b. conditioned suppression, insectivore

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HEARING IN PRIMITIVE MAMMALS, II: HEDGEHOG
(*Hemiechinus auritus*)[1]

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INTRODUCTION

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

The hedgehog's inclusion in this series relies on conclusions from morphology and paleontology. Comparative anatomy has revealed that the hedgehog brain and ear are close approximations to the brain and ear that probably existed in the common ancestry of Eutheria–mankind's own subclass of Mammals (Cf. Smith, 1910; Young, 1950). Paleontology has established that Insectivores resembling the modern hedgehog in most essential characters did, in fact, exist during the Paleocene and probably long before that (Gregory and Simpson, 1926). These facts mean first, that the hedgehog brain and ear are probably good approximations of the brain and ear that existed in the Paleocene ancestors of mankind and further, that the common ancestry of man and hedgehog is more recent than the common ancestry of man and opossum, which was the subject we chose for the first report in this series (Fig. 1). Therefore, a comparison of auditory capacities of opossum and hedgehog might suggest at least one of the directions that was followed in the early mammalian stage of the evolution of human hearing.

Our ability to measure auditory thresholds in the hedgehog depended once more on the practicality and generality of the behavioral technique called conditioned suppression (Estes and Skinner, 1941; Sidman et al., 1966; Hendricks, 1966).

METHOD

Subjects.

Two adult wild-born and experimentally naive hedgehogs (*Hemiechinus auritus*) were used, each weighing about 250g-300g.

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 esewhere (Ravizza, et al., 1969). Briefly, the hedgehogs were trained to lick a water spout in order to abtain a food reward. When the lick rate became stable, a pure tone was presented for 10 sec with a mild shock to the feet accompanying its offset. After a few repetitions, the hedgehog would stop licking whenever a tone was present. In test trails this stoppage or suppression was used as evidence that the hedgehog perceived a tone.

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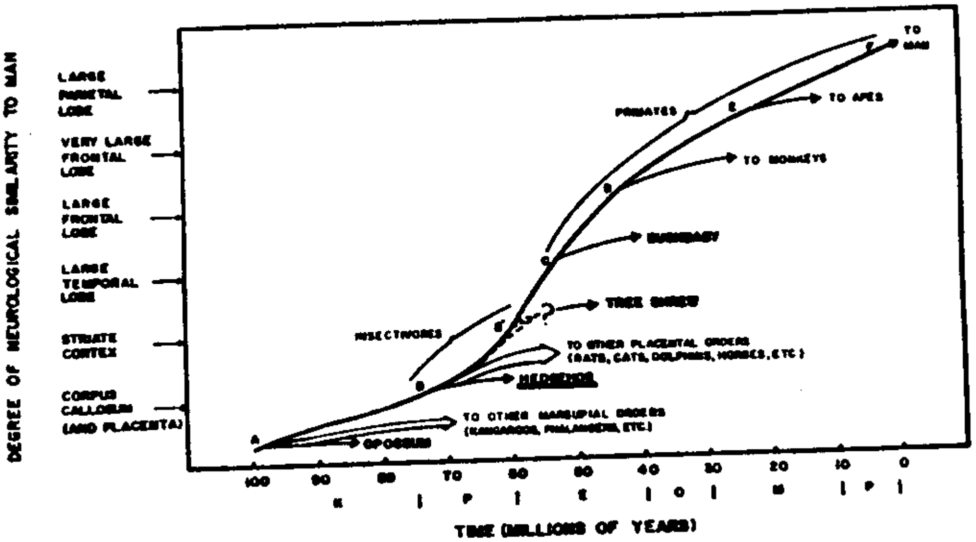

Fig. 1. Phylogenetic relations of hedgehog to some other extant mammals. Letters along main branch represent common ancestry of Man and animals in phyletic sequence.

RESULTS

Figure 2 shows that the hedgehog hears pure tones from .250 to 45 kc/s. If the audiograms were to be extrapolated to 80 db, the frequency range of audibility would probably extend from .125 to about 60 kc/s.

To evaluate the possibility that the hedgehog might be employing an unusual mechanism for high-frequency hearing, we included a frequency limen (ΔF) test in our procedure (Ravizza et al., 1969 Roeder and Treat, 1961; Corso, 1963). At 42 kc/s (40 db above threshold) the ΔF is about 1 kc/s. Since this value is within the limits that can be expected on the basis of results in other animals and also well within the limits expected on the basis of Weber's Law extrapolated from results on human subjects, we have no reason to believe that the hedgehog makes use of a different mechanism for high-frequency hearing (Ravizza, et al., 1969; Geldard, 1953).

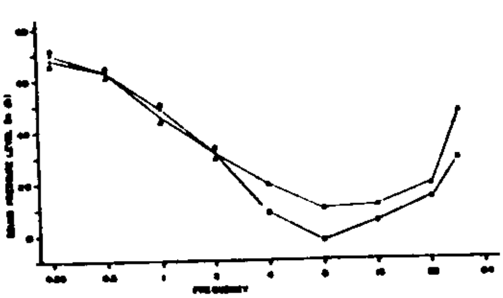

Fig. 2. Audiograms from 0.25 to 64 kc/s; SPL re 2 x 10^{-4} μbar.

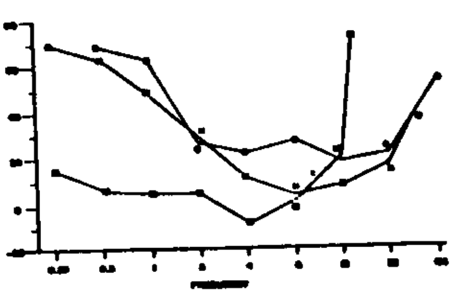

Fig. 3. Average audiograms through 64 kc/s of 2 opossums (O), 2 hedgehogs (H) and 2 men (M) measured with the same audio system.

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DISCUSSION

Two features of the hedgehog's audiogram merit comparison with opossum: the upper frequency limit and the overall sensitivity. To allow comparison, Figure 3 shows the average audiograms of hedgehog and opossum and, for reference, the average audiogram of two human subjects tested with the same audio system.

High-frequency hearing.

We did not extend threshold testing in the hedgehogs (45 kc/s) to as high a frequency as we did for opossum (60 kc/s). Nevertheless, the high-frequency cut-off in opossum and hedgehog appear to be quite similar. In fact, the hedgehogs average sensitivity at the highest frequency tested (45 kc/s) is exactly the same as the average sensitivity of the two opossums interpolated to the same frequency. This striking convergence leads us to conclude that the probable upper frequency limit of hedgehog is not much different from that of opossum–probably 60 kc/s at SPLs greater than 80 db. Whether or not the hedgehog's upper limit is the same as the opossum's however, the convergence of their audiograms at high frequencies suggests that high-frequency hearing may be a much more commonplace characteristic in primitive mammals than is usually assumed. If this proves to be the case, comparative inference of characters-in-common would imply that high-frequency hearing was also a characteristic of man's ancient mammalian ancestors.

Overall sensitivity.

Figure 3 shows that from 2 to 32 kc/s, the average threshold intensity is lower for the hedgehog than it is for opossum (14 db vs 24 db SPL). Although this difference in overall sensitivity is due to a relative insensitivity of opossum rather than a hyper-sensitivity of hedgehog compared with most other mammals, the important fact for inquiries into the evolution of human hearing is that the hedgehog is a measureable grade more similar to advanced mammals than is the opossum (Cf. Fujita and Elliott, 1965; Gourevitch and Hack, 1966; Neff and Hind, 1955; Stebbins, et al., 1966). Making use of the fact that the common ancestry of man and hedgehog is more recent than the common ancestry of man and opossum, it does not appear unreasonable to suggest than an increase in overall sensitivity accompanied the evolution of early placental mammals from their more marsupial-like ancestors.

Previously we suggested that this general increase in sensitivity may have been a result of changes in the suspension of the tympanum (Ravizza et al., 1969). At that time we were impressed with the relative insensitivity of opossum compared with advanced mammals and sought an obvious parallel in the anatomy of their middle ears. However, since we now know that even the most primitive placental mammal (hedgehog) is markedly more sensitive than the opossum, and yet it also possesses only little more rigid support for its tympanic ring, we are inclined to expand the scope of the search for possible anatomical correlates beyond the suspension of the tympanum.

SUMMARY

The hedgehog hears tones from 250 c/s to 45 kc/s, has a best frequency near 8 kc/s, and frequency discrimination of about 2.5% at 42 kc/s. If the audiogram is extrapolated to +80 db, it can be concluded that pure tone sensitivity ranges from a low of 200 c/s to a high near 60 kc/s. In comparison to opposum, the hedgehog is measurably more sensitive throughout most of this range but is, nevertheless, less sensitive than most other mammals.

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