

The Evolution of Human Hearing

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Five descriptive parameters of hearing—high-frequency and low-frequency sensitivity, lowest threshold, best frequency, and area of the audible field—are compared statistically, first, among mammals in general, and, then, among seven animals selected to approximate a phylogenetic sequence of man's ancestors. Three potentially explanatory parameters—body size, maximum binaural time disparity, and recency of common ancestry with man—are also explicitly included in the analysis. The results show that: high-frequency hearing (above 32 kHz) is a characteristic unique to mammals, and, among members of this class, one which is commonplace and primitive. Being highly correlated with functionally close-set ears, it is probably the result of selective pressure for accurate sound localization. Low-frequency hearing improved markedly in mankind's line of descent, but the kind and degree of improvement are not unique among mammalian lineages. High sensitivity developed in the earliest stages of man's lineage and has remained relatively unchanged since the simian level. The frequency of the lowest threshold has declined in Man's lineage—the greatest drop probably occurring during the Eocene. The total area of the audible field increased until the Eocene and has decreased since then.

INTRODUCTION

IN the course of experiments on the perceptual contributions of the mammalian cerebrum, we have had occasion to test the auditory abilities of some of the most primitive mammals now in existence. The results of these tests have revealed that there are several dimensions of hearing on which mammals are either strikingly similar or strikingly dissimilar. Since these dimensions may prove to be of importance in reconstructing the evolution of human hearing, we have collected the results of comparable tests in other animals and arranged the array of results in a manner that allows statistical comparison along three other dimensions, one phylogenetic and two morphological.

Because of the generality of some newly invented behavioral techniques, we have been able to include data from four species of primitive mammals: opossum (*Didelphis virginiana*), hedgehog (*Hemiechinus auritus*), tree shrew (*Tupaia glis*), and bushbaby (*Galago senegalensis*) (Ravizza *et al.*, 1969a,b; Heffner *et al.*, 1969a,b). Our choice of these particular animals as experimental subjects relies entirely on morphological and paleontological conclusions regarding their phylogenetic relationship (Fig. 1). Since it is reasonably likely that an ordered sequence in time was formed by the

common ancestry of man with each of these four animals in turn, comparison of their auditory characteristics with each other and with monkeys, apes, and men provides information relevant to questions concerning the evolution of human hearing.

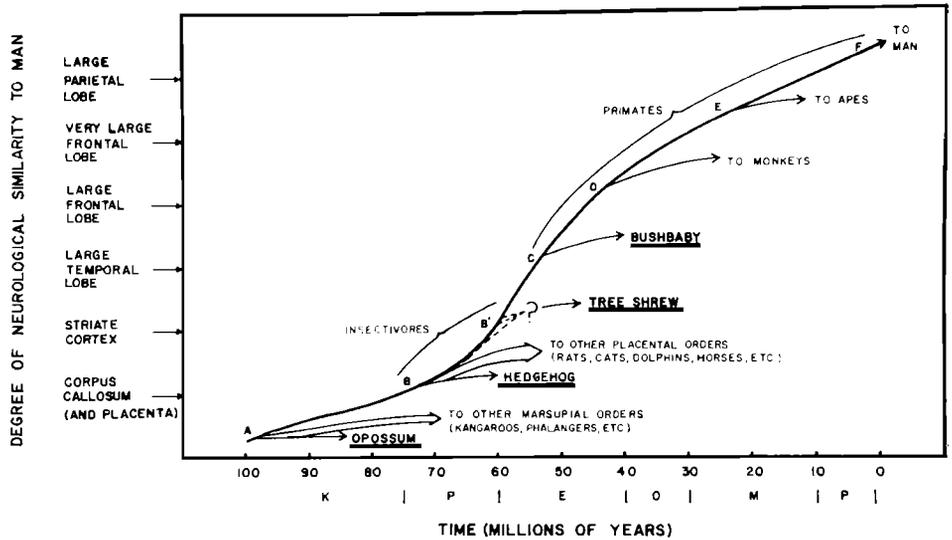
I. METHOD

In this report, two separate statistical comparisons are made among mammals for each of five quantifiable features of hearing: high-frequency cutoff, low-frequency sensitivity, lowest threshold, best frequency, and total area of the audible field. *First*, the distribution of each of these auditory parameters has been derived for all mammals in which comparable data are available. These distributions provide the basis: (1) for comparing mammals with nonmammals; (2) for estimating the breadth of variation of the parameters among mammals so that significant differences among lower taxa can be recognized; and (3) for correlating the auditory parameters with morphological parameters.

Second, the values of each auditory parameter have been arranged according to phyletic level for seven mammals that are the best available approximation of a phylogenetic sequence. These arrays provide the basis: (1) for demonstrating the significant differences between levels of the phyletic sequence and (2) for recognizing the evolutionary changes in hearing that are

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FIG. 1. Phylogenetic relationship between some living mammals and mammals in Man's ancestral lineage. A, B, B', C... represent ancestors whose characteristics can be inferred through comparison of animals in phyletic sequence.



most likely to have taken place during the mammalian segment of man's ancestral lineage.

The primary data in this report are standard audiograms that circumscribe the intensity-frequency boundary of pure-tone audibility in 22 different mammals. The audiograms have been drawn from behavioral experiments in our own laboratory and also from the published reports of others.

A. Audiograms of Primitive Mammals

The audiograms of primitive mammals have been obtained through the technique of conditioned suppression (Estes and Skinner, 1941; Kamin, 1967). A detailed description of the apparatus and general procedure for testing sensory capacities by this technique is available elsewhere (Sidman *et al.*, 1966; Hendricks, 1966). In one of our adaptations of this technique for primitive mammals, the subjects are trained first to lick a water spout. This response is maintained by an occasional reward of dry food. After a few daily hour-long sessions, the animal licks the spout at a rapid rate, only momentarily interrupting its licking to eat the rewarding food pellet. This persistent licking provides the background upon which hearing tests are imposed.

In the final stage of training, a tone is presented for 10 sec and at its offset, a low-intensity shock is delivered to the animal's feet. This pairing of tone with weak but unavoidable shock results in a reliable *cessation* of licking whenever an audible tone occurs (Fig. 2). Thus, in test trials, the cessation (or suppression) of licking can be used as evidence that the animal has perceived a tone.

After this training, daily threshold test sessions are begun. Each session typically includes 30 randomly spaced, 10-sec test trials. During these sessions, the intensity of the tone is systematically varied from trial to trial while the rate of licking is recorded. This procedure generates a smooth graph of changes in lick rate

as a psychophysical function of tone intensity, which, in turn, allows a precise definition of threshold (Fig. 3). After repeating this procedure at each of several different frequencies, an audiogram showing the limits of the animal's audible field can be constructed. The audiograms that describe hearing in opossum, hedgehog, tree shrew, and bushbaby were determined in this manner, each in the same apparatus and in concurrent daily sessions.

B. Criteria for Selecting Other Audiograms for Statistical Comparison

The discussion that follows deals with similarities, structural parallels, and evolutionary trends in the hearing abilities of mammals. Part of this discussion depends on strict statistical comparisons of the audiograms of primitive mammals with each other and with those of more specialized or more advanced mammals. For audiograms of mammals other than the four primitive ones, we have relied on results published by more than 150 other investigators. However, an audiogram was not included for statistical purposes unless two technical and one practical criteria were satisfied:

- (1) Thresholds were obtained from normal animals by a currently acceptable behavioral technique requiring an overt response on the part of the animal.
- (2) The audiogram was obtained with pure tones that were generated, controlled, and measured by currently acceptable techniques (e.g., stable generator, keyer, monitoring system, etc.).
- (3) The audiogram was the most recent or most complete one available for a particular animal, and the report from which it was taken included an explicit discussion of any deviations from previously published reports on the same animal.

The first criterion not only eliminated several quasi-behavioral audiograms but it also eliminated all reports

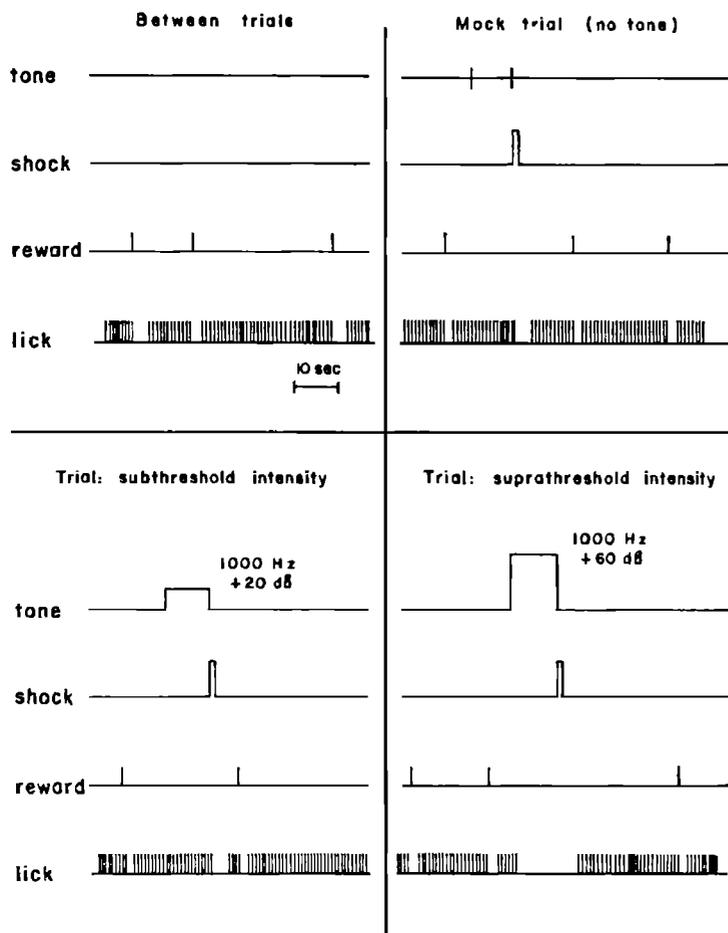


FIG. 2. Segment of a typical behavioral record during threshold test trials using technique of conditioned suppression. Time runs from left to right on horizontal dimension; events are represented by short vertical strokes. From top to bottom in each quadrant: tone, shock, reward, tongue contact with lick spout. Note that animal stops licking only after reward, shock, or onset of a suprathreshold stimulus.

based solely on measurements of cochlear-microphonic (CM) responses. The reasons for excluding this large body of data can be derived from Wever (1958). These exclusions reduced the number of potentially usable audiograms to 85 in 25 different genera. The second criterion eliminated audiograms obtained with uncalibrated sound systems or with sound equipment that was likely to have allowed audible transients during onset or offset of a tone. Its application reduced the number of

potentially usable audiograms from 85 to 31 in 20 genera. Application of the final criterion in most cases resulted in acceptance of only one audiogram for indistinguishable species or varieties of the same species. In a few cases, however, data from one report were used to complete an audiogram in another report. This last criterion reduced the list to 18 audiograms in 15 genera. The sources of these 18 audiograms are designated by an asterisk in the bibliography.

Thus, the statistical analyses are derived from all or part of comparable audiograms in 22 different mammals, 4 of the 22 from our own experiments and 18 of the 22 from the work of others. In this total, 21 species, 19 genera, 17 families, 8 orders, and 2 subclasses of Mammalia are represented by at least one audiogram.

The sample of mammalian genera acquired by this means deviates from the natural distribution of mammalian genera by less than 5% for every order except Primates and Rodentia. These deviations can be seen in Table I. Instead of one genus of Primates in the sample, which is all that would be expected on the basis of the proportion of primate genera within Mammalia, six genera are included. Instead of an expected seven genera of Rodentia, three are included in the sample.

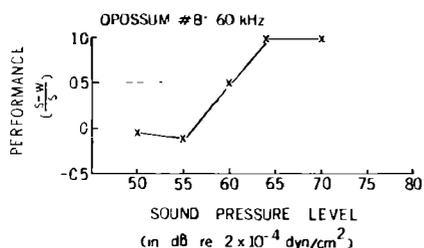


FIG. 3. Change in lick rate as a psychophysical function of intensity of a 60-kHz tone in opossum. For performance score, W is number of licks in 10-sec (warning) period during which tone is present; S is number of licks in 10-sec (safe) period immediately preceding warning period. Performance axis is scaled so that perfect suppression (tone was invariably heard) yields a score of 1.0 and no suppression (tone was never heard) yields a score near 0. Dashed lines show threshold calculation.

EVOLUTION OF HUMAN HEARING

TABLE I. Population and sample distributions of living mammals in genera per order.

True distribution (after Simpson, 1945)			Sample distributions											
Order	No.		Entire Sample		High Freq.		Low Freq.		Lowest Threshold		Best Freq.		Area of Audible Field	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Monotremata	3	0.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Marsupalia	57	6.1	1	5.3	1	5.9	1	6.3	1	5.6	1	5.6	1	8.5
Insectivora	71	7.6	2	10.5	2	11.8	2	12.5	2	11.1	2	11.1	2	17.0
Dermoptera	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Chiroptera	118	12.7	2	10.5	2	11.8	0	0.0	2	11.1	2	11.1	2	17.0
Primates	59	6.3	6	31.6	6	35.3	6	37.5	6	33.3	6	33.3	3	25.5
Edentata	19	2.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Pholidota	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Lagomorpha	10	1.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Rodentia	344	36.9	3	15.8	2	11.8	3	18.8	3	16.7	3	16.7	1	8.5
Cetacea	35	3.8	1	5.3	1	5.9	0	0.0	0	0.0	0	0.0	0	0.0
Carnivora	114	12.2	2	15.8	3	11.8	3	18.8	3	16.7	3	16.7	2	17.0
Tubulidentata	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Proboscidea	2	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Hyracoidea	3	0.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Sirenia	2	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Perissodactyla	6	0.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Artiodactyla	86	9.2	1	5.9	1	5.9	1	6.3	1	5.6	1	5.6	1	8.5
Total 18	932	99.8	19	100.1	17	100.2	16	100.2	18	100.1	18	100.1	12	100.0

Although this overweighting of Primates is useful for the primary purpose of this report, for statistical purposes it is a simple sampling bias and one that becomes more marked in lesser subsamples. Therefore, the groups of animals used here as statistical samples of the Class Mammalia cannot be considered to be subject to only random sampling error and inferences from them to the entire population of mammals must be weakened accordingly.

C. Auditory Dimensions of Comparison

The results are divided into five sections corresponding to each of five descriptive parameters of hearing. These five parameters and their relation to an audio

gram can be seen in Fig. 4. They are: (1) *high-frequency cutoff*—arbitrarily defined as the highest frequency (in kilohertz) that an animal can hear at a sound-pressure level (SPL) of +70 dB; (2) *low-frequency sensitivity* (in decibels)—the intensity threshold at 1 kHz; (3) *lowest threshold* (or best intensity, in decibels)—the intensity coordinate of the lowest point on the audiogram; (4) *best frequency* (in kilohertz)—the frequency coordinate of the lowest point on the audiogram; and (5) *area of audible field* (in decibels by octave)—the area of the region in the frequency-intensity plane bounded by the audiogram below and the +70 dB horizontal above.

The reasons for choosing these particular parameters instead of others, the interrelations between them, and

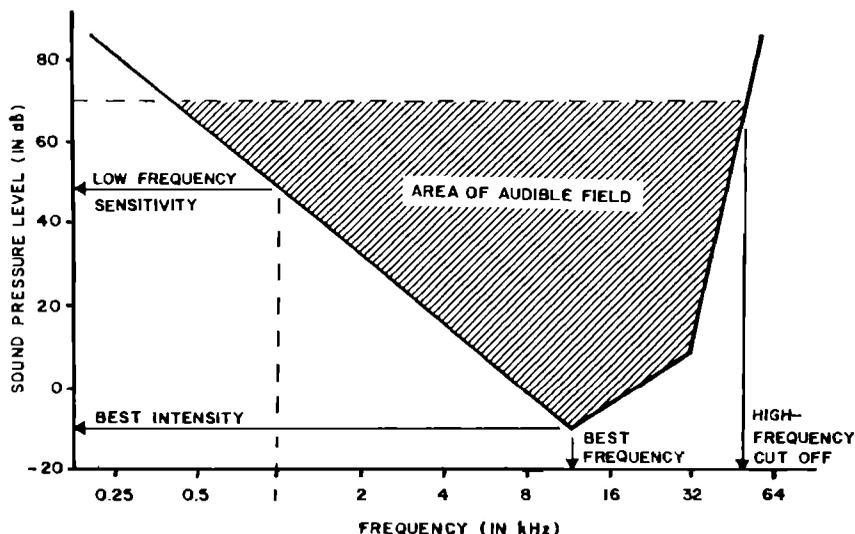


FIG. 4. Idealized audiogram showing the five descriptive parameters included in the analysis. The two frequency parameters, Best Frequency and High-Frequency Cut-off, are scaled in kilohertz or log kilohertz; the two intensity parameters, Low-Frequency Sensitivity (or Threshold at 1 kHz) and Best Intensity (or Lowest Threshold) are scaled in decibels *re* 2×10^{-4} dyn/cm²; the Area of the Audible Field is scaled in decibels \times octave.

the method of estimating specific values for cases with incomplete audiograms are discussed within the appropriate sections.

D. Ancestral and Morphological Dimensions

1. Ancestry

In addition to the five descriptive parameters of hearing, we explicitly included in the statistical analyses three parameters that might be expected to have explanatory power. The first of these, "recency of common ancestry with man," or *Ancestry* for short, provides the main focus of this report. For statistical purposes, Ancestry is represented by an ordinal scale, one through seven, with one representing animals having the most remote common ancestry with man (opossums) and seven representing most recent common ancestry (mankind itself). Values for particular animals can be derived from Fig. 1, where they are represented by letters (A,B,C...) along the main limb of the phylogenetic tree. Even though paleontological and morphological data now permit little argument about the ordering of five of the seven branch points in Fig. 1, two of the seven points (tree shrew and monkey) required arbitrary decisions.

Tree shrews have been described as Primates with many Insectivora characters by some (e.g., Clark, 1959; Simpson, 1945), and as Insectivora with many Primate characters by others (e.g., Osman-Hill, 1953; Simpson, 1965; Campbell, 1966a,b). This difference of opinion reflects, in part, a lack of information about the ancestry of modern tree shrews. That is, the line connecting extant tree shrews with the main limb leading to man may have followed any one of several paths (see dashed lines and query in Fig. 1). Despite this lack of paleontological verification, however, most authorities now agree that tree-shrewlike animals once occupied a pivotal position in the evolution of mankind and that modern tree shrews are the best approximation of this unique stage in mankind's line of descent (e.g., Simpson, 1965; Romer, 1967). Thus, the position of the modern tree shrew in the phyletic sequence, with Insectivora below and Prosimian Primates above, is probably correct, even though the evolutionary route traced by ancestral tree shrews and the classification of modern tree shrews may still be open to question.

Nevertheless, in order to avoid conclusions about the evolution of human hearing that might be negated by new information regarding the ancestry of tree shrews, all inferential statistics were calculated twice—*first*, as if the common ancestry of man with tree shrew were at Point B in Fig. 1 (this assumption results in a six-point scale for Ancestry over all), and *second*, as if the most appropriate point were at B' (resulting in a seven-point scale). As it turned out, these alternatives (and the subsequent renumbering of Primate branches) resulted in only very small and insignificant statistical differences. Therefore, the conclusions derived from the

analysis of the five auditory characteristics included here do not depend on the accurate affinitation of tree shrews and, conversely, the auditory characteristics analyzed here provide no important information on the affinities of tree shrews.

Monkeys required a second decision. In several morphological characters, new-world monkeys are less humanoid than old-world monkeys (cf., Osman-Hill, 1953; Clark 1959). This observation suggests that the common ancestry of man with new-world monkeys may be more remote in time and, for the present purpose, should possibly be represented in the phyletic sequence by a lower ordinal value than old-world monkeys. We have *not* adopted this position for two reasons. *First*, the characteristics usually cited as more primitive in new-world monkeys are neither otological nor neurological. *Second*, since the entire ancestry scale spans at least 100 million years in only seven discrete steps, the differences between the two families of monkeys do not seem large enough to warrant different numerals, even though the scale is only an ordinal one. Therefore, the two families have been grouped together as "Monkeys" and assigned a single value for Ancestry throughout. In the phyletic sequence, this level is represented by the old-world genus, *Macaca*.

2. Morphology

The final two parameters explicitly included in the statistical analyses are estimates of morphological dimensions: *Body Weight* and *Maximum Binaural Time Disparity*. The inclusion of Body Weight as a possible explanatory parameter is indicated by previous investigations that have shown that physical stature may be correlated with some auditory characteristics (e.g., von Békésy and Rosenblith, 1951). For animals whose body weights were not reported along with their audiograms and for whom specimens were not available, estimates have been obtained from Walker (1964).

The second morphological parameter, Maximum Binaural Time Disparity or *Maximum Δt* , is a measure of the availability of time cues for sound localization. It has been included here because of the conclusions of recent physiological and anatomical investigations into neural mechanisms of sound localization in mammals (e.g., Harrison and Irving, 1966; Masterton and Diamond, 1967a,b; Neff, 1968). Values for land mammals have been calculated by dividing an estimate of the minimum interaural distance (around the head) by the velocity of sound in air. The value used for the dolphin is an estimate of the interaural distance (through the head) divided by the velocity of sound in water.

E. Interrelations between Ancestral and Morphological Dimensions

Of the three pairs of potentially explanatory parameters (i.e., Ancestry, Maximum Δt , and Body Weight),

only one pair is correlated in the comparisons among the 22 different mammals included here: Ancestry and Maximum Δt ($r=0.69$, $p<0.01$). But in the phyletic sequence, that is, among the seven mammals selected from the total of 22 for their close approximation to successive ancestors of Man (Fig. 1), all three pairs of potentially explanatory parameters are correlated (Fig. 5). This close interrelation of alternative explanations has been in the past, and still is, the primary source of frustration in attempts to identify the main factors underlying the adaptive modifications of the mammalian auditory system. A partial resolution of this problem has now become possible due solely to the increase in variety of mammals with known audiograms. The increase in raw data permits the mathematical extraction of the relation of a single explanatory parameter to a single auditory characteristic by the procedure known as partial correlation (e.g., Nunnally, 1967). In order to help choose among several plausible relations of ancestry, morphology, and ecology with hearing, we have computed partial correlations whenever the number of data permits.

II. RESULTS AND DISCUSSION

Audiograms of opossum, hedgehog, tree shrew, bushbaby, and man are shown in Fig. 6. The Figure reveals several marked departures from expectations based on human psychophysics alone. Perhaps the most obvious of these is the upper frequency limit of hearing. Each of the four animals hears tones whose frequencies are more than an octave above the upper limit of humans. Further, the animals show a striking convergence in high-frequency cutoff. A comparison of this feature between mammals and birds, and between primitive and advanced mammals is presented in Sec. II-A.

At the low-frequency end of the audiograms in Fig. 6, no uniformity among the primitive mammals is seen. Instead, the four audiograms show wide but diminishing differences in sensitivity up to 4 kHz. Within the array, however, there appears to be a trend toward better

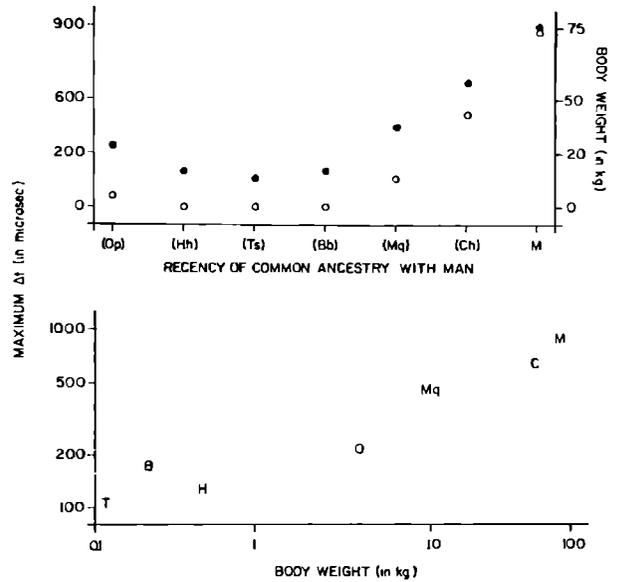


FIG. 5. Interrelations between morphological and ancestral parameters. *Top*: Relations of Ancestry with Maximum Δt (left scale, filled circles) and Body Weight (right scale, open circles). *Bottom*: Relation of Maximum Δt with Body Weight. Note logarithmic scaling of axes. O or Op, opossum; H or Hh, hedgehog; T or Ts, tree shrew; B or Bb, bushbaby; Mq, macaque; C or Ch, chimpanzee; M, man.

low-frequency hearing in the more advanced animals. For example, at 1 kHz, the bushbaby and the tree shrew have about the same threshold, but both have a threshold lower than the hedgehog, and each of these three have a threshold lower than the opossum. The relation between low-frequency sensitivity and an animal's degree of primitiveness is the topic of Sec. II-B.

The lowest threshold of the four animals in Fig. 6 ranges from -12 dB for the tree shrew to $+20$ dB for the opossum, with the hedgehog and bushbaby intermediate. Although this parameter shows no obviously ordered distribution nor trend among the four primitive mammals, the expectation of an evolutionary trend

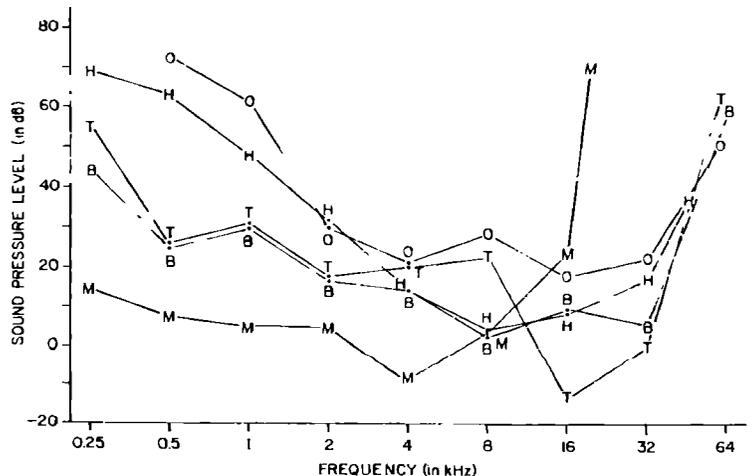


FIG. 6. Audiograms of four primitive mammals and Man tested with the same audio equipment. O, opossum (*Didelphis virginiana*); H, hedgehog (*Hemiechinus auritus*); T, tree shrew (*Tupaia glis*); B, bushbaby (*Galago senegalensis*); M, man. Sound-pressure level is scaled in decibels $re 2 \times 10^{-4}$ dyn/cm².

toward better general sensitivity is not unreasonable. This feature is analyzed in Sec. II-C.

The best frequencies of the four primitive mammals are also shown in Fig. 6. The hedgehog has its lowest threshold at 8 kHz and the tree shrew at 16 kHz. Both opossum and bushbaby have a broad range of frequencies where their audiograms are within a few decibels of their lowest threshold but they too have best frequencies at 16 and 8 kHz, respectively. This concentration of lowest thresholds in the 8-16-kHz range stands in marked contrast to man's best frequencies in the 3-4-kHz range and suggests another possible evolutionary trend. An analysis of this feature is the topic of Sec. II-D.

The final obvious difference among the four audiograms is the over-all size of the audible field: that is, the area between the audiogram and a horizontal line at +70 dB. Figure 6 reveals a trend toward an increasing area that follows the degree of advancement of the four animals. This feature is the topic of Sec. II-E.

A. High-Frequency Cutoff

The uniformity of high-frequency cutoff among the four primitive mammals and the contrast between them and man prompt the analysis of this feature among more advanced mammals, particularly those approximating man's line of descent. Comparisons of high-frequency hearing among mammals are difficult to make, however, because most published audiograms are incomplete at the high-frequency end. Until the 1950's, these high-frequency truncations were the direct result of the unavailability of appropriate audio equipment (Neff and Hind, 1955). Even today, high-frequency transducers are scarce enough that audiograms rarely extend beyond 32 kHz. In order to begin a discussion of the upper limit of hearing in mammals, therefore, it is first necessary to estimate the range of the high-frequency cutoff by extrapolation.

Among the high-frequency data that follow, six upper limits (two bats, two monkeys, dolphin, and man) have been determined empirically. To these we have added 13 others from audiograms, or fragments of audiograms,

that obviously approach an upper limit even though they do not reach it. In these cases, the upper limit is estimated by completing the audiogram with an almost vertical straight line (i.e., SPL in decibels as a linear function of frequency in octaves). The origin of the line coincides with the highest-frequency point on the audiogram, and its slope is equal to the average slope of the cut offs in the animals in which high-frequency limits have been empirically determined (569 dB/oct). Although any one of these extrapolations does not evoke a high degree of confidence in its accuracy, this method of estimation is very conservative for the comparative conclusions that follow, i.e., it probably yields a *low* estimate of the upper limit in every case.

1. High-Frequency Hearing in Mammals

When the thirteen estimates are combined with the six empirical determinations, the distribution in Fig. 7 is obtained. As might be expected, the range of high-frequency limits of hearing (at +70 dB) extends from a low near 18 kHz for man to about 120 kHz for dolphin and one bat.

Certainly less predictable, though perhaps not wholly unexpected, is the *average* high-frequency cutoff for the nineteen mammals. At 53 kHz, it is more than an 1½ oct above man's upper limit. Further, this average would be still higher if the sample were not biased by the inclusion of so many primates. Thus, even though these nineteen animals do not constitute a truly random sample of Mammalia, it seems safe to conclude that the ability to receive what were once called "ultrasonic" frequencies and considered to be the bizarre adaptation of a few is, in fact, a commonplace characteristic among mammals.

The distribution of high-frequency limits in mammals, centered at 53 kHz, is far higher than the corresponding distribution for nonmammalian vertebrates. For example, the modal high-frequency cutoff for birds appears to be in the region of 8-12 kHz (Schwartzkopf, 1955) with few, if any, species extending as high as 20 kHz. For the only reptile available (turtle), the cutoff is about 0.8 kHz (Patterson, 1966). Although CM have been recorded to higher frequencies in some other nonmammals (e.g., Wever and Peterson, 1963), the separation of the distributions of high-frequency cutoff in mammals and nonmammals still remains nearly perfect. Apparently, high-frequency hearing in vertebrates is a uniquely mammalian trait.

The most obvious anatomical difference between the ears of mammals and nonmammals that parallels this striking difference in upper limits of frequency is the presence of an ossicular linkage in the middle ear of mammals. It has long been known that amphibians, reptiles, and birds have only a single functional bone in their middle ear for conducting sounds from tympanum to cochlea (columella or stapes) and three bones in their lower jaw (dentary, angular, and articular). In

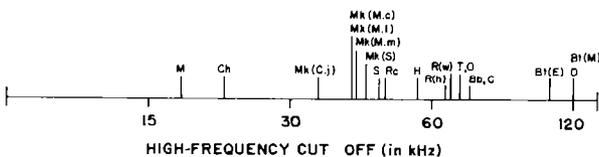


FIG. 7. Distribution of High-Frequency Cutoff among 19 mammals. Bb, bushbaby; Ch, chimpanzee; H, hedgehog; O, opossum; T, tree shrew; and M, man; as in Fig. 5. Bt(E), bat (*Eptesicus fuscus*); Bt(M), bat (*Myotis lucifugus*); C, cat (*Felis catus*); D, dolphin (*Tursiops truncatus*); Mk(C,j), marmoset (*Callithrix jacchus*); Mk(M,c), monkey (*Macaca cynomolgus*); Mk(M,i), monkey (*Macaca irus*); Mk(M,m), rhesus monkey (*Macaca mulatta*); Mk(S), squirrel monkey (*Saimiri sciureus*); R(w), laboratory white rat; R(h) laboratory hooded rat; Rc, raccoon (*Procyon lotor*); S, sheep (*Ovis aries*).

contrast, all mammals have a series of three bones in their middle ear (malleus, incus, and stapes) and only one in their lower jaw (dentary) (Young, 1962). This clear morphological distinction among modern vertebrates allows the presence (or absence) of a three-ossicle middle ear to be used as *prima facie* evidence for (or against) the inclusion of a living or fossilized animal in the class of Mammalia (Colbert, 1955). Further, physiological experimentation in modern mammals has shown that the ossicular linkage acts as a simple lever providing mechanical transformation that matches the impedance of air to the impedance of cochlear fluid (von Békésy, 1960). Since the transmission of high-frequency vibrations from eardrum to cochlea is known to require this matching of impedances, there seems little reason to look beyond the evolution of the middle-ear ossicles for one explanation of the radical difference between mammals and nonmammals in the upper limit of hearing.

Returning to mammals themselves, Fig. 7 shows that, anthropomorphic conclusions to the contrary notwithstanding, it is more parsimonious to consider high-frequency sensitivity as the rule for mammals and lack of this sensitivity as an exception. In this sense, Man and Chimpanzee are clearly exceptional mammals. The Figure also illustrates the well-known fact that bats and dolphins are exceptional in the opposite way—their upper limit is much higher than the mammalian mode. Since these animals are also known to depend on their auditory systems for locating objects in space, they are commonly (and according to Fig. 7, correctly) considered to be auditory anomalies (Kellog, 1961; Griffin, 1959). However, comparing the degree to which bats and dolphins deviate from the mammalian average to the degree of deviation by men and chimpanzees, it can be concluded that hominoids are more of an auditory anomaly among mammals than either bats or dolphins.

In seeking evidence of the adaptive value of high-frequency sensitivity in mammals, it is necessary to turn to correlational data. Among the 19 animals in Fig. 7, High-Frequency Cutoff is correlated with Maximum Δt ($r = -0.86$, $p < 0.01$) and, surprisingly perhaps, it is *not* correlated with Body Weight ($r = 0.02$). Because a small body is often considered the best rule-of-thumb for predicting high-frequency sensitivity, this lack of correlation warrants further comment before turning to a discussion of the significance of the high correlation between High-Frequency Hearing and Maximum Δt .

The existence of a (negative) correlation between High-Frequency Sensitivity and Body Weight has previously been suggested mostly on the basis of results from a sample of laboratory animals (e.g., rats, cats, monkeys) that at the time was also the best available phyletic sequence for approximating the successive levels achieved by man's ancestors (e.g., von Békésy and Rosenblith, 1951). As in the phyletic sequence used

to approximate man's lineage here, these previous sequences yield a correlation between High Frequency Sensitivity and Ancestry or Phyletic Level and also between each of these parameters and Body Weight. Thus, the increase in body size was an obvious alternative to Ancestry for explaining the observed decrease in high-frequency sensitivity across the sequence of animals.

The reason that High-Frequency Sensitivity and Body Weight are uncorrelated in the sample of mammals in Fig. 7 and yet are highly correlated in previous samples, lies solely in the wider variety of animals that are represented here. For example, the dolphin, large in body size but sensitive to high frequencies, gives direct contradiction to the large-size low upper-limit hypothesis, and thus its inclusion here contributes to a lower correlation. Because its upper limit had not yet been determined, the dolphin was missing from previous samples, with the result that the large-size low-upper-limit hypothesis went uncontradicted.

It should be noted, however, that arguments opposing the inclusion of the dolphin in the present sample can be made on the grounds of its aberrant ecology. Because of such arguments, and because of the small but real bias in this sample as well as in previous ones, we do not feel that the relation between body weight and high-frequency hearing should yet be entirely dismissed. There are many mammals available, other than the possibly aberrant dolphin, in which large body size (suggesting a low upper limit) is combined with a disproportionately small maximum Δt (suggesting a high upper limit): Artiodactyla (cattle or deer) and Perissodactyla (horses or rhinoceroses) are two examples. Until the upper limits of hearing are determined in some of these critical cases, the conclusion that Body Size contributes to an animal's High-Frequency Cutoff independently of Maximum Δt remains tenable.

The negative correlation between Maximum Δt and High-Frequency Sensitivity is by far the strongest of the three potentially explanatory correlations and remains the strongest when the other two are mathematically eliminated ($r = -0.83$ $p < 0.01$). Therefore, it can be concluded that Maximum Δt provides the most direct clue to the biological significance of high-frequency hearing. The negativity of the correlation means that the narrower the range of binaural time disparities that an animal can experience, the higher the animal's upper limit of hearing. Since the significance of the binaural time disparity lies in sound localization, this correlation suggests that an explanation for the presence or absence of high-frequency sensitivity might be profitably sought in sound localization also.

2. Relation between Sound Localization and High-Frequency Sensitivity

It is now well known that many animals combine two natural cues for determining the direction of the source

of a brief sound. One cue is the difference in the time of arrival of the sound waves at the two ears (Δt). The other is the binaural disparity in frequency-intensity spectra in the stimulation reaching the two ears (Δf_i). Further, it has been shown that both of these cues are encoded in the difference between the discharges of the two auditory nerves (Teas, 1962; Masterton *et al.*, 1967). Since the larger the difference between the discharges of the auditory nerves, the easier the brainstem's task of analyzing the direction of a sound source, it follows that accurate sound localization can be maintained in the absence of one of the two cues by the maximization of the difference in neural discharge produced by the other cue (Masterton *et al.*, 1967). This means that Δt and Δf_i are alternative cues for achieving a given level of accuracy in sound localization and a lack of one can be compensated by the other.

Returning to the question of high-frequency hearing, two physical facts become pertinent: High frequencies are more quickly attenuated over distance and are more effectively shadowed by the head than are low frequencies. Therefore, the reception of high frequencies is tantamount to an expansion of the range of binaural spectra disparities (Δf_i), because even little heads induce a large disparity at high frequencies.

Combining these physiological and physical facts with the existence of a negative correlation between Maximum Δt and High-Frequency Sensitivity, we are led to the conclusion that mammals that have available to them only small binaural time disparities, either because of close-set ears or a marine environment, increase their accuracy in localizing a sound source by maximizing the availability of binaural spectra disparities. This cue is maximized, in turn, through sensitivity to high frequencies. By this line of reasoning, the coincidence of a large maximum Δt with a low upper limit on the one hand, and a small maximum Δt with a high upper limit on the other hand, is a consequence of persistent selective pressure on mammals to maintain the better mechanism for localizing a sound source regardless of their size, ancestry, or ecology.

Bringing to bear two paleontological conclusions concerning the nature of ancient mammals, one final inference about high-frequency hearing now becomes plausible. Available data suggest that all of the mammals of the Cretaceous were small and had close-set ears (Simpson, 1949; Romer, 1954). Therefore, either through the relation between small maximum Δt and high-frequency sensitivity, or through comparative triangulation of characters-in-common, it follows that ancient mammals were also capable of hearing high frequencies. This inference, which can be made without specific reference to the relative primitiveness of either opossum or hedgehog, is supported by the observation that both of these limiting cases within the sample are capable of hearing high frequencies.

3. Evolution of High-Frequency Cutoff in Man's Lineage

Figure 8 shows the high-frequency cutoffs for the phyletic sequence of opossum, hedgehog, tree shrew, bushbaby, macaque, chimpanzee, and man. The Figure shows that the upper limit of hearing is high and relatively constant across the first four positions in the sequence and then drops markedly across the last three positions. The similarity in the shape of this graph with those in Fig. 5 illustrates the correlation of High-Frequency Cutoff with Maximum Δt ($r = -0.96$, $p < 0.01$) and with Body Weight ($r = -0.94$, $p < 0.01$) within the phyletic sequence. Although the absolute size of the correlation between High-Frequency Cutoff and Body Weight illustrates the basis for previous explanations once again, it has already been shown that Maximum Δt alone accounts for practically all of the variance in upper limit for the more inclusive sample in Fig. 7, as well as for this select seven (Fig. 8). Therefore, there seems to be no reason for reopening the question of its more indirect relation with body weight within the phyletic sequence.

Accepting as fact for the moment that high-frequency sensitivity is a characteristic of primitive mammals living now, and was also a characteristic of ancient mammals, the absence of this sensitivity in the higher levels of the phyletic sequence and its loss in the later stages of the inferred phylogenetic sequence remains to be explained. The question can be stated in this manner: If the ancient mammalian forbears of mankind were sensitive to high frequencies by virtue of their newly evolved middle-ear linkage, why did this great achievement become vestigial in hominoids? One possible

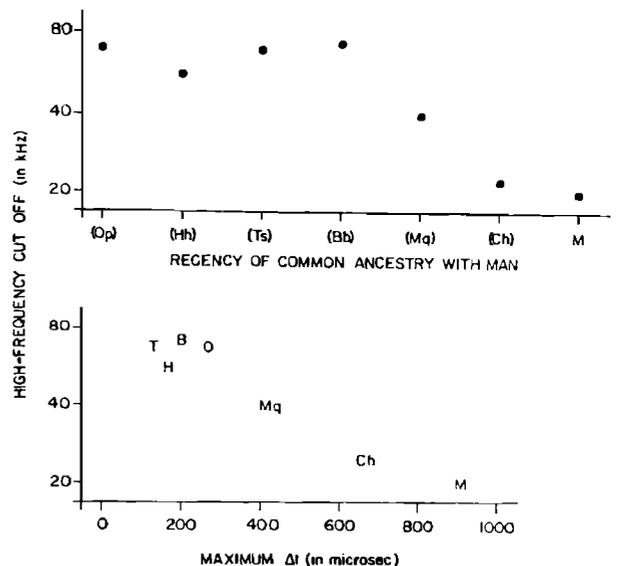


FIG. 8. *Top*: High-Frequency Cutoff in animals of phyletic sequence. *Bottom*: Relation of High-frequency Cutoff to Maximum Δt . Note logarithmic scaling on vertical axis. See Fig. 5 for animal labels.

answer to this question is that some mammals have lost their high-frequency sensitivity in order to gain low-frequency sensitivity (von Békésy, 1960). This idea implies that high-frequency sensitivity and low-frequency sensitivity are incompatible, or at least conflicting, characteristics. It is tenable because *Threshold at 1 kHz* is negatively correlated with High-Frequency Cutoff ($r = -0.58$, $p < 0.05$); therefore, a conflict between the two characteristics may indeed exist. Thus, it can be argued that high-frequency sensitivity may have been lost in the evolution of Hominoids through selective pressure for low-frequency sensitivity and consequently, *against* high-frequency sensitivity. However, in Sec. II-B, it is shown that at least three animals (cats, raccoons, and monkeys) possess high frequency sensitivity along with low-frequency sensitivity. Therefore, the two characteristics are certainly not incompatible, either in mammals or in primates as a whole.

A second possible explanation of the loss of high-frequency sensitivity in hominoids stems from a consideration of the ecological demands for accurate sound localization: once the ears became sufficiently wide set to provide accurate sound localization without necessitating special benefit from high frequencies, sensitivity to high frequencies became passively vestigial, i.e., through lack of selective pressure to maintain it rather than any specific selective pressure against it. Unlike the former possibility, this one has no immediate contradictions in any of the animals included here, but it carries with it the worrisome implication that there is little, if any, useful information unique to high frequencies beyond that used for localizing the source of a sound or an echo.

4. Conclusions

Physics, physiology, comparative morphology, paleontology, and comparative psychology converge on three conclusions regarding high frequency sensitivity in mammals.

- High-frequency hearing (e.g., above 32 kHz) is a distinctively mammalian characteristic, common to all but a few anomalous species (Man and Ape are the only exceptions yet known). This special ability of mammals depends on the ossicular linkage in the middle ear and may have been one of the primary sources of selective pressure that resulted in the evolutionary transformation of reptilian jaw bones into mammalian auditory ossicles.

- Among mammals, a high upper limit of hearing is probably necessitated more by the demand for accurate sound localization than by any other single source of selective pressure. In combination with the previous conclusion, this one suggests that selective pressure for accurate sound localization may have been the primary driving force behind the final stages in the evolution of the mammalian variety of middle ear.

- In the evolution of Man, high-frequency sensitivity was retained until its benefits for sound localization were replaced by the benefits of wide set ears. From the early Eocene onward, progressively wider-set ears (and the more effective interaural sound shadows that are their consequence) released man's ancestors from selective pressure for high-frequency hearing and resulted in regression of the upper limit to a point that is now so low that man bears artificial resemblance to nonmammalian vertebrates.

B. Low-Frequency Sensitivity

An analysis of low-frequency sensitivity is prompted by the observation that thresholds at the low-frequency end of the audiogram tend to decrease across the sequence of primitive mammals (Fig. 6). In seeking a parameter to quantify this characteristic for statistical analysis, several preliminary problems arise. Certainly for ease of interpretation, one of the best parameters to describe low-frequency sensitivity would be some measure of the lower frequency limit of hearing analogous to that just discussed for high-frequency hearing, e.g., the lowest frequency at which the audiogram intersects the +70-dB horizontal. Unfortunately, this type of measure is rarely available. Further, when it is available, it is often subject to wide laboratory-to-laboratory variability for animals of the same species. Besides offering a statistical annoyance, this variability also prevents adequate estimation by extrapolation.

Beyond the variation that is contributed by real differences between individuals or between species, the chief source of variability in thresholds at very low frequencies is ambient low-frequency noise. Within any animal testing chamber, noise is always present and is progressively louder at lower frequencies. As background, this noise tends to mask low frequency test tones and can sometimes result in the inadvertent measurement of differential thresholds (noise versus noise and tone) instead of absolute thresholds (silence versus tone). Because an experimenter can depend on his own hearing to assess the adequacy of the sound shield for tests on animals with relatively poor low-frequency hearing, background noise is rarely a source of error in these animals. But for animals that have low-frequency sensitivities rivaling man's (e.g., cats, raccoons, monkeys), background noise sometimes proves to be the limiting factor. In these cases, the low-frequency end of the resulting audiogram may parallel the spectrum of background noise and parallel its day-to-day or laboratory-to-laboratory variations.

Since it is impossible to achieve a fair comparison between animals tested in the presence of different levels of background noise, the discussion of low-frequency sensitivity is best confined to thresholds for frequencies above 500 Hz. We have chosen the threshold at 1 kHz. This parameter provides an adequate safeguard against the influence of ambient noise since 1

kHz is high enough to be effectively shielded by most sound chambers now in use. At the same time, it is low enough to be a truly "low" frequency, in the sense that 1 kHz is far beneath the best frequency in 16 out of the 18 mammals included in the comparison (cf. Sec. II-D, on best frequency).

1. Low-Frequency Sensitivity in Mammals

Figure 9 shows the distribution of thresholds at 1 kHz for 18 mammals. The distribution in Fig. 9 ranges from a low of -15 dB for raccoon to a high of +61 dB for opossum. The mean is +17 dB, and the standard deviation is 22 dB. Bats are not on the scale because they cannot hear tones as low as 1 kHz (Dalland, 1965). Rather than assign them an infinite value that would obviate all correlations, they have been omitted from the statistical analysis. The effect of this bias is discussed below.

Before seeking correlates of this characteristic among mammals themselves, it should be noted that the distribution of low-frequency sensitivities (in contrast to high-frequency sensitivities) is apparently quite similar for birds and mammals (Schwartzkopf, 1955). Although this similarity provides no evidence concerning the rôle of low-frequency sensitivity in the evolution of mammalian hearing, it does demonstrate that the nonmammalian ear provides no insurmountable anatomical barrier to sensitivity at low frequencies.

Returning to the evolution and significance of low-frequency hearing among mammals, Threshold at 1

kHz proves to be modestly correlated with Ancestry ($r = -0.49$, $p < 0.05$) and Maximum Δt ($r = -0.50$, $p < 0.05$) and it is not significantly correlated with Body Weight ($r = -0.34$).

The negative correlation of Threshold at 1 kHz with Ancestry means that there is a tendency for mammals with more recent common ancestry with man to have better low-frequency hearing. The reason for this apparent tendency among Mammals in general will become clear in the discussion of the phyletic sequence below.

Although the negative correlation between Threshold at 1 kHz and Maximum Δt suggests that there might be an important relation between low-frequency sensitivity and sound localization, two other facts serve to weaken this interpretation. First, it has already been seen that Maximum Δt is very closely related to High-frequency Sensitivity ($r = -0.86$). We have noted, also, that High-Frequency Sensitivity and Low-Frequency Sensitivity are negatively correlated ($r = -0.58$). The existence of these two stronger correlations suggests that the modest correlation between Maximum Δt and Threshold at 1 kHz obtained here may be merely their product and therefore much too indirect to provide an independent clue to the significance of low-frequency sensitivity. Thus, for one reason or another, neither Maximum Δt nor Body Weight yields a sufficiently striking correlation with low-frequency hearing among the animals in the sample to warrant discussion at the present time. This general conclusion is supported by partial correlations of Threshold at 1 kHz with the two morphological parameters alone: Each correlation is diminished still further when the other parameter is held constant (for Max Δt , $r = -0.17$; for Body Weight, $r = -0.27$). However, it should be noted that Body Weight, at least, is not eliminated as a factor contributing to low-frequency hearing in Mammals despite the fact that these two parameters are not well correlated in the present sample. With the exclusion of bats and an obvious shortage of large mammals, the sample is far from adequate for testing a *body-weight-low frequency* hypothesis. On the other hand, it is also clear that Body Weight is probably not a very strong correlate of low-frequency hearing in the way that Maximum Δt is for high-frequency hearing. Thus, at the present time, it seems likely that the search for the adaptive significance of low-frequency sensitivity within the entire class of mammals might be profitably pursued in somewhat different directions [e.g., see Busnel (Ed.), 1963, or Marler, 1967].

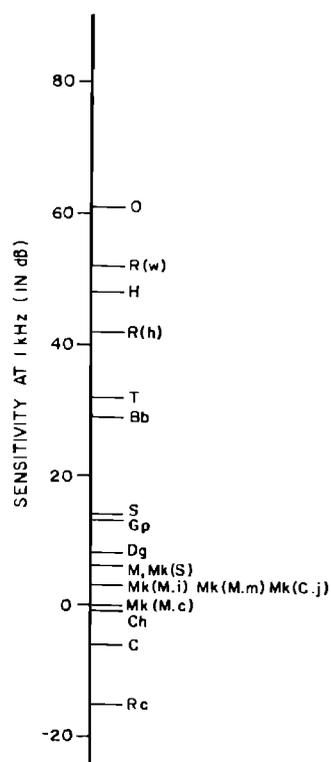


FIG. 9. Distribution of sensitivity (threshold) at 1 kHz among 18 mammals. Gp, laboratory guinea pig (*Cavia*); Dg, dog (*Canis familiaris*). See Fig. 7 for other labels.

2. Evolution of Low-Frequency Sensitivity in Man's Lineage

Although there exists no overwhelming relationship between low-frequency hearing and Ancestry for the entire class of mammals, Threshold at 1 kHz is closely related to Ancestry in the seven mammals of the phy-

letic sequence ($r = -0.95$, $p < 0.01$). Further, when Maximum Δt and Body Weight are held constant, the partial correlation of Threshold at 1 kHz and Ancestry increases to -0.96 ($p < 0.01$). Therefore, among the animals in the phyletic sequence "recency of common ancestry with man," by itself, accounts for more than 92% of the total variance in Threshold at 1 kHz. This relationship is shown in Fig. 10.

In the face of this strong relationship within the phyletic sequence, it is difficult to avoid the conclusion that Man's ancestors were exposed to strong and persistent selective pressure for low-frequency hearing. Apparently, sensitivity to low-frequencies was achieved gradually during the earliest periods of mammalian and primate evolution—from the opossumlike stage in the Cretaceous to the monkeylike stage in the Eocene.

Since Ancestry is so strongly correlated with Threshold at 1 kHz in the phyletic sequence, and yet the two are only slightly correlated among other mammals, it is tempting to conclude that the selective pressure exerted on Man's ancestors may have been *unique* to that lineage. However, this conclusion is not implied by the statistic and it is quickly denied by specific cases. To begin with, Fig. 9 shows that raccoon and cat are more sensitive at 1 kHz than any Primate including Man. Further, cats have been shown to be as sensitive as man at most lower frequencies as well. Only at frequencies below 0.3 kHz can it be claimed that humans may be uniquely sensitive, and even here the difference between humans and cats is so slight as to be seriously doubted (Neff and Hind, 1955). Thus, at least some ancestors of cats, and possibly the entire order of Carnivora, must also have been exposed to selective pressure for low frequency hearing. Therefore, some mammalian lineages have increased their low-frequency sensitivity since their divergence from Man's lineage while others have not. It follows that although man's lineage may prove to be *unusual* in its degree of improvement, it certainly is not unique.

Finally, Fig. 10 provides data that serve to cast further doubt on one of the alternative interpretations of the loss of high-frequency sensitivity in Man's lineage

that was discussed in the Sec. II-A. If Fig. 10 (showing the decrease in threshold at 1 kHz) is compared to Fig. 8 (showing the decrease in the upper limit of hearing), it can be seen that the two curves are far from coincident, despite the fact that they each start high at opossum and end low at man. This lack of coincidence means that low-frequency sensitivity and lack of high-frequency sensitivity, though statistically correlated, are not either a cause nor an effect of each other, at least among the animals within the phyletic sequence. Thus, the idea that *man's* ancestors lost high-frequency sensitivity in order to gain low-frequency sensitivity is not supported. At the same time, a similar comparison between Figs. 7 and 9 shows the validity of the observations that generated this idea: The sequence—rat, monkey, and man—shows a decrease in high-frequency sensitivity that parallels an increase in low-frequency sensitivity. With the improvement in approximation provided by the phyletic sequence used here, however, it would seem that the possibility of the existence of an important clue in this statistical relationship could now be ruled out.

3. Conclusions

The distribution and correlates of sensitivity to low-frequency tones among mammals warrant four tentative conclusions:

- Low-frequency sensitivity is *not* a primitive mammalian characteristic.
- Animals in Man's line of descent showed marked improvement in low-frequency hearing, but neither the kind nor the degree of improvement was unique among mammals.
- The increase in low-frequency sensitivity, though almost linear across the phyletic sequence, was probably *not* steady in time. If the phyletic sequence is equated to a phylogenetic sequence, low-frequency hearing improved slowly until the Paleocene, then quickly through the Eocene—after which it remained relatively unchanged until the present.

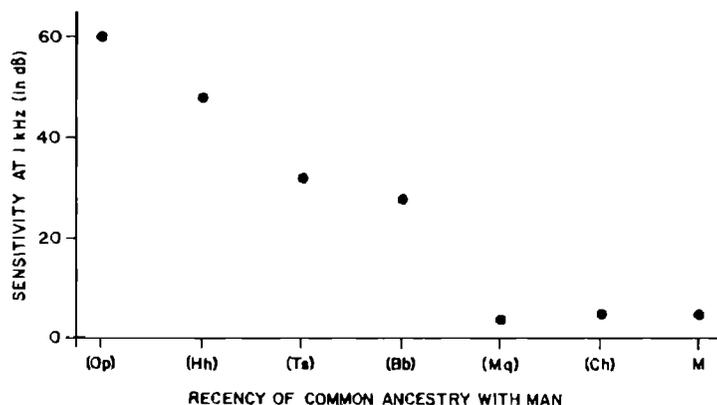


Fig. 10. Sensitivity (threshold) at 1 kHz in animals of phyletic sequence.

Unlike high-frequency sensitivity, the biological significance of low-frequency sensitivity is probably not related to sound localization, but, excepting possibly Body Weight, the parameters included in this analysis provide no immediate clue to what this significance might be.

C. Lowest Threshold

Figure 6 shows that opossum is relatively insensitive compared to the other primitive mammals. Since the opossum is also the most primitive of the four, this observation suggests that the evolution of human hearing might have been accompanied by an increase in sensitivity. The parameter we have chosen to describe sensitivity is the intensity coordinate of the lowest point on the audiogram.

Like the previous parameter, this one is also subject to variation other than that due to real differences between animals. Perhaps the most important source of error in estimation results from the practice of obtaining thresholds only at frequency octaves. That is, by necessity the frequency axis of an empirical audiogram is scaled discretely instead of continuously. This means that an animal's lowest threshold certainly occurs at an untested frequency and can be as far as 1/2 oct from the nearest test frequency. Since some mammals are known to have abrupt changes in their sensitivity from one octave to the next (cf., tree shrew at 8 kHz and 16 kHz in Fig. 6), an estimate of the lowest point of an animal's audiogram is always several decibels, and possibly many decibels, higher than the true value. In addition to this persistent bias, ambient noise is also a source of error in estimation. Since sound-treated chambers leak low-frequency noise, an animal whose lowest

threshold is at the low end of the frequency scale must contend with direct masking noise, while animals with lowest thresholds at high frequencies do not. Taken together, these considerations mean Lowest Threshold is always subject to a significant amount of measurement error. Certainly, differences as small as 5 dB should be viewed with scepticism.

1. Lowest Threshold in Mammals

The distribution of Lowest Threshold for 20 mammals is shown in Fig. 11. The distribution ranges from -17 dB for cat to +18 dB for opossum. The mean is -2 dB and the standard deviation is 9 dB. This distribution is essentially similar to that for birds, whose Lowest Threshold appears to average about +1 dB (Schwartzkopff, 1955). However, it is set quite apart from the one reptile (turtle, +40 dB) that has been tested (Patterson, 1966). This value (+40 dB) is sufficiently different from the mammalian average that even with only one representative of Reptilia and twenty representatives of Mammalia, it can be safely concluded that the two classes of Vertebrates will prove to be different in auditory sensitivity. Thus, in Lowest Threshold, birds and mammals are essentially similar but each is probably different from reptiles. In any event, it is clear that selective pressure for lower thresholds was not confined to the ancient reptilian line that gave rise to mammals; at least one later line—that leading to birds—was also subjected to similar pressure.

In Mammalia, Lowest Threshold is not significantly correlated with Ancestry or with either of the two morphological parameters. Nor does a significant value appear after partial correlation of Lowest Threshold with each parameter alone. Thus, no clue to a general explanation of the variation in sensitivity among mammals can be offered. Apparently, high sensitivity (i.e., low thresholds) has been acquired by too many different mammalian lineages and, perhaps, for too many different ecological reasons to be uncovered by the present statistical analysis of the entire class.

2. Evolution of Sensitivity in Man's Lineage

Among the animals of the phyletic sequence, neither Ancestry nor either of the two morphological parameters is correlated with Lowest Threshold when they are allowed to covary. Under partial correlation, however, Ancestry stands out as a possible source of variation ($r = -0.83, p < 0.10$). This relationship is shown in Fig. 12. After a trend toward an increase in sensitivity across the opossum-hedgehog-tree shrew stages, Lowest Threshold seems to vary about a mean of -5 dB. Since the variation inherent in current techniques for testing hearing in animals necessitates particularly skeptical interpretation of Lowest Threshold, the only difference that can be properly accepted as real at this time is that between the animals at the lowest levels of the phyletic sequence.

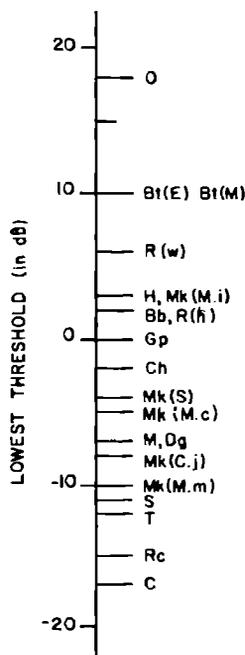


FIG. 11. Distribution of Lowest Threshold among 20 mammals. See Figs. 5, 7, and 9 for labels.

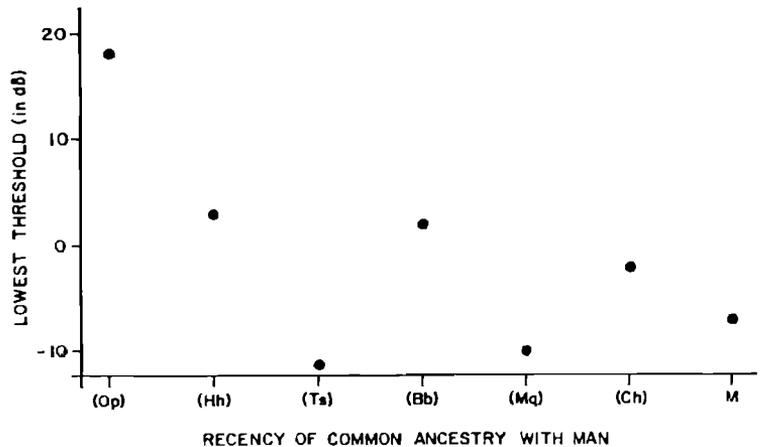


FIG. 12. Lowest Threshold in animals of phyletic sequence. Note large drop at lower levels.

This apparent increase in general sensitivity is paralleled by several changes in the structure of the middle ear (Tumarkin, 1955). Two of these differences are directly related to the degree of rigidity in the suspension of the tympanic membrane and may account for at least a part of the observed differences in sensitivity (e.g., van der Klaauw, 1929). For example, in opossum, the ring of bone (ectotympanic) that supports the eardrum is incomplete. In hedgehog, it is more complete and in tree shrew it is still more complete. This progressive encirclement of the tympanum is accompanied by the development of a sturdy auditory bulla, which, still later, fuses the tympanic ring laterally with the skull medially. It seems reasonable to expect that the lack of rigid support for the tympanic membrane in primitive mammals might result in a loss of energy during the first link in the transmission of air movements to movements of the cochlear fluid and at least account in part for the relative insensitivity in these animals. Before this possibility can be accepted, however, further assurance of a significant trend toward greater sensitivity would seem to be required. This assurance can only be provided by audiograms of several more marsupials, insectivores, and prosimians.

3. Conclusions

In spite of a relatively high degree of bias and uncontrolled variation in estimates of Lowest Threshold, two tentative conclusions seem warranted.

- The mammalian version of the ear and auditory system bestows no unique general sensitivity to sound.
- The only large differences in general sensitivity among animals in the phyletic sequence that may be both real and significant occur between levels at the lowest stages (i.e., opossum-hedgehog-tree shrew levels, phyletically; Cretaceous to Paleocene, historically). These differences in sensitivity may be related to differences in the rigidity of tympanic suspension.

D. Best Frequency

Although Fig. 6 reveals no great difference in the frequency coordinates of the lowest points on the audiograms (hedgehog and bushbaby are at 8 kHz, opossum and tree shrew are at 16 kHz), the past popularity of discussions concerning the significance of an animal's Best Frequency prompts its analysis here. As is the case with the other descriptive parameters, an estimate of Best Frequency is subject to several sources of error beyond that due to real differences between individuals or species. *First*, the practice of measuring thresholds only at octaves results in a discrete and relatively crude scale of Best Frequency. *Second*, the shielding characteristics of sound chambers bias results toward higher best frequencies. *Third*, sound shadows and standing waves created by the testing apparatus and the animal itself, often result in what appear to be abrupt differences in sensitivity from octave-to-octave and can give a mistaken impression of a sharply-tuned Best Frequency where none really exists. Finally, and by far the most important for statistical purposes, the audiograms of some mammals show either double peaks of sensitivity or a broad range of sensitivity where thresholds at widely disparate frequencies are within only a few decibels of each other. For example, in Fig. 6, it can be seen that the thresholds for opossum at 4, 8, 16, and 32 kHz are all within 8 dB of each other. Obviously, the claim that opossum is uniquely sensitive at 16 kHz rather than at 4, 8, or 32 kHz places severe strain on the confidence evoked by animal testing techniques. For these several reasons and for some more that appear below, comparisons of Best Frequency require cautious interpretation.

1. Best Frequency in Mammals

The distribution of Best Frequency for 20 mammals is shown in Fig. 13. The mean of the distribution is about 13 kHz and its range extends from a low of 1 kHz for raccoon and one species of Macaque to a high of 50 kHz for one bat.

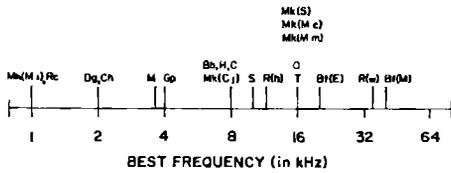


FIG. 13. Distribution of Best Frequency among 20 mammals. See Figs. 5, 7, and 9 for labels. Note wide variation among monkeys (Mk) and rats (R).

A large amount of variation in Best Frequency within low-level taxa can be seen in Fig. 13. Note that among the three species of Macaque, the best frequency of one is at 1 kHz while the two others are at 16 kHz—a full 4 oct higher. If the criteria used for selecting audiograms were to be relaxed so that 11 audiograms in 8 species and 6 genera of monkeys would be included, Best Frequency is found to be 1 kHz for one species, 2 kHz for one species, 4 kHz for no species, 8 kHz for three species, and 16 kHz for two species, with one species, *Macaca mulatta*, reported at four different frequencies (2, 8, 12, and 16 kHz) by four different investigators. Thus, the range of Best Frequency among Monkeys appears to be 3 oct within a single species and 4 oct within a single genus. Obviously, a particular best frequency is neither a specific nor a generic attribute in monkeys.

Figure 13 also shows that the two varieties of laboratory rats—*R(h)* (hooded rats) and *R(w)* (white rats)—have best frequencies more than an octave apart. Since the two rats are subspecies of the same species, this wide difference implies that a particular best frequency is not a specific attribute among rodents either. With such large variations between varieties of the same species and between species of the same genus, comparisons between higher-level taxa, such as between primates and nonprimates or between mammals and nonmammals are obviated. Since its wide variation within the lowest taxonomic levels stands in marked contrast to that of the other four parameters used in this analysis, Best Frequency is, at present, the least useful indicator of a mammal's general mode of adaptation. Whether its variability proves to be due mostly to measurement error, or to a true supersensitivity to ecological pressures, conclusions based on comparisons of Best Frequency between two or three diverse species are certainly premature.

For the two morphological parameters, the only correlate of Best Frequency that gains statistical significance is Maximum Δt ($r = -0.55$, $p < 0.05$), but even this relationship may be trivial. It can be accounted for, statistically, by noting that High-Frequency Cutoff is correlated with both Maximum Δt and Best Frequency ($r = -0.62$, $p < 0.01$): An animal with a high best frequency always has a high upper limit. For purposes of explanation, therefore, either Best Frequency or High-Frequency Limit could be claimed as the chief effect of Maximum Δt and con-

sequently the chief effect of selective pressure for sound localization. But since Maximum Δt accounts for 69% of all the variance in High-Frequency Limit among mammals and only 30% of the variance in Best Frequency, it can be seen that there is at least one more factor influencing a mammal's best frequency than there is influencing its high-frequency limit.

Thus, for mammals as a whole, no obvious clue to the significance of Best Frequency appears beyond the almost trivial observation that animals with a high best frequency always have a high upper limit of hearing, and animals with a high upper limit usually have a high best frequency. Further, the statistical method employed here provides no convincing information about which one of these two characteristics is the primary attribute paralleling functionally close-set ears. However, the relation of these two parameters to each other and to Maximum Δt reinforce the more general conclusion based on the analysis of High Frequency Cutoff alone: The uniquely mammalian capacity for high-frequency hearing is probably the result of selective pressure for accurate sound localization.

2. Evolution of Best Frequency in Man's Lineage

Figure 14 shows Best Frequency for the animals in the phyletic sequence. Over the first four phyletic positions, Best Frequency alternates between 8 and 16 kHz. At the level represented by Macaque, Best Frequency ranges from 1 to 16 kHz. At the last two levels, Best Frequency is low, though higher for Man than for Chimpanzee. As is the case for mammals in general, no regression line results in a significant reduction of variation, whether it is based on Ancestry as in Fig. 14, on Maximum Δt , or on Body Weight, either singly or in combination.

However, Best Frequency and High-Frequency Cutoff are highly correlated once more ($r = -0.96$,

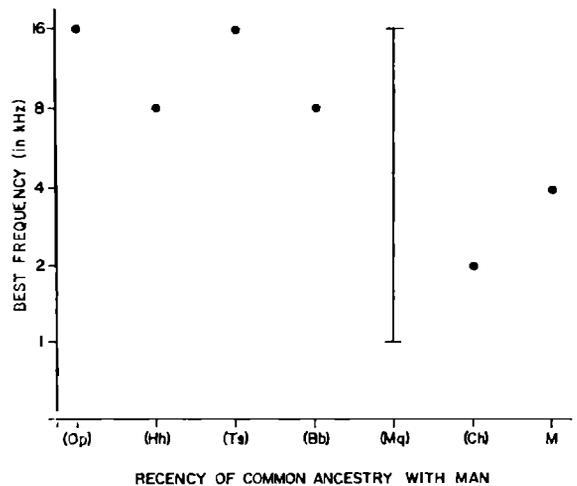


FIG. 14. Best Frequency in animals of phyletic sequence. Vertical line above Mq brackets range of best frequencies reported for single genus of monkeys (*Macaca*).

$p < 0.01$). Although this correlation is higher within the phyletic sequence than it is for mammals as a whole, no clue to the possible primacy of one or the other of these two parameters is evident. Therefore, as in the case of mammals in general, we are inclined to group the two characteristics together under the more neutral and inclusive term "high-frequency hearing" and conclude that the animals in the phyletic sequence, and man's ancestors in the inferred phylogenetic sequence, were not shielded from selective pressure for accurate sound localization and the result has been the same for them as for any other mammal.

3. Conclusions

● Best Frequency proves to be subject to a high degree of variation within genera where more than one species has been tested, and within species where more than one variety has been tested. Since this variability may be the result of differences in experimental technique, no great significance can yet be properly attached to it. The relations between Best Frequency and High-Frequency Cutoff, and between each of these parameters and Maximum Δt , suggest that high-frequency hearing is related to, and possibly the direct effect of, selective pressure for accurate sound localization. Perhaps more substantial clues to the special significance of best frequency might be gained by experimentation in animals possessing a high upper limit of frequency in combination with an unusually low best frequency (e.g., raccoon or *Macaca irus*).

E. Area of Audible Field

The final parameter included in the statistical analysis is the area of the region bounded by the audiogram below and the +70 dB horizontal above. The reason for including this measurement can be seen in Fig. 6, where there appears to be a gradual enlargement of the audible field paralleling the phyletic sequence of primitive mammals. The area of the audible field for a particular audiogram has been approximated by summing the differences (in decibels) between the threshold intensity and +70 dB at each frequency octave. This procedure can be visualized by imagining the audiogram to be a bar graph (instead of a continuous curve) with each bar an octave wide, centered on a frequency octave, and extending from the intensity threshold below upwards to +70 dB. The value used as the total area of the audible field is the sum of the areas of the individual bars. Although this procedure generates estimates that are too inexact for other purposes, the deviation from the true area of the audible field proves to be quite small for all but the most tortuous audiograms.

Before considering the distribution of this parameter among mammals, it should be noted parenthetically that the scaling of frequency in octaves results in an obvious bias in favor of animals that are sensitive to

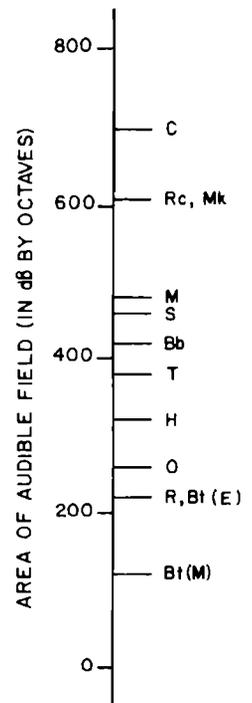


FIG. 15. Distribution of Area of Audible Field among 12 mammals. See Figs. 5, 7, and 9 for labels.

low frequencies. For example, bats have much smaller areas of audibility (120) than do humans (480) even though their hearing spans a much wider frequency range when measured in kilohertz instead of octaves. Although in abstract the logarithmic bias accompanying an octave scaling may seem much too large to allow fair comparison, there are many more mathematical, physical, physiological, and psychological reasons for scaling frequency in octaves than there are for scaling it linearly.

1. Area of the Audible Field in Mammals

The distribution of the Area of the Audible Field for 12 mammals is shown in Fig. 15. It ranges from a low of 120 for one variety of bat to a high of 700 for cat. The average of the distribution is 400 and its standard deviation is about 180.

Although this distribution is statistically quite different from the corresponding one for birds, which appears to range only as high as 345, there is a great deal of overlap between the two distributions (cf. Schwartzkopf, 1955). For example, the area of the audible field in pigeon is about 250, which falls above three of the 12 mammals in Fig. 15. In marked contrast to either birds or mammals, however, the one reptile (turtle) that has been tested behaviorally has an audible field whose area is only 75 (Patterson, 1966). Whether this constitutes a real difference between reptiles and mammals or birds or is just an aberrancy of turtles cannot be answered until data on more reptiles become available. However, even with only 12 mammals and one reptile represented, the probability that the areas of the audible field in the

two classes will eventually prove to be the same is less than 0.05. Thus, the present state of knowledge provides more evidence to support the existence of a real difference between mammals and reptiles as well as between mammals and birds than to refute it.

Although the area of the audible field is statistically different for mammals and birds, it is not greatly different. Thus, this dimension is not one on which strong arguments concerning the special contribution of the primitive mammalian ear can yet be based. Nevertheless, the way in which the two classes differ is in high-frequency sensitivity. As has been already discussed, this capacity is bestowed on mammals by their middle-ear linkage and it is by this means that some lineages of mammals (e.g., cats, raccoons, monkeys) eventually increased their total audible field to a size almost certainly unprecedented and unmatched among Vertebrates.

At present, audiograms are complete enough to estimate safely the area of audible fields in only 12 mammals. Partly due to this relatively small number, no correlation between the size of audible field and any of the three explanatory parameters reaches statistical significance for mammals as a whole. Thus, no further clues to the anatomical means nor the adaptive value of large audible fields are provided beyond those that apply directly to the more refined parameters discussed previously. At this time, only the differences between the audible fields of mammals, birds, and, possibly, reptiles seem quantitatively great enough to warrant speculation.

2. Evolution of the Audible Field in Man's Lineage

The area of the audible field of animals in the phyletic sequence appears in Fig. 16. It can be seen that the area increases across the first five levels, peaks at the Monkey stage and then drops once more at Man. Most of this change is explainable in terms of the two more refined parameters—Low-Frequency Sensitivity and High-Frequency Cut Off. The area increases over the first few stages because low-frequency sensitivity increases while the high-frequency limit remains high

and almost constant (cf. Figs. 8 and 10). The decrease in area from Monkey to Man is due mostly to a decrease in the upper limit while low-frequency sensitivity remains relatively constant.

Despite the decrease in the last stages in Fig. 16, the size of the audible field in the phyletic sequence is well correlated with "Ancestry" ($r=0.81, p < 0.05$), but not with either Maximum Δf nor Body Weight. Further, the correlation between Ancestry and Area increases when Maximum Δf and Body Weight are held constant ($r=0.98, p < 0.05$). Thus, the increase in area across the first five levels of the phyletic sequence is probably not a matter of chance, nor does it merely parallel differences in the sizes of heads or bodies.

From this observation, it is tempting to assume that a large audible field is somehow generally better than a small one and, therefore, the increase in area across the sequence is a sign of an increase in some general auditory competence. However, this argument does not explain the decrease in area at the highest levels of the sequence without suggesting that Man is somehow less competent than other anthropoids. This question is reopened below.

3. Conclusions

- The average audible field of mammals is larger than that of birds and probably larger than that of reptiles. These differences are due mostly to the mammalian capacity for high-frequency hearing. Although the mammalian version of the middle ear allowed the expansion of the audible field into high frequencies, a large audible field is *not* a primitive characteristic of mammals.
- Apparently Man's ancestors gradually attained more extensive audible fields by increasing their sensitivity to low frequencies until the Eocene. Since that time the audible field has slightly regressed due to the loss of high-frequency hearing.

III. HUMAN HEARING

Although the primary goal of this paper is to identify the significant changes in hearing capacity that accom-

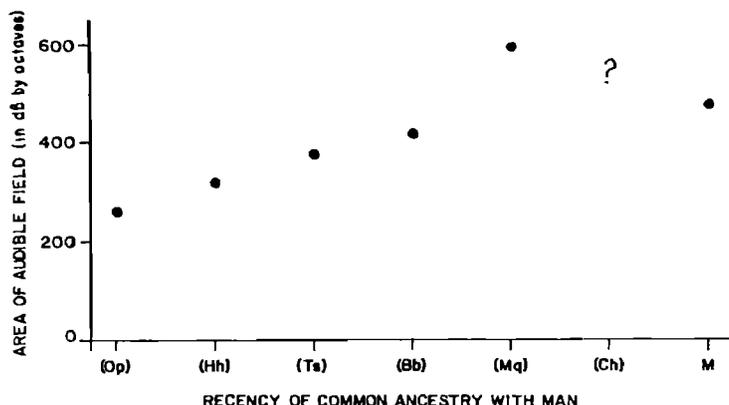


FIG. 16. Area of Audible Field in animals of phyletic sequence. Query locates estimate for chimpanzee based on an incomplete audiogram.

panied the evolution of mankind, the Figures also allow Man's auditory capacities to be compared to those of other mammals. In the past, comparisons of this kind have typically concluded that human hearing is somewhat different from that of other animals, and yet it is clearly superior in certain important ways. For example, most textbooks and popular periodicals, and even a surprisingly large number of scientific journals, contain statements such as: "Some animals hear higher frequencies than man, but man hears lower frequencies much better than animals." In these statements, terms such as the "but," instead of a neutral "and," are used either to imply that low-frequency sensitivity is known to be an important evolutionary advancement over high-frequency sensitivity or, more generally, that for every ostensible inferiority of human hearing, there is a still more important superiority to redeem it.

Ignoring the underlying subscription to a *scala naturae* that prompts such statements in the first place, the parameter distributions in the foregoing Sections (Figs. 7, 9, 11, 13, and 15) serve to deny emphatically the idea of a general human auditory superiority. To begin with, human hearing is certainly *not* superior to other mammals' along any of the strictly physical dimensions included here. Of the mammals for which comparable data are available, 35% are more sensitive (Lowest Threshold), 39% are more sensitive at 1 kHz, 100% have higher upper limits, and most important, 25% have larger audible fields. Indeed, only *after* the human audiogram is carefully compared to all of the other audiograms can a potentially significant "superiority" be found in it. For example, at 0.06 kHz, it can be claimed without fear of immediate contradiction that humans may be more sensitive than any other mammal. However, as has already been discussed, there are no adequate data for comparison at so low a frequency. Without the careful control of irrelevant noise that is provided only by earphones, and without the lowest possible estimates of threshold intensity that are gained only from knowledgeable and cooperative subjects, audiograms of animals do not now, and may never, approximate the human audiogram at low frequencies. Thus, the possible uniqueness of human audition at very, very low frequencies is not yet denied. With technological advances in sound delivery systems and behavioral testing methods, combined with an ever-increasing variety of animal subjects, however, it would not be surprising if man's fabled low-frequency sensitivity were soon to be seriously rivaled or even flatly exceeded. Therefore, if evidence is sought for man's general "superiority," audition is probably not the place that it will be found. If any mammal can be rated as inferior or superior, it is opossum that is inferior and cat that is superior.

When the distribution of mammalian audiograms is the standard to which Man's hearing is compared and anthropocentric bias set aside, it can be concluded that

frequencies low enough to be in man's range of (possibly) superior sensitivity are truly *subsonic*, by the same argument that the bat's or dolphin's are *supersonic*. At the present state of knowledge, both capacities must be considered to be about equally aberrant—the result of adaptation to equally bizarre ecological niches.

At present, human hearing can be *demonstrated* to be extreme in only one way: Man's high-frequency limit is certainly the lowest of all mammals yet tested. The biological significance of this fact remains elusive. Since the very high correlation of the upper limit of frequency with the functional distance between the ears is the only clue to its general significance known to us, it seems that Man's low upper limit is likely to be related to his ability to localize sounds accurately on the basis of binaural time cues alone (Δt). This same correlation, however, also implies that Man does not have the lowest upper limit among mammals because he does not have the widest-set ears. Thus, even this characteristic is probably not a unique one. It would seem that that the only safe conclusion at the present time is a dissatisfyingly weak and restricted one: Among mammals, Man has the lowest frequency range of sensitivity yet discovered—whether his range is unique and aberrant or, instead, just unusual, is not known.

IV. SUMMARY

Five descriptive parameters of hearing—High-Frequency and Low-Frequency Sensitivity, Lowest Threshold, Best Frequency, and Area of the Audible Field—have been compared statistically, first, among mammals in general, and, then, among seven animals selected to approximate a phylogenetic sequence of man's ancestors. Three potentially explanatory parameters—Body Size, Maximum Binaural Time Disparity (Δt), and Recency of Common Ancestry with Man—have also been explicitly included in the analysis.

The results show that: (1) High-frequency hearing (above 32 kHz) is a characteristic unique to mammals, and, among members of this class, one which is commonplace, primitive, and highly correlated with functionally close-set ears. It is concluded that high-frequency hearing is a result of selective pressure for accurate and instantaneous localization of the source of brief sounds. (2) Good low-frequency hearing (1 kHz and below, is neither unique to mammals, nor is it commonplace nor a primitive characteristic of the Class. Low-frequency hearing improved markedly in Man's line of descent, but the kind and degree of improvement are not unique among mammalian lineages. (3) The over-all sensitivity (or lowest threshold) of mammals is not greatly different from birds, and high sensitivity is not a general nor, probably, a primitive characteristic among mammals. High sensitivity developed in the earliest stages of man's lineage and has remained relatively unchanged since the simian (Eocene) level. (4) The frequency of the lowest threshold has declined in Man's lineage—

the greatest drop probably occurring near the simian level during the Eocene. This change was most closely related to the drop in the upper frequency limit of hearing. (5) The total area of the audible field probably increased until the Eocene and has decreased since then. The increase at the early stages was due to an increase in low-frequency sensitivity while high-frequency sensitivity remained unchanged. The decrease at the later

stages was due to a loss of high-frequency sensitivity while low-frequency sensitivity remained unchanged.

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