HEARING IN PRIMITIVE MAMMALS, III:
TREE SHREW (*Tupaia glis*)[1]

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INTRODUCTION

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

The tree shrew has been included in this series by virtue of its curious collection of primitive and advanced anatomical characters. On the one hand, its primitive characters are similar to those usually associated with Insectivores; on the other, its more advanced characters, especially its visual system, are reminiscent of features found in Primates. Some morphological authorities have interpreted this combination of characteristics as sufficient to admit tree shrews into the order of Primates (e.g., Clark, 1959; Simpson, 1945); while others have concluded that tree shrews are simply Insectivores with a primate-like visual system (e.g., Osman-Hill, 1953; Campbell, 1966a, b; Simpson, 1965). Despite this difference in opinion concerning taxonomic status, most agree that the tree shrew approximates a pivotal stage of evolutionary development through which mankind's ancestors probably passed in the Paleocene (Romer, 1967). Consequently the tree shrew is a proper candidate for inclusion in a phyletic sequence of mammals at a stage intermediate to ground-dwelling Insectivores below and prosimian Primates above (Simpson, 1965). With some reservation due to lack of paleontological verification then, comparison of the auditory capacities of tree shrew first with those of the opossum and then with those of the hedgehog, might reveal some directions that were followed during the earliest stages in the evolution of human hearing (see Fig. 1, Reference 21).

As in the case of opossum and hedgehog, the hearing of tree shrews was tested with the technique of conditioned suppression (Estes and Skinner, 1941; Sidman et al., 1966). In addition, other tree shrews were tested on similar tasks with a shock-avoidance technique in a double-grill box (e.g., Masterton and Diamond, 1964).

METHOD

Subjects

In all, four wild-born tree shrews (*Tupaia glis*) were used in this experiment. Two were tested with conditioned suppression and two with shock avoidance. All were adults weighing between 150g and 250g.

Apparatus and procedure

The behavioral apparatus, the sound production, monitoring and measuring equipment, and the procedures for training and testing primitive mammals with the technique of conditoned suppression are described in detail elsewhere (Ravizza et al., 1969). In all essentials the method used for measuring absolute thresholds and frequency difference (ΔF) thresholds in tree shrews was identical to that used for opossums and hedgehogs, the first two species of this series.

In addition to this standard testing procedure, two other tree shrews were tested with a more usual shock-avoidance technique. The method employed for these tests was essentially similar to that used by Butler et al. (1957) in their tests on cats. Briefly, the tree shrews were trained to cross from one compartment of a double grill box to the other whenever a "safe" signal was replaced with a "warning" signal. For absolute thresholds, the safe signal was silence and the warning signal was a pure tone of a given frequency and intensity. For ΔF thresholds, the safe signal was a 1/sec train of tone pulses of a fixed frequency 30 or 40 db above the previously determined threshold. The warning signal was a train of tone pulses identical in all respects to the pulses in the safe signal except that the test frequency alternated with the fixed frequency, i.e., high-low-high-low . . . .

If the animal crossed to the opposite compartment within 10 sec after the onset of the warning signal, the warning signal was replaced by the safe signal, shock was not delivered, and a correct response was recorded for the trial. Of, on the other hand, the tree shrew did not respond within 10 sec after the onset of the warning signal, the warning signal was continued and intermittent shock was administered through the grill box floor until the response was made. As soon as the tree shrew entered the opposite compartment and escaped shock, the warning signal was replaced by the safe signal. In this event an incorrect response was recorded for the trial. Because the safe signal occupied the entire interval between successive warning signals, a tree shrew occasionally responded during the safe signal. These spontanious responses or false-positives were also recorded and served as a baseline by which discrimination between the safe and warning signals could be measured.

In order to minimize intensity gradients within the apparatus in shock-avoidence testing, the speaker from which the tones were projected was placed about 15 feet from the grill-box. But the distance from speaker to subject and the sound shadows produced by the barred walls limited the range of frequencies that could be tested and undoubtedly influenced the reception of even moderately high frequencies beyond a point that is detectable by sound pressure level equipment.

RESULTS

Figure 1 gives the audiograms of the two tree shrews obtained with conditioned suppression, showing that tree shrews can hear pure tones from 0.250 to 60 kc/s. If the audiograms are extrapolated to +80 db, it can be concluded that tree shrew hearing ranges from about 0.125 to about 70 kc/s.

Figure 2 summarizes the audiograms obtained with the two different testing techniques. Although some of the thresholds differ by 10 db, the similarity of shape, low-frequency limit, and range of best frequencies inspires confidence in both techniques.
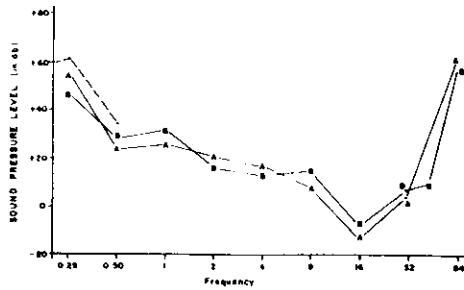
Fig. 1. Audiograms through 64 kc/s of two tree shrews obtained with the conditioned suppression technique; SPL re 2×10^{-4} μbar. Dashed line shows average ambient noise level.
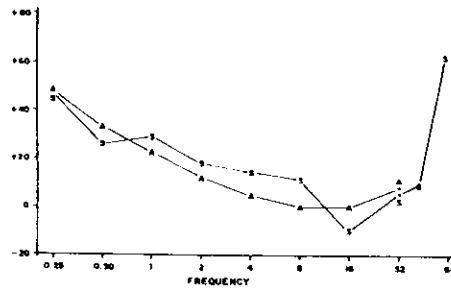
Fig. 2. Average audiograms through 64 kc/s of two tree shrews obtained with shock-avoidance (A) and two obtained with conditioned suppression (S). Apparent superiority of hearing in tree shrews tested by shock-avoidance is probably due to slight bias in measurement of true SPL within grill box.

Because of the difficulties inherent in the interpretation of false-positive responses and also in measuring effective SPLs in the shock-avoidance apparatus, we place greater confidence in the audiograms obtained by the conditioned suppression technique. In this latter technique it is possible to train an animal to a point where there are virtually no false-positive responses. Further, the animal's head is fixed in locus and attitude relative to the speaker throughout testing due to the physical requirements for licking the water spout. These features of the technique allow less arguable interpretation of the behavioral data and also much more accurate measurement of SPLs—the measuring microphone can be located and oriented within the region actually occupied by the animal's head during testing.

Figure 3 shows the ΔF thresholds plotted as Weber fractions (ΔF/F) as a function of the frequency of the fixed or comparison tone. For ease of comparison the same fractions are plotted for humans (Geldard, 1953) and also, at 42 kc/s, for opossum and hedgehog (Ravizza et al., 1969a, b). As can readily be seen, ΔF thresholds in tree shrew, and also in opossum and hedgehog at 42 kc/s, are almost ten times wider than those in man.

For the main purposes of this report, however, the important result in the figure is that ΔF/F is about the same at 42 kc/s as it is at the lower frequencies. From this data we conclude that, like the opossum and hedgehog, the tree shrew probably does not make use of a grossly different mechanism for high-frequency hearing than it does for low-frequency hearing (cf. Corso, 1963; Roeder and Treat, 1961).

DISCUSSION

There are at least three features of the tree shrew audiogram that merit comparison with opossum, hedgehog and ultimately, with man: high-frequency limit, overall sensitivity and best frequency.

High-frequency limit.

The results show that the tree shrew has an upper limit of hearing higher than 60 kc/s, probably about 70 kc/s at SPL of +80 db. Although at first this limit might seem to be unusually high (only dolphins and bats are known to hear higher), we have shown previously that both opossum and hedgehog also hear tones in the same range. Thus the

tree shrew is the third of three primitive mammals capable of high-frequency hearing. Apparently the reception of ultrasonic frequencies is not as rare an occurence as might be expected solely on the basis of human psychophysical data. We are led to suggest that high-frequency hearing may prove to be a general characteristic of mammals rather than a bizarre specialization of a few.

Combining the fact that opossum, hedgehog and tree shrew have about the same upper limit, with the fact that they are among the most primitive of extant animals, we also suggest that high-frequency hearing is a primitive character of mammals of the Cretaceous and Paleocene. If this were the case, the common ancestors of all placental mammals at least, and possible, of all marsupial mammals as well, were capable of high-frequency hearing. Therefore we feel that the possibility that this capacity has been merely retained by modern mammals is more likely than the possibility that it is a new and parallel achievement in the independent lines. Through this line of reasoning, it follows that apes and man may be more anomalous among mammals by virtue of their low upper limit than other mammals by virtue of their high upper limit.

Only three mammals have yet been rigorously shown to have an upper limit higher than the three primitive mammals in this series: dolphin (Schevill and Lawrence, 1953; Lilly et al., 1968) and two bats (Dalland, 1965). Since these animals also use their auditory system for echolocation (Kellog, 1961; Griffin, 1959). echolocation has usually been assumed to be the source of selective pressure for high-frequency hearing. Since
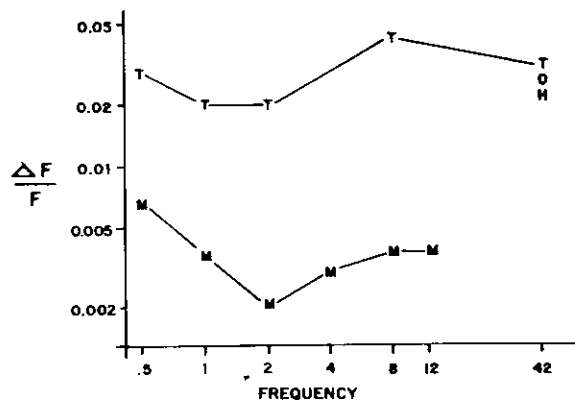

Fig. 3. Frequency difference thresholds in kc/s as a function in tree shrew (T), opossum (O), hedgehog (H), and man (M).

some other mammals may also be capable of echolocation, it is not impossible that all primitive mammals are capable of echolocation (e.g., Gould, 1964; Riley and Rosenzweig, 1957; Cotzin and Dallenbach, 1950). But the chance that each of these animals depends on echolocation to the same degree as dolphins and bats seems too remote, at present, to conclude that this mode of adaptation is the only, or even a major, source of selective pressure for high-frequency hearing in most mammals. Therefore, we are inclined to look elsewhere for the significance of high-frequency hearing in those mammals where echolocation is not easily demonstrable.

Overall sensitivity

The sensitivity of the tree shrew is greater than opossum at every high frequency except the highest one tested (60 kc/s) (cf. Ravizza et al., 1968a). The tree shrew is also more sensitive than hedgehog at seven of the nine frequencies tested. Only at 4 and 8 kc/s are the thresholds of hedgehog lower than the thresholds of tree shrew (cf. Ravizza et al., 1969b). In addition to this general superiority in sensitivity, the lowest threshold of tree shrew (−15 db SPL at 16 kc/s) is about 20 db lower than the lowest threshold of the hedgehog (+5db at 8 kc/s) and more than 30 db lower than the lowest threshold of opossum (+18 db at 16 k/cs).

This clear increase in sensitivity across the sequence, opossum-hedgehog-tree shrew, parallels both "recency of common ancestry" (i.e., phyletic level) and also several anatomical modifications in the middle ear. For example, the opossum possesses a tympanum incompletely encircled by a thin tympanic ring (ectotympanic) and is also the least sensitive to sound. The hedgehog's tympanum is more completely encircled by a tympanic ring and this animal is measurably more sensitive than the opossum. Finally, the tree shrew's tympanum is still more rigidly supported and proves to be still more sensitive than the others (Van der Klaauw, 1925, 1929; Clark, 1925, 1926). Although it is not inpossible that this relation between overall sensitivity and rigidity in the support of the tympanum is the key to the increase in sensitivity observed, there are also many other differences between the ears of the three animals that may contribute to more sensitive hearing (e.g., differences in absolute area of the tympanum). Certainly, the sifting of these many alternative possibilities is now premature.

The increase in sensitivity paralleling the phyletic level of the three animals suggests that highly sensitive ears were not a characteristic of ancient animals but instead, gradually evolved during the Cretaceous and Paleocene. But since man's hearing of low frequencies is markedly still more sensitive than either of the primitive mammals, it seems safe to conclude that selective pressure resulting in greater sensitivity in man's lineage must have persisted for at least some time after the Paleocene too. However, the source of this selective pressure and the reason for its persistence is not now apparent.

Best frequency

In the audiogram obtained with the conditioned suppression technique, the tree shrew shows a sharply tuned best frequency at 16 kc/s. Although this feature does not appear in the shock-avoidance audiogram, 16 kc/s is well within the range of frequencies where the barred walls of the grill box and the distance of the speaker from the apparatus makes SPL measurements imprecise and of doubtful accuracy. Since opposum, hedgehog and tree shrew audiograms were each obtained in the same apparatus in the conditioned suppression tests, however, comparisons of best frequencies there are not as risky.

By the conditioned suppression technique, the opposum and tree shrew have a best frequency of 16 kc/s and the hedgehog has a best frequency of 8 kc/s. Thus, at first glance, it appears that the best frequency may have alternated between 16 kc/s and 8 kc/s over the three stages of the phyletic sequence. But before this conclusion is accepted, it is noteworthy that best frequency is subject to at least two sources of uncontrolled variance each of which tempers conclusions based on only one-octave differences. The first of these derives from the fact that thresholds were obtained only at octaves. This means it is possible that all three animals have a best frequency intermediate to 8 and 16 kc/s and may, in fact, have the same one (e.g., 12 kc/s). The second source of potential error derives from the fact that both opossum and hedgehog have closely similar thresholds at

more than one frequency (opossum at 16 and 32 kc/s, hedgehog at 8 and 16 kc/s). This means that even with an estimated error as low as ±5 db in absolute threshold, the apparent best frequency of opossum or hedgehog might shift an octave upwards with the result that a slight trend toward lower best frequencies across the phyletic sequence would appear. For these reasons we are not now inclined to attach any great significance to the apparent alteration of best frequency across the sequence. However, the range of best frequencies of these mammals (8 to 16 kc/s) stands in marked contrast to that of man (3 to 4 kc/s) and a real shift of best frequency sometime during the later stages in the evolution of man is implied.

SUMMARY

The tree shrew hears tones from 0.25 to 60 kc/s and has a best frequency in the region of 16 kc/s. Further, the tree shrew is capable of discriminating frequencies which differ by about 0.3% over most of the range. Through comparison to opossum and hedgehog it is concluded that high-frequency hearing was probably a common-place trait among ancient mammals and may be a common-place trait now, and that overall sensitivity and sensitivity at low frequencies improved during the earliest stages in man's lineage.

ACKNOWLEDGEMENT

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