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Short Communication

Audiogram of the hooded Norway rat

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Abstract

The behavioral audiogram of the hooded Norway rat was determined for frequencies from 250 Hz to 70 kHz. The resulting audiogram is virtually identical to the albino rat audiogram obtained by Kelly and Masterton (1977), indicating that there is no detectable effect of albinism on the audiogram of the Norway rat. The two audiograms also indicate the degree of replicability that can be obtained with current behavioral techniques.

Key words: Albino; Audiogram; Hooded rat; Psychophysics

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1. Introduction

In the course of studying the hearing ability of rodents, we have had occasion to determine the auditory thresholds of hooded rats. Although the original purpose of obtaining these thresholds was for comparison with those of other rodents tested under the same conditions, the results are of interest in their own right.

Previous audiograms of the Norway rat were determined using albino animals and no complete audiograms for pigmented Norway rats are available. Because the lack of pigmentation in animals is associated with subtle changes in the nervous system (e.g., Conlee et al., 1983), it has been suggested that their sensory abilities may differ from those of pigmented strains (Bock and Steel, 1984; Creel, 1980). Thus, the question arises as to whether the audiogram of the albino differs from that of pigmented Norway rats.

In addition, although the audiogram by Kelly and Masterton (1977) is the currently accepted standard for the albino rat, it should be noted that there exist large and significant differences between it and previously published audiograms for Norway rats (for a review, see Kelly and Masterton, 1977). Although these differences have been attributed to variation in the accuracy of sound measurements and differences in the sensitivity of behavioral techniques, the question arises as to the replicability of behavioral audiograms. As will be seen, the present results also have a bearing on this question.

2. Methods

A conditioned avoidance procedure was used in which a thirsty animal was trained to make continuous contact with its mouth on a water spout in order to receive a slow, steady trickle of water. Tones were presented at random intervals and followed at their offset by a mild electric shock delivered through the water spout. By breaking contact with the spout during tone presentations, an animal both avoided the shock and indicated that it had heard the tone. Although differing in details, this procedure is similar to the method of conditioned suppression used by Kelly and Masterton (1977) in which their animals licked a spout for water and ceased licking when they heard a tone which signalled impending shock.

2.1. Subjects

Four male Long-Evans hooded rats (designated as A, B, C and D) were used in this study. Animals A and B were 3 months and animals C and D were 9 months old at the beginning of testing, which lasted for an additional 20–80 days. Each animal was housed in a

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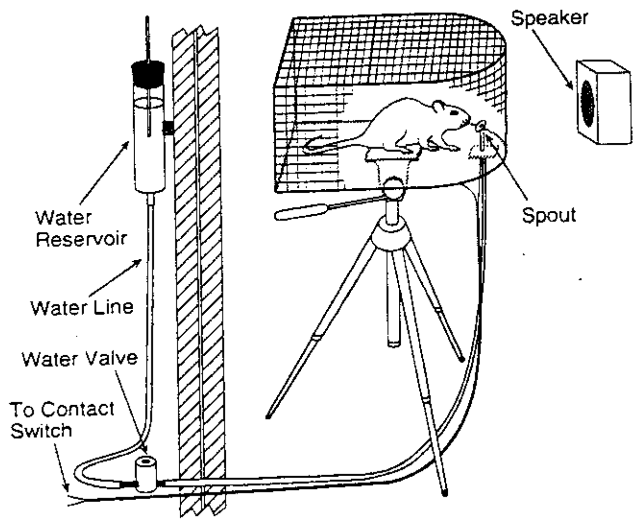

Fig. 1. Diagram illustrating the arrangement of the behavioral test apparatus (not to scale).

standard rat cage and given free access to food. The animals received water daily during testing and were given small slices of fresh fruit or vegetables (e.g., apples, carrots, potatoes) in their home cage as supplements. The ears of the animals were inspected and found to be free of disease or obstruction.

2.2. Behavioral apparatus

Testing was conducted in a carpeted double-walled acoustic chamber (Industrial Acoustics Company model 1204; 2.55 × 2.75 × 2.05 m) the walls and ceiling of which were covered with eggcrate foam to reduce sound reflection. The electronic equipment and microcomputer used for behavioral control were located outside the chamber and the animals were observed over closed-circuit television.

The rats were tested in a cage (38 × 24 × 24 cm) constructed of 1/2-inch (12-mm) hardware cloth (Fig. 1). The cage was mounted on a camera tripod 92 cm above the floor. A water spout (15-gauge stainless steel tubing) was mounted vertically up through the floor of the front of the cage so that it projected 9 cm above the cage floor. An oval stainless steel disk (1.5 × 2.5 cm) was mounted on top of the spout at a 30° angle. This arrangement permitted an animal to lick water off the spout while holding its head in a normal position facing the front of the cage.

The water spout was connected via plastic tubing to an electrically operated water valve and a 25-ml constant-pressure water reservoir located outside the chamber. A contact switch, connected between the cage and the water spout, served to detect when the animal made contact with the spout. A 3–5/s train of 50-ms pulses was used to operate the water valve whenever an animal made contact with the spout. The animals typically received 7–15 ml in sessions lasting 30–60 min. Mild electric shock was provided by a constant-current shock generator connected between the water spout and the cage floor. A 25-W light bulb located beneath the cage was turned on whenever the shock was turned on.

2.3. Acoustical apparatus

Sine waves were generated by an oscillator (Hewlett-Packard 209A) which was calibrated with a frequency counter (Fluke 1900A). The electrical signal was gated on and off with a rise-fall gate (Coulbourn S84-04), attenuated (Hewlett-Packard 350D attenuator), bandpass filtered at 2/3 octave centered on the test frequency (Krohn-Hite 3202 filter), and connected via either an impedance-matching transformer or an amplifier (Crown D75) to a loudspeaker. The electrical signal to the loudspeaker was monitored with an oscilloscope.

A loudspeaker was placed in front of the cage and oriented toward the position occupied by the animal's head when it was drinking from the spout. The distance of the speaker was varied from 0.5 to 1.5 m as needed to achieve a sound field of sufficient intensity and homogeneity (±1 dB in the area occupied by the animal's head). The loudspeakers used included a 15-in (38-cm) woofer for 4 Hz to 500 Hz, an Infinity RS2000 speaker for 1 kHz to 4 kHz, and a Foster ribbon tweeter for higher frequencies.

Pure-tone thresholds were obtained at octave intervals from 250 Hz to 64 kHz. Additional thresholds were obtained at 2.4, 3.2, 22.4, 38, 45, and 70 kHz. The animals were also tested for their ability to detect 4, 8, 16, 32, 63, and 125 Hz at 100 dB SPL.

Tones from 125 Hz to 70 kHz were pulsed, 400 ms on and 100 ms off, with a rise-fall of 80 ms (125 Hz), 40 ms (250 Hz), 20 ms (500 Hz) or 10 ms (1–70 kHz). Frequencies from 4 to 63 Hz were presented with a rise-fall time of 150 ms, an on-time of 500 ms, and an off-time of 160 ms.

The sound pressure level (re 20 $\mu N/m^2$) was measured daily with a Brüel and Kjaer (B&K) 1/4-in (0.64-cm) microphone (B&K 4135), preamplifier (B&K 2618), microphone amplifier (B&K 2608) and filter (Krohn-Hite 3202) set to pass one octave above and below the test frequency. Measurements were taken by placing the microphone in the position occupied by an animal's head when it was drinking and orienting it towards the loudspeaker (0° incidence). The acoustic signal was checked for distortion with a spectrum analyzer (Zonic 3525) and the measuring system was calibrated with a pistonphone (B&K 4230). Overtones, which were present in the signal when high intensities were used (i.e., at the highest and lowest frequencies tested), were at least 20 dB below the animals' thresholds and did not influence the results.

2.4. Behavioral procedure

An animal which had been deprived of water for 23 h was placed in the test cage and allowed to drink from the water spout. Tones were presented at random intervals and followed at their offset by a mild electric shock delivered through the spout. The animal quickly learned to avoid the shock by breaking contact with the spout whenever it heard a tone. The shock was adjusted for each individual to the lowest level that would reliably produce an avoidance response. The mildness of the shock was attested by the fact that none of the animals developed a fear of the spout and returned to it without hesitation after the shock had been delivered.

Test sessions were divided into 2.5-s trials separated by 1.5-s intertrial intervals. Each trial contained either a pulsing tone ("warning" signal) or silence ("safe" signal) with 22% of the trials containing a tone. A response was recorded if an animal broke contact for more than half of the last 150 ms of a trial (as determined by the microcomputer). The response was classified as a hit if the trial contained a tone and as a false alarm if no tone was presented. Both the hit and false alarm rates were determined for each block of 6–8 warning trials (which also included approximately 25 safe trials) for each stimulus condition. The hit rate was corrected for false alarms according to the formula: Performance = Hit rate − (False alarm rate × Hit rate), with the hit and false alarm rates expressed in proportions of 1. This measure proportionately reduces the hit rate by the false alarm rate observed under each stimulus condition and varies from 0 (no hits) to 1 (100% hit rate and 0% false alarm rate) (see Heffner and Heffner, 1988).

Absolute thresholds were determined by reducing the intensity of a tone in successive blocks of 6–8 warning trials until the animal no longer responded to the signal above the 0.01 chance level (binomial distribution). Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity in 5-dB increments extending from 10 dB below to 10 dB above the estimated threshold. Threshold was defined as the intensity corresponding to a performance of 0.50. Threshold testing for a particular frequency was considered complete when the thresholds obtained in at least two different sessions were within 3 dB of each other. Once an audiogram had been completed, each threshold was rechecked to ensure reliability.

The care and use of the animals used in this study were approved by the University of Toledo Institutional Care and Use Committee which adheres to the guidelines of the Declaration of Helsinki (NIH grant DC00179).

3. Results and discussion

The avoidance task is an easy one for rats to learn and the animals were reliably avoiding the shock within the first 10–15 min of the first session. The animals trained quickly and were giving reliable and valid thresholds within 5–7 sessions.

The thresholds of the four hooded rats are shown in Fig. 2 together with the average audiogram of Sprague-Dawley albino rats (from Fig. 2 in Kelly and Masterton, 1977). The hooded rats were able to respond to frequencies from 250 Hz to 70 kHz, but could not hear lower frequencies (4, 8, 16, 32, 63, and 125 Hz) even at 100 dB SPL.

Comparison of the audiograms for the hooded and albino rats reveals that they are virtually identical. Between 500 Hz and 64 kHz, the two audiograms vary on average by less than 3 dB. Indeed, both audiograms show the same general structure: a rapid increase in sensitivity beginning in the low frequency end which slows above 1 kHz; a point of best hearing at 8 kHz; a leveling or slight decline in sensitivity between 8 and 32 kHz; a second point of best hearing at 32–38 kHz; and a rapid decrease in sensitivity above 38 kHz.

The largest differences between the two audiograms are at their extremes. At a level of 60 dB SPL, the low-frequency limits are 530 Hz for the hooded rats and 400 Hz for the albinos. At the other end, the high-frequency limits are 68 kHz for the hooded rats with an estimated 76 kHz for the albino rats. However, these differences represent less than half an octave and

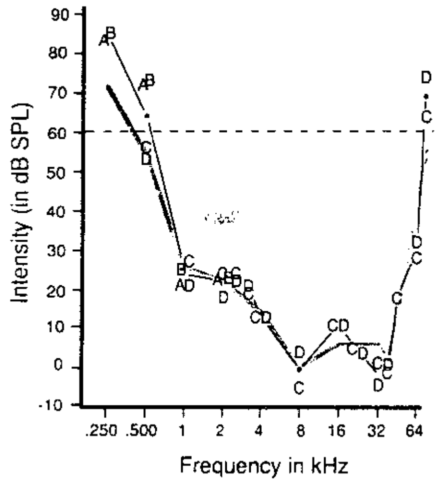

Fig. 2. Absolute thresholds of four hooded rats (A, B, C, and D). Average albino rat audiogram from Kelly and Masterton (1977) is shown by shaded line. Dashed line indicates the 60-dB SPL level.

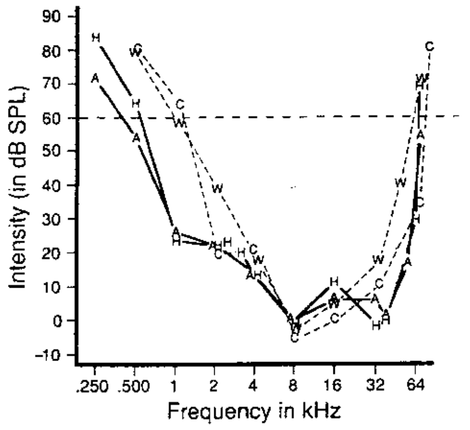

Fig. 3. Average audiograms of the hooded rat (H, this study), albino rat (A, Kelly and Masterton, 1977), cotton rat, *Sigmodon hispidus* (C, Heffner and Masterton, 1980), and wood rat, *Neotoma floridana* (W, Heffner and Heffner, 1985a).

may simply reflect individual variation in the extreme ends of the audiogram.

Fig. 3 compares the audiograms of the hooded and albino rats with those of the cotton rat (*Sigmodon hispidus*) and the wood rat (*Neotoma floridana*), two species from the same superfamily (Muroidea) and of approximately the same size as the Norway rat. Inspection of this figure reveals that although the audiograms of the three species are similar, the hooded and albino rat audiograms resemble each other more closely than they resemble either of the other two species. Thus, it appears possible to observe species differences between the audiograms of closely related rats when reliable techniques are used.

There are two main conclusions that can be drawn from these results. First, there are no significant differences between the audiograms of pigmented and albino Norway rats. Thus, absolute sensitivity is one more auditory feature which, in rats, is not affected by albinism (cf. Godfrey et al., 1987; Heffner and Heffner, 1985b).

Second, it should be noted that both of the audiograms were obtained using procedures which combine the use of a positive reward with a mild electric shock punisher. Such a combination provides good control over an animal's response criteria and allows the experimenter to maximize an animal's detection rate and minimize its false alarm rate by adjusting the reward and shock levels. This control facilitates the task of ensuring that an animal is performing at its optimal level. In addition, the response of drinking from a spout keeps an animal's head in a fixed position so that the sound field can be precisely specified. Such procedures yield highly replicable results (see also Borg, 1982).

4. Acknowledgement

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