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# HEARING IN PRIMITIVE MAMMALS, IV: BUSHBABY (*Galago senegalensis*)

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## INTRODUCTION

This report is the fourth in a series concerned with the general question of the evolution of human hearing. The goal of the series and the equipment and procedures employed have already been described elsewhere (Ravizza, et al., 1969).

The bushbaby (Galago senegalensis) has been included in this series because it is a member of the most primitive suborder (Prosimii) of the order Primates (see, for example, Simpson 1945; Osman-Hill; 1953). Although the bushbaby is not the most primitive member of this suborder and, consequently, not the most primitive of Primates, it is little, if any, more advanced over the Lemurs which are the most primitive Primates, in either otological or neurological characteristics (Osman-Hill, 1953). Thus, for the purposes of tracing the phylogenetic history of human hearing by comparative inference from a phyletic sequence of extant mammals, the bushbaby ear and auditory system is probably as good an approximation to the ear and auditory system of the most ancient Primates that is now (or ever will be) available. Consequently, the bushbaby is a proper candidate for inclusion when placed at a phyletic level intermediate to Insectivores below and Anthropoid Primates above. It follows that a comparison of the auditory capacities of the bushbaby first with opossum, hedgehog, and tree shrew and then with those of Anthropoids, might reveal some of the adaptations that were made during the earliest stages in the primate period of the evolution of human hearing (see Fig. 1, Reference 7).

As in the case of the first three experiments in this series, the hearing of bushbabies was tested with the technique of conditioned suppression (Estes and Skinner, 1941; Sidman et al., 1966).

## METHOD

*Subjects.*

Two adult wild-born and experimentally naive bushbabies (*Galago senegalensis*) were used, each weighing about 150g-200g.

*Apparatus and procedure.*

The behavioral apparatus, the sound production, measuring and monitoring equipment, and the procedures for training and testing primitive mammals are described in detail elsewhere (Ravizza, et al., 1969). Briefly, the bushbabies were trained to lick a water spout in order to obtain a food reward. When the lick rate became stable, a pure

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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 bushbaby would stop licking whenever a tone was present. In test trials this stoppage or suppression of licking was used as evidence that the bushbaby perceived a tone.

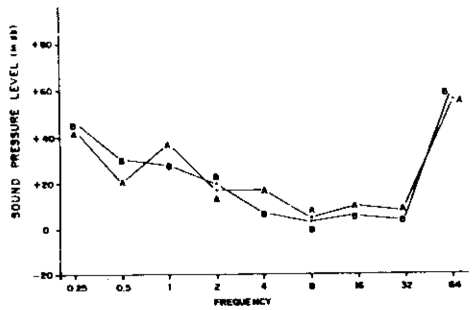


Fig. 1. Audiograms through 64 kc/s of two bushbabies; SPL re 0.0002 μbar.

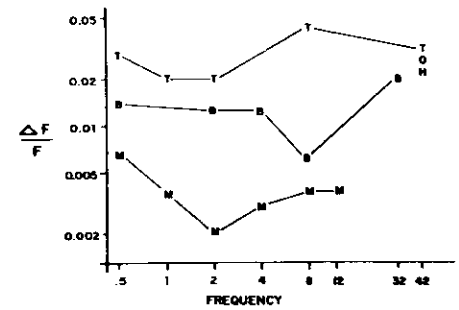


Fig. 2. Frequency difference limens in bushbaby (B), tree shrew (T), man (M), opossum (O), and hedgehog (H). Dips in the value of ΔF/F in bushbaby and man occur near their best frequency.

## RESULTS

Figure 1 gives the audiograms of two animals showing that the bushbaby can hear pure tones from 0.25 to 60 kc/s with best frequencies in the range from 8-32 kc/s. If the audiograms were to be extrapolated to 80 db, the range of audibility would extend from less than 0.1 to more than 70 kc/s.

In order to obtain evidence on whether or not the bushbaby might employ an unusual mechanism for high-frequency hearing (e.g., Roeder and Treat, 1961), frequency limen (ΔF) tests were also performed. The results of these tests are shown in Fig. 2 as Weber fractions (ΔF/F) as a function of the frequency in kc/s of the fixed tone. For ease of comparison the same fractions are plotted for humans (Geldard, 1953), for tree shrews (Heffner, et al., 1969), and at 42 kc/s for opossums and hedgehogs (Ravizza, et al., 1969a, b). The bushbaby is measurably more sensitive to small changes in frequency than the tree shrew, but less sensitive than man. For the main purpose here, however, the important result in Figure 2 is that the Weber fraction is about the same across the entire range of frequencies. We conclude that the bushbaby, like the opossum, hedgehog, and tree shrew, probably does not make use of an unusual mechanism for high-frequency hearing (Corso, 1963; Roeder and Treat, 1961).

## DISCUSSION

*High-frequency limit.*

The bushbaby can hear tones of 60 kc/s and can probably hear tones as high as 70 kc/s at a SPL of 80 db. Although this characteristic may appear bizarre at first, we have already shown that opossum, hedgehog, and tree shrew hear tones in this range also. Thus, the bushbaby becomes the fourth of four primitive mammals which have proved to be capable of high-frequency hearing.

In the face of this unanimity it is profitable to turn the question around: are there any mammals that cannot hear high-frequencies? A wide (though probably not exhaustive) search of the pertinent literature reveals that only two mammals, chimpanzee and man, have been shown *not* to hear frequencies above 32 kc/s. At least 17 other mammals, including the four in this series, have undergone tests that have included behavioral thresholds to tones of 32 kc/s or higher. In every case, sensitivity to frequencies above 32 kc/s has been persuasively demonstrated. Thus, even though the four mammals discussed here and the thirteen others in the literature are not a random selection of extant mammals, it can no longer be argued that high-frequency hearing is a rare occurrence. Apparently, the reverse is true: the *lack* of sensitivity to tones above 32 kc/s is a rare occurrence. Therefore, the 2 (chimps and men) out of 19 species that have low upper limits are more safely considered to be auditory anomalies than are the 17 out of 19 that have high upper limits.

*Low-frequency sensitivity.*

Table I allows thresholds at low-frequencies to be compared for opossum, hedgehog, tree shrew, bushbaby, and man. The table shows a clear decrease in threshold that corresponds closely to the phyletic level of the animals. With this strong trend toward higher sensitivity, it is difficult to escape from the obvious inference that man's ancestral lineage must have been exposed to strong and persistent selective pressure for low-frequency sensitivity. This idea is not a new one, of course (see von Bekesy and Rosenblith, 1951, for example). Even a small sample of low-frequency thresholds in Mammals reveals a marked difference between man and other mammals. With the strong

**TABLE I**

ABSOLUTE THRESHOLDS IN db SPL re 0.0002 μBAR FOR LOW FREQUENCY TONES

| | Frequency in c/s | | |
|---|---|---|---|
| Animal | 250 | 500 | 1000 |
| Opossum | >80 | 72 | 62 |
| Hedgehog | 69 | 63 | 48 |
| Tree Shrew | 55 | 27 | 30 |
| Bushbaby | 43 | 25 | 28 |
| . | . | . | . |
| . | . | . | . |
| . | . | . | . |
| Man | 15 | 8 | 6 |

support of this conclusion provided by the data in Table I, however, it would seem that attention could now be turned to the identification of the anatomical changes accompanying this change in hearing capacity and the sources of selective pressure which caused them.

*Overall sensitivity.*

Because high-frequency sensitivity remains relatively constant while low-frequency sensitivity increases, the range of audible frequencies also increases across the sequence of four primitive mammals. In addition to this increasing frequency range, the audiograms of the first three animals in the sequence show marked increase in sensitivity at their best frequency. This combination of differences can be reduced to one comparable parameter: the *area* of each animal's audible field. Using an octave scale for frequency and the usual decibel scale for SPL the areas are 260, 320, 380, and 420 for opossum, hedgehog, tree shrew, and bushbaby, respectively. Thus, overall sensitivity as measured by the area of the audible field shows a consistent increase from each level of the phyletic sequence to the next. It is tempting to interpret this widening area of audibility as evidence of an increase in general auditory competency. But this conclusion is probably best reserved until comparable figures become available for a larger array of species.

*Best frequency.*

The frequency of the lowest point on the audiograms for the four animals does not parallel phyletic level. Instead, it alternates between 16 and 8 kc/s. Thus we see no significant trend nor important conclusion to be derived from this parameter. Since it is possible that the best frequency of each of the four animals may, in fact, lie at an untested frequency between 8 and 16 kc/s, the lack of either an obvious trend or an obvious constancy may be due merely to the lack of refinement in the octave scale for frequency that was used. However, the collection of best frequencies in the 8-16 kc/s range stands in marked contrast to man's best frequency which is 2 or 3 octaves lower. Therefore, a real shift in best frequency almost certainly occurred sometime during man's phylogenetic history. However, the similarity of best frequencies in the four primitive mammals suggests that this shift probably occurred after a prosimian level was achieved.

*Frequency discrimination threshold.*

Figure 2 shows that the bushbaby is capable of more refined frequency discriminations than is the tree shrew, but still is less sensitive than man. Although few comparable data are available on this point, it seems that the difference between tree shrew, bushbaby, and man may be a real one, and if so, of evolutionary significance. There are several potential anatomical and physiological explanations for this increase in discriminatory capacity: the length of the basilar membrane, the density of its innervation, and lateral inhibition are some of the more obvious. However, we have no verification for any of these possibilities at present.

## SUMMARY

The bushbaby hears tones ranging in frequency from 0.250 to 60 kc/s with a best frequency near 8 kc/s. Throughout most of this range, the bushbaby is capable of discriminating frequencies which differ by less than 2%. Through comparison with opossum, hedgehog, tree shrew, and man it is concluded that 1) high-frequency sensitivity is almost certainly a usual characteristic among non-Hominoids; 2) sensitivity to low-frequencies and overall sensitivity improved markedly at least until the prosimian stages of man's mammalian lineage; 3) the best frequency of animals in man's lineage probably remained in the 8-16 kc/s range until after the prosimian stage was achieved.

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