .125 kHz. Thus, the apparent low-frequency superiority of Lorisinae is probably not a real one. Similarly, the sensitivity of the Galaginae at 16 kHz. and 32 kHz. is only slightly less than their sensitivity at 8 kHz. and thus, best frequency for both the Lorisinae and Galaginae ranges from 8 kHz. to about 16 kHz. The lowest threshold for the two subfamilies does not differ much at all and the somewhat larger area of audible field of the Galaginae is a direct result of their high-frequency superiority. It is only along the dimension of high-frequency cut-off that the Galaginae differ from the Lorisinae significantly. Since the Galaginae have a smaller mean ear separation than the Lorisinae (69.9 mm. vs. 71.9 mm.), the difference in high-frequency hearing again seems to be adequately explained by selective pressure for accurate sound localization.

Turning now to comparisons between higher level taxa, Table 2 shows two notable differences between primitive Primates and Primates as a whole. First, Lorisidea have a higher than average high-frequency cut-off. Once more, this difference is correlated with their more closely set ears as is the difference between the Galaginae and Lorisinae themselves. Second, Lorisidea are less sensitive to low frequencies than the average for Primates. Since the Primate average is only slightly biased by the presence of one or two too many hominoids, this difference between primitive Primates and higher Primates will probably prove to be a real one. Other than the relation of low-frequency sensitivity to primitiveness or "recency of common ancestry with Man," which is reopened below, the significance of this difference remains elusive.

DISCUSSION

From the data in Table 2, it is difficult to avoid the impression that the subfamilies

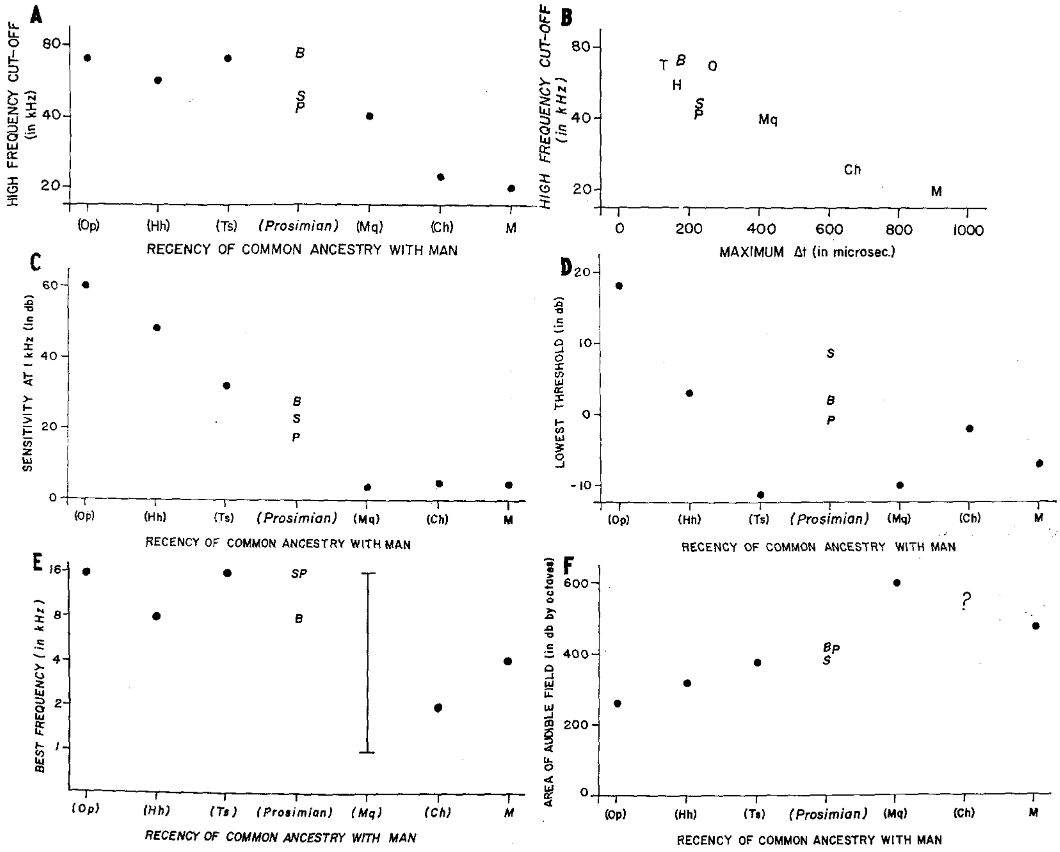

FIG. 4. Comparison of animals in a phylectic sequence on five auditory dimensions and the relation of "high-frequency hearing" to maximum interaural-time-disparity. (A: high-frequency cut-off [$r = -.84, p < .01$]; B: relation of high-frequency cut-off to maximum Δt [$r = -.87, p < .005$]; C: sensitivity [threshold] at 1 kHz. [$r = .95, p < .01$]; D: lowest threshold [$r = -.63, p > .05$]; E: best frequency [$r = -.62, p > .05$]; F: area of audible field [$r = .81, p < .01$]. OP or O, opossum; Hh or H, hedgehog; Ts or T, tree shrew; Bb or B, bushbaby; S, slow loris; P, potto; Mq, macaque; Ch, chimpanzee; M, man. In Graph B, "maximum Δt" is the maximum disparity in time of arrival of sound waves at the two ears. Vertical line above Mq in Graph E brackets the range of best frequencies reported for a single genus of monkeys [Macaca]. Query in Graph F locates the best estimate for chimpanzee based on an incomplete audiogram.)

of the family Lorisidea have highly similar audiograms in spite of individual variation. Low-frequency sensitivity, lowest threshold, best frequency, and area of the audible field are nearly the same. Only high-frequency cut-off is obviously different. Since the close similarity in four out of five auditory characteristics stands in marked contrast to the many morphological and behavioral differences that distinguish Lorisinae and Galaginae (Osman-Hill, 1953), the conclusion can be drawn that these four characteristics of hearing are relatively conservative behavioral traits. This conclusion in turn implies that (*a*) the variation in these auditory characteristics among more diversified mammals may be due more to wide differences in their ancestral lineage than to differences in their present ecology; and (*b*) these four auditory characteristics evolve relatively slowly, in response to persistent selective pressure extending over long time periods. Of the five auditory characteristics considered here the only exception to this conclusion is the extended high frequency range of the bushbaby. This characteristic is apparently much less conservative than the others, but it seems to be adequately accounted for in terms of selective pressure for accurate sound localization.

Turning finally to the evolution of human hearing, Figure 4 allows assessment of the effect of refining the Prosimian estimates by adding the potto and slow loris data to the previous bushbaby data. It can be seen that the two new data points fall near obvious regression lines in four out of six graphs. The large size of the correlation coefficient along with the small probability of Type I error in each of these four graphs suggest that the previously discovered relationships are reasonably precise and probably not a matter of chance. In the two remaining graphs, lowest threshold in Figure 4d and best frequency in Figure 4e, adding the loris and potto data provides little useful information because no obvious regression line exists either before or after the addition. Furthermore, these two characteristics that show a large degree of variance which remains uncorrelated with phylogeny alone, are also the two which show the largest amount of intrageneric variance (Masterton et al., 1969). For example, the best frequency of a single genus of monkeys, Macaca, has been reported at four different frequencies spanning four octaves. Therefore, once the possibility of measurement error is reduced, it is not unlikely that even these parameters might show a clear relationship with ancestry.

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