Sound localization in wild Norway rats (*Rattus norvegicus*)

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The ability of three wild Norway rats to localize sound was determined for single clicks and 100-ms white noise bursts. Chance level localization thresholds were 12° for clicks and 9.7° for white noise. A comparison of these results with published localization thresholds for the domestic albino rat yielded no significant differences. It appears that the combined effects of domestication and albinism have not affected the ability of the laboratory rat to localize sound. Instead, the relatively poor localization acuity of these rats appears to be part of the normal variation in sound localization acuity found among different species of mammals.

albino rat, wild Norway rat, sound localization, domestication

Introduction

Although the albino laboratory rat has often been used in the study of hearing, there has been some concern regarding its appropriateness as an experimental animal. This concern has arisen from the fact that the laboratory rat is not only a domesticated animal, but an albino as well. Specifically, the long period of inbreeding and adaptation to a laboratory environment have resulted in physiological as well as behavioral changes which have caused the laboratory rat to differ from its wild ancestors not only visually, but also in the size and function of its internal organs [5,13]. Furthermore, it now appears that albinism in other species of mammals is not only associated with abnormal development of the inner ear, but with subtle changes in brainstem nuclei as well [4,8]. Because one of the nuclei most severely affected is the superior olivary complex where binaural interactions important for sound localization take place, the use of albino animals for studies involving sound localization might be particularly misleading. These findings have led some investigators to recommend against the use of albino animals in sensory studies [2] and has cast some doubt on the generalizability of the results of auditory investigations using the domesticated albino rat even though no specific auditory abnormalities have been reported.

Yet the albino rat is a convenient subject for sensory studies and a large amount of information has accumulated concerning its central auditory functioning. Indeed, the albino rat is a key animal in the study of auditory cortex as it is the only species so far examined in which auditory cortex ablation appears to have no dramatic effect on the ability to localize sound (cf. [11,12,14]). As a result, it is important to know whether the auditory ability of the albino rat is representative of its wild ancestors or whether it may be somewhat aberrant due to domestication or albinism. Thus, the purpose of the present study was to determine the generality of previous data on sound localization in the laboratory rat by comparing it with the ability of wild Norway rats to localize sound.

Methods

A conditioned avoidance procedure was used in which an animal was trained to drink steadily from a water spout while sounds were emitted from a loudspeaker on its right side. The animal was trained to cease drinking when a sound was emitted from a loudspeaker on its left side in order to avoid impending shock.

Subjects

Three rats (*Rattus norvegicus*) trapped in Labette County, KS, were used in these tests. The animals weighed 280, 320 and 350 g and their interaural distances (as measured around the head from the opening of one auditory meatus to the other) were 42, 45 and 43 mm, respectively. Each animal was housed in an activity wheel and given free access to food. Water was available only in the test situation. The ears of the animals were inspected upon acquisition and at the time of killing and were found to be free of disease or obstruction.

Behavioral apparatus

In order to minimize ambient noise and reduce sound reflections, the rats were tested in a double-walled acoustic chamber (IAC) the walls and ceiling of which were lined with acoustic foam. An adjacent room housed the test equipment and the animals were observed over closed-circuit television.

The rats were tested in a 1/2-inch (12 mm) hardware cloth cage (43 × 25 × 31 cm) which had a small compartment (19 × 10 × 16 cm) attached to the front. The cage was placed on 16-cm legs and positioned on a small table 69 cm above the floor of the chamber. A 20-gauge hypodermic needle with a blunted tip served as a water spout and was placed at the front of the compartment in a position that allowed the rat to drink while centering its head in front of the loudspeakers. The spout was connected via plastic tubing to a water valve and water reservoir located outside the chamber. A touch-sensing switch, connected at one end to the water spout and at the other end to the floor of the cage, served to detect when the animal made contact with the spout. Mild electric shock was provided by a shock generator connected to the water spout and the cage floor.

Acoustical apparatus

Both broad-band noise and clicks were used as stimuli. Broad-band noise was generated by a noise generator (Grason Stadler 1285, 100 kHz band width), led to a programmable attenuator (Coulbourn S85-08), a rise–fall gate (Grason Stadler 1287), then through an impedance-matching transformer to a pair of matched wide-range dual loudspeakers. Each dual loudspeaker consisted of a 3-inch (7.6 cm) paper cone speaker mounted in a 500 ml enclosure and a piezoelectric tweeter with a 3-inch (7.6 cm) horn mounted directly above such that the centers of the speakers were 3.5 inches (8.9 cm) apart. To produce the clicks, square waves of 25 μs duration were produced by a pulse generator (Coulbourn S52-22), led to the programmable attenuator, then to the impedance-matching transformer and loudspeakers. The speakers were mounted on a perimeter bar (102 cm radius) which was centered on the middle of an animal's head when it was drinking. In order to reduce the possibility that the animals could distinguish the loudspeakers on the basis of intensity differences, the stimuli were randomly attenuated by ±2 dB in 1 dB steps. That the animals did not use a non-locus cue to solve the discrimination was demonstrated by their inability to distinguish between the left and right speakers at the smallest angles tested. All stimuli were presented at 50 dB above threshold as estimated by attenuating the stimuli until the animals' performance fell to chance.

The acoustic spectra of the noise and click were measured with a 1/4-inch (0.64 cm) Brüel and Kjaer (B&K) microphone (B&K 4135) with the protective grid removed to obtain linearity, pre-amplifier (B&K 2618), measuring amplifier (B&K 2608) and band-pass filter (Krohn-Hite 3202). The microphone was placed in the center of the position normally occupied by an animal's head and oriented directly towards the loudspeaker. Measurements were taken at 1/6-octave steps (24 dB/octave attenuation) with the high and low pass filter settings set at the same frequency (6 dB was added to each measurement to compensate for the resulting insertion loss). Measurement of the click spectrum was facilitated by pulsing the clicks at a rate of 10/s. The spectra of the stimuli are shown in Fig. 1.

Psychophysical procedure

The avoidance procedure used here is similar to that described elsewhere [9]. A thirsty animal was trained to make steady contact with the water spout by providing a steady trickle of water (0.5 ml/min) as long as the animal maintained contact with the spout. The rats were initially trained to drink steadily while a 2 s train of broad-band
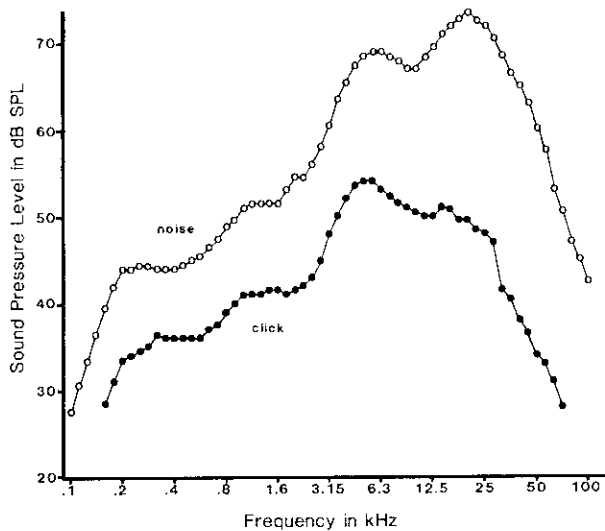
Fig. 1. Acoustic spectra of the noise (O) and click (●) stimuli.

noise bursts (5/s) was presented once every 5 s from a loudspeaker located 90° to the right of the animal, the stimulus side that was never paired with shock. By the fifth session, the animals had learned to maintain steady contact for 20 min or more. Further training consisted of occasionally switching the auditory stimulus to a loudspeaker 90° to the animal's left side and following its offset 2 s later with a mild electric shock delivered between the water spout and the floor of the cage. After only a few pairings of the left sound with shock, the animals learned to avoid the shock by breaking contact with the spout whenever the noise burst was presented from the left side. In order to provide feedback for successful avoidance, a light in the darkened test room was momentarily flashed on each time shock was delivered. Thus, the light served to indicate that a warning trial was over and that the animal could return to the water spout. In the following tests, cessation of spout contact was used as an indication of an animal's ability to perceive a shift in locus.

The presentation of right (safe) and left (warning) trials was randomized, with a warning trial likely to occur anywhere from 1 to 10 trials after the previous warning trial. Longer intervals between warning trials were inserted to prevent an animal from using the time since the last warning trial as a cue. No trial was given in the 5 s immediately following a warning trial in order to

allow an animal sufficient time to return to the water spout.

For the purpose of quantifying an animal's response, the duration of spout contact was measured in 0.02 s increments beginning 1.8 s after stimulus onset until 0.2 s later at the end of the trial. This measured 'time in contact' was then averaged separately for the right or (S) trials and the left or warning (W) trials for each angle of separation. A measure of discrimination could then be expressed in the form of a ratio $(S - W)/S$ for each angle. In trained animals this measure varies from near zero (failure to discriminate) to unity (perfect discrimination). In order to reduce the effects of spurious pauses, the results of a trial were automatically discarded if the animal was not in contact with the spout at any time during the 1 s immediately preceding the trial, though the trial and shock were presented as usual. Because this criterion was applied equally to safe and warning trials, it did not bias the results.

Sound-localization thresholds were determined by reducing the duration of the stimulus to a single noise burst or click and then reducing the angular separation between the left and right loudspeakers until the animal could no longer distinguish the two stimuli. Once a preliminary threshold had been obtained, threshold testing was continued while the shock level and the animal's deprivation level were varied. Psychophysical functions were then plotted by taking the average of the scores from each animal's best three sessions (asymptotic performance) with a minimum of 25 warning trials per angle. Threshold was arbitrarily defined in both of two ways: (a) as the smallest angle yielding a performance ratio of 0.5 (i.e., 50% detection) and (b) as the smallest angle at which the animal could discriminate between the two stimuli at the 0.01 one-tailed level of statistical reliability (Mann–Whitney U test; [16]) which in this case was a performance ratio of 0.30.

A typical session lasted 30 min during which an animal received 90–150 trials (18% of which were warning trials) and consumed 10–20 ml of water.

Results

Broad-band noise localization

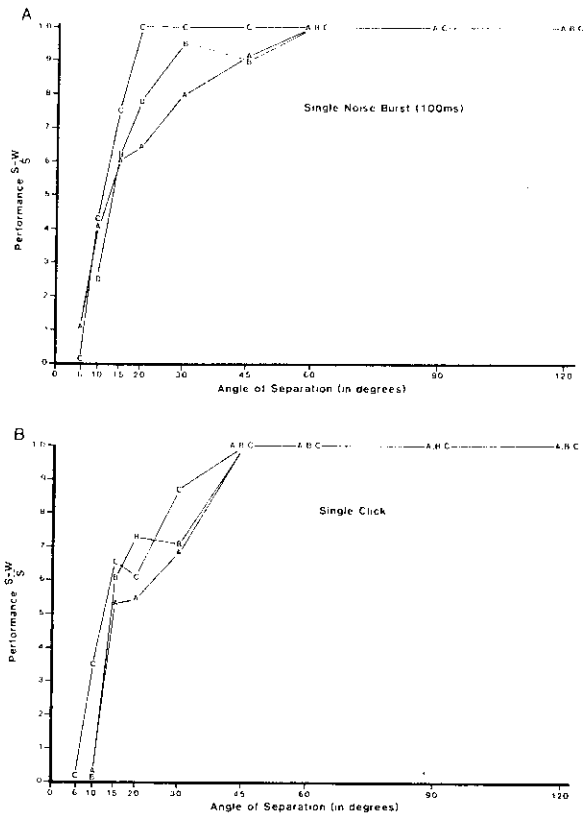The ability of the three wild Norway rats to

Fig. 2. Sound-localization performance of three wild Norway rats for a single 100 ms noise burst (A) and a single click (B). A, B and C within the panels indicate the three animals.

localize a single, 100 ms burst of noise at angles ranging from 0° to 120° separations is shown in Fig. 2A. Each point represents an animal's asymptotic performance at a given angle. All of the rats were capable of perfect detection of the shift in locus at large angles of separation. As the angle of separation was reduced below 45° their performance began gradually to fall reaching the 0.50 performance level between 11° and 13.5° and falling to chance at angles of 9° to 11°. Overall, the three rats showed good agreement.

Click localization

The performance of the three rats on the single-click localization test was also perfect at large angles (Fig. 2B). Performance began to fall at angles smaller than 45° for this stimulus also, but somewhat more sharply than for the noise stimulus. The thresholds for the click stimulus were

slightly poorer with the 0.50 performance level being reached at angles of 12.5–15° and chance performance occurring at angles of 10–13°. Again there were no major differences between individual thresholds.

A comparison of the performances of the animals on the two stimuli shows that the rats localized the 100 ms noise burst more accurately than the clicks. This is a common finding among animals and is generally attributed to the fact that the noise burst has a longer duration than the click [9,10].

Discussion

Given the above results, the question turns to the issue of whether the ability of domestic albino rats differs from that of the wild rats. A comparison of the sound localization thresholds of the two varieties of rats is shown in Table I. To facilitate comparison between the different methods used by these studies, threshold is defined in each as the smallest angle which could be discriminated at the 0.01 level of chance. In the two-choice procedure [11] this threshold was at 68% correct while in a conditioned suppression task [12] it is usually the 0.30 suppression ratio $((S - W)/S)$.

The click localization thresholds of wild and albino rats are 12° and 14°, respectively. These values are sufficiently similar to conclude that there are probably no significant differences in their abilities to localize clicks. As there are no published thresholds for albino rats for wide band

TABLE I

COMPARISON OF SOUND LOCALIZATION THRESHOLDS IN WILD AND ALBINO RATS

Source	Stimulus	Chance detection threshold
Wild rats	Single click	12°
Albino rats [a]	1/s clicks	14°
Wild rats	White noise burst	9.7°
Albino rats [b]	Low-frequency noise burst	10°
Albino rats [b]	High-frequency noise burst	8°

[a] From [12], conditioned suppression procedure.
[b] From [11], two-choice procedure.

noise localization, the noise localization threshold of the wild rat is compared with those of the albino rat for low- and high-frequency noise. Again, such a comparison yields similar thresholds (Table I) with the wild rat threshold of 9.7° falling between the albino rat thresholds of 8° and 10° for high- and low-frequency noise, respectively.

The close similarity between the sound localization abilities of wild and albino rats has two main implications. First, despite anomalies in the anatomy and physiology of the brainstem auditory nuclei reported for albino individuals of other species (i.e., cats and humans) [4–7], it would appear that the auditory system of the albino rat has not undergone changes which could disrupt this complex task. Though the albino rat is known to differ from the wild rat in other ways [5,13], its auditory localization ability does not appear to have been altered. Thus, on the basis of their normal sound localization ability, there does not seem to be any reason for believing that the auditory system of the domestic albino rat deviates significantly from that of wild rats.

Second, these results confirm the finding that the Norway rat is notably poorer at localizing sounds than many other mammals (for a review, see [9]). Specifically, the cat [3], opossum [15], macaque [1], elephant [10], seal [18], and dolphin [17] all have 50% detection thresholds of 5° or less for noise bursts while the equivalent threshold for the rat is 10–14°. With the addition of these results, it is no longer possible to argue that the rat's comparatively poor localization thresholds are the result of domestication, nor, for that matter, the result of a particular behavioral testing procedure. Instead, it appears that there exists significant interspecific variation in the sound localization abilities of mammals.

Acknowledgement

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