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Research papers

Sound-localization ability of the Mongolian gerbil (*Meriones unguiculatus*) in a task with a simplified response mapLaurel H. Carney^{a,b,c,d,e,*}, Srijata Sarkar^{a,b}, Kristina S. Abrams^{a,e}, Fabio Idrobo^f^a Institute for Sensory Research, Syracuse University, Syracuse, NY 13244, USA^b Department of Biomedical & Chemical Engineering, Syracuse University, Syracuse, NY 13244, USA^c Department of Electrical Engineering & Computer Science, Syracuse University, Syracuse, NY 13244, USA^d Department of Biomedical Engineering, University of Rochester, 601 Elmwood Ave., Box 603, Rochester, NY 14642, USA^e Department of Neurobiology & Anatomy, University of Rochester, 601 Elmwood Ave., Box 603, Rochester, NY 14642, USA^f Department of Psychology, Boston University, Boston, MA, USA

ARTICLE INFO

Article history:

Received 4 June 2010

Received in revised form

30 November 2010

Accepted 6 December 2010

Available online xxx

ABSTRACT

The characterization of ability in behavioral sound-localization tasks is an important aspect of understanding how the brain encodes and processes sound location information. In a few species, both physiological and behavioral results related to sound localization are available. In the Mongolian gerbil, physiological sensitivity to interaural time differences in the auditory brainstem is comparable to that reported in other species; however, the gerbil has been reported to have relatively poor behavioral localization performance as compared with several other species. In this study, the behavioral performance of the gerbil for sound localization was re-examined using a task that involved a simpler response map than in previously published studies. In the current task, the animal directly approached the speaker on each trial, thus the response map was simpler than the 90°-right vs. 90°-left response required in previous studies of localization and source discrimination. Although the general performance across a group of animals was more consistent in the task with the simpler response map, the sound-localization ability replicated that previously reported. These results are consistent with the previous reports that sound-localization performance in gerbil is poor with respect to other species that have comparable neural sensitivity to interaural cues.

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1. Introduction

A complete understanding of sound localization requires knowledge of both behavioral and neural responses to sounds in space. A puzzle in the literature concerning sound localization is that the neural responses of mammals that have been studied typically show comparable sensitivity to interaural differences, yet behavioral abilities to discriminate sounds from different locations vary considerably across species and do not necessarily correspond closely to neural sensitivity (Heffner and Heffner, 1992). The Mongolian gerbil is an example of a mammal with particularly poor sound-localization performance as compared to other species [e.g. 75% correct discrimination for speakers separated by 27° (Heffner

and Heffner, 1988b) or 23° (Maier and Klump, 2006)]. However, the gerbil has neural sensitivity to interaural time differences (ITDs) that is generally comparable to that of several other mammals for which the slopes of discharge rate vs ITD for binaural neurons in the brainstem or midbrain have been reported (gerbil: Brand et al., 2002; Spitzer and Semple, 1998; cat: Yin and Chan, 1990; McAlpine et al., 1996, 2001; rabbit: Batra et al., 1997; Kuwada et al., 1987; Langford, 1984). Species with comparable physiological ITD curves have been demonstrated to have very different sound-localization ability; for example, the cat has a threshold of approximately 6° separation for speaker discrimination (Heffner and Heffner, 1988a), and a threshold of <1° for directing gaze to an acoustic target (Tollin et al., 2005), whereas in rabbit the threshold for speaker discrimination is about 22° (Gandy et al., 1995; Heffner, 1997), consistent with the behavioral ITD-discrimination threshold for rabbit (Ebert et al., 2008).

One reaction to the apparent discrepancy between neural and behavioral sensitivity to sound localization cues in gerbil is to question the extent to which the discrimination procedures and apparatus influence the behavioral results. Indeed, behavioral

Abbreviations: ITD, interaural time difference; LED, light-emitting diode; VI, variable interval; MRA, minimum resolvable angle.

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doi:10.1016/j.heares.2010.12.006

studies involve a host of complex factors that can influence estimates of behavioral ability. In this study, the response mapping aspect of the task used by Heffner and Masterton (1980) and Heffner and Heffner (1988b) was hypothesized to be a potential factor in the estimate of sound-localization ability. Response mapping, which is related to the spatial contiguity between the sound source and the required response, has been shown to be a significant behavioral factor in other tasks (Downey and Harrison, 1972, 1975; Harrison et al., 1971; reviewed in Harrison, 1992). In this study, a task with a simple response map was designed that allowed the comparison of localization ability in this task to that in the Heffner and Heffner (1988b) task, which involved a more complex response map. The simpler response map was a direct approach by the animal from an observing platform in the center of the cage to the target speaker. The more complex task required the animals to back out of an observing compartment after stimulus presentation and then to make a response in a compartment located either 90° to the right, for trials in which the stimulus came from any speaker location on the right-hand side of the test apparatus, or to make a response 90° to the left, for any stimulus presented from speaker locations on the left-hand side (Heffner and Heffner, 1988b). A related response map was used in the task of Maier and Klump (2006), except that rather than making responses directly to the right or left, the animals responded by approaching one arm of a Y-maze, in which the arms were separated by approximately 90°, regardless of stimulus location. A recent study employed a task in which each trial was initiated with a nose poke, after which the animal was required to back away from the observing response site and then approach a speaker target (Lesica et al., 2010).

The results presented here suggest that response mapping may have influenced the performance of some animals; for example, there was more variance in results across animals in the more complex task. However, there were no significant differences in sound-localization ability between the two tasks or between these results and those of Heffner and Heffner (1988b) and the other studies mentioned above. Thus, the difference in response mapping may have influenced training and performance for some animals, but it cannot explain the relatively poor sound-localization performance of the gerbil as compared to other mammals.

2. Materials and methods

2.1. General methods

Mongolian gerbils were weighed daily and maintained at approximately 80% of their *ad lib* weights. Six animals (3 males, 3 females) were tested in Experiment I, and 4 animals were tested in Experiment II (2 males, 2 females). Two animals were members of both groups. Animals were not selected based on sound-localization ability but rather were chosen randomly from the available animals in the vivarium. An additional 3 animals from the Experiment I group were studied at a later date in the apparatus for Experiment II, but training was not completed in this group of older animals (see below).

In both experiments, food rewards during training and testing were 20 mg pellets (Noyes Precision Pellets PJA1-0020, Research Diets) delivered by two pellet dispensers (ENV-203-20, Med Associates) into containers inside the response compartments. Infrared LED emitter–detector pairs (Radio Shack 276-142) were used to detect the animals' observing and reporting responses. The interface between the apparatus, pellet dispensers, and the computer was based on a PCI-6503 24 channel digital I/O board (National Instruments). The program used to control stimulus

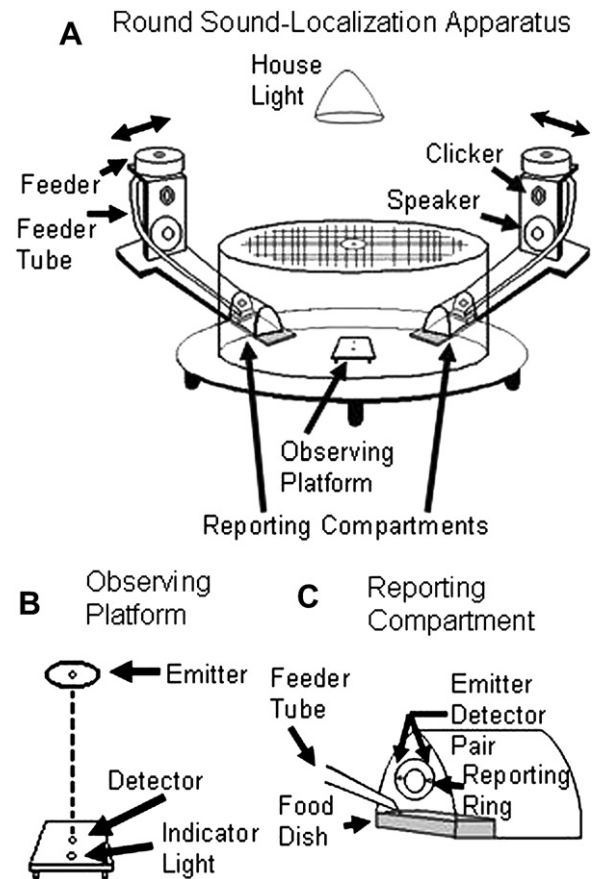


Fig. 1. Drawing of apparatus used for Experiment I. A) Overview of entire apparatus. B) Observing platform used to initiate each trial. C) Reporting compartment used for detecting responses and delivering reinforcement. See text for dimensions and other details.

presentation and data acquisition in each experiment was written in LabVIEW version 6i.

In both experiments, sounds were presented using a sound card (Creative Sound Blaster Live 5.1, Model No SB0220), an amplifier (RCA SA-155), and dome tweeters (MOREL MDT-33, matched pair of 1-1/8 inch soft dome tweeters). Stimuli for both experiments were wideband Gaussian noises, generated in MATLAB and presented at a 44.1 kHz sampling rate; the energy in the stimulus was mainly between 1 and 20 kHz, with energy rolling off (as expected) at low frequencies and above 22 kHz. The overall levels of the noises were approximately 71 dB SPL, as measured with an Ivie IE-35 sound-level meter placed in the center of the cage. The spectra of the stimuli from the two speakers were matched within 2–3 dB across all frequencies, and the overall levels were within 1 dB of each other. Egg-crate foam was placed on all surfaces of the test booth to minimize sound reflection. An incandescent light positioned approximately 60 cm above the cage provided light during the sessions and was turned off to create timeouts, as described below.

The methods used in both experiments were approved by the Institutional Animal Care and Use Committee at Syracuse University.

2.2. Experiment I

2.2.1. Apparatus

Fig. 1 is a schematic illustration of the apparatus used for Experiment I, referred to below as the round apparatus. The main

cage and the reporting compartments were constructed from 1/3 inch (0.7 cm) hardware cloth. The diameter of the main round cage was 46 cm, and its height was 18 cm. The main compartment rested on a perforated plastic platform that was raised 12 cm above the table top, which was covered with egg-crate foam.

The reporting compartments, speakers, and feeders were attached to plastic arms that pivoted around the center of the round cage. The reporting compartments were located directly in front of the speakers, and the cage was constructed such that when the speaker locations were varied, the reporting compartments were also shifted (and then fixed into place with wire ties.) Speakers were positioned 61 cm from the center of the cage; the centers of the speakers were 6 cm above the cage floor. The small clicker was positioned 14 cm above the cage floor. The feeder was 22.5 cm above the cage floor.

The observing platform (6 cm long \times 4.5 cm wide \times 2 cm high) was constructed from 0.3 cm Plexiglas, positioned in the center of the main cage. The observing platform was modeled after that used in an operant task designed to study discrimination in the gerbil (Sinnott et al., 1992). A white light-emitting diode (LED) was added on the end of the observing platform that pointed toward 0° (in an effort to orient the animal towards the “front” of the apparatus). At all separations, the speakers were positioned symmetrically to the left and right of 0°, the front of the apparatus. An emitter–detector pair of infrared LEDs (RadioShack 276-142) was mounted in the center of the observing platform and on top of the round cage to detect the animal's presence on the platform. Early during the training process, the animals began to consistently orient their body on the observing platform with their head toward the front of the cage; however, the detailed orientation of the head was not controlled in this apparatus. Head position for each trial was not documented.

The reporting-response compartments were 7 cm deep \times 6 cm wide \times 9.5 cm high. The reporting rings (2 cm diameter) were positioned in the back wall of the reporting compartment, directly above the feeder cup. An emitter–detector pair of infrared LEDs was mounted in the left and right sides of the reporting ring to detect reporting responses, made by poking the nose/head into the ring. A small clicker (8-ohm mini speaker, Radio Shack 273-092) was activated upon each reporting response to provide feedback for a valid response.

2.2.2. Procedure

Six gerbils were tested in the apparatus for Experiment I (3 males, 3 females). The animals were approximately 2–4.5 months old when training began, and 3–7 months old when testing began.

Training began with magazine training: a single reporting compartment was available, positioned at 0°, and a nose poke into the reporting ring was reinforced with a click and delivery of a food pellet. After approximately 50 trials of magazine training, acoustic stimuli were introduced. Long-duration noise bursts were presented with a variable interval (VI) from a single speaker located behind the reporting compartment, positioned at 0°. A nose poke into the reporting ring during the noise stimulus was reinforced with a click, food delivery, and cessation of the noise. The VI was gradually increased over several sessions to a 2–6 s range. During training, reaction times and numbers of reporting responses made in silence, which were reinforced by a click but no food, were measured to monitor stimulus control of behavior.

The next stage of training was to introduce the observing platform into the cage; an LED on the platform was illuminated when the animal jumped onto the observing platform, and a long-duration noise burst was initiated after a VI. The VI was gradually increased from 0 to a range from 2 to 6 s. Reporting responses made during the noise were reinforced with the click, food, and cessation of the noise. After animals reliably initiated and responded to

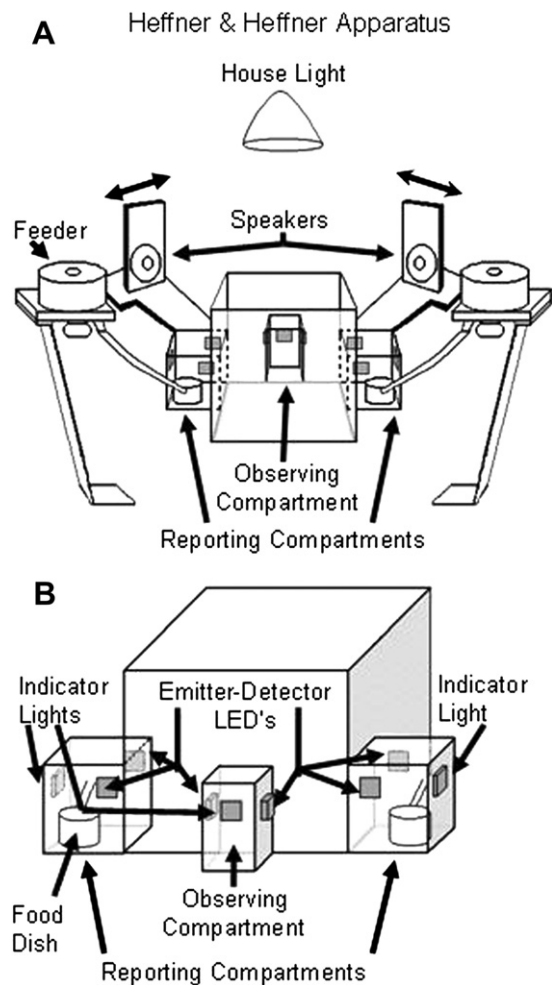


Fig. 2. Drawing of apparatus modeled after that of Heffner and Heffner (1988b) used for Experiment II. A) Overview of entire apparatus. B) Close-up view (from opposite angle) of observing compartment used to initiate each trial, and reporting compartments located at 90° to the right and left of observing compartment.

noises coming from a single speaker, the second speaker was introduced; the speakers were initially separated by 180°. Each observing response initiated a noise from one or the other speaker, with equal probability. Initially, noises were sustained until the reporting response was made. Reporting responses made to the compartment in front of the active speaker were reinforced by a click, food delivery and cessation of the noise. Reporting responses made in the other compartment resulted in a click and noise cessation, but no food reinforcement was provided.

Once an animal reliably discriminated between stimuli from the two speakers, the duration of the noise stimulus was gradually reduced to 100 ms, with a reaction-time window of 3 s allowed for valid reporting responses. To discourage reporting responses made in the absence of the stimulus (e.g., anticipatory responses during the VI), a 15-s timeout (house light off) was introduced in the next stage of training. A 1.5-s protected period followed each food-reinforced trial; during this protected period, reporting responses did not result in timeouts (to avoid timeouts for ‘double-responses’ or activity associated with eating the food pellet).

Animals were trained with speakers at 180° separation until 80% correct performance was observed. The entire training period (from magazine training through 80% correct performance with 180° speaker separation) lasted approximately 6–8 weeks (this period

was extended by development and debugging of the setup and software.). After training was completed, animals were tested with speaker separations of 20°, 30°, 45°, 60°, 90°, and 180°. The order of testing was randomly varied across animals; each animal was tested at 3 different angles per day, with approximately 50 trials in each test block. Results shown below are based on the average performance of the best two test blocks for each animal at each angle of separation.

2.3. Experiment II

2.3.1. Apparatus

Fig. 2 is a schematic illustration of the apparatus used for Experiment II, which intended to replicate the apparatus described in Heffner and Heffner (1988b) and Heffner and Masterton (1980). The main compartment was constructed from ½-inch (1.27 cm) hardware cloth, and was 20 cm long × 15 cm wide × 10 cm high. The observing response compartment (6 cm long × 4 cm wide × 7 cm high) was located in the center of the cage on one end. On either side of the cage, at the same end as the observing response compartment (at 90° to the right and the left of an animal facing forward in the observing compartment), two reporting-response compartments were positioned. Each of these compartments was 6 cm long × 7 cm wide × 7 cm high. Two plastic arms pivoted around a position just below the observing compartment and held the speakers at a distance of 61 cm from the center of the observing compartment. Infrared emitter–detector pairs mounted at the entrance of the reporting and observing response compartments indicated when the gerbil entered the compartment. White LED indicator lights were mounted in all three compartments (Radio Shack 276-320).

2.3.2. Procedure

Four gerbils (2 males, 2 females) were tested to completion in this apparatus. Two of these animals had been previously tested in Experiment I, and two were novices. The animals were 5–6 months old when training was initiated, and 6–7 months old when testing began. Training lasted approximately 4–5 weeks from magazine training until testing began. An additional 3 animals that were previously tested in Experiment I were trained in the apparatus for Experiment II for approximately 8 weeks, but their testing was not completed because of their poor performance (similar to that observed for 2 other animals, see below). These animals were 16–17 months of age when training began, which may have contributed to their performance.

Training and testing in this apparatus intended to replicate the methods described in Heffner and Heffner (1988b), except as mentioned below. In the first step of training, an indicator light in either the right or left reporting-response compartment was illuminated at random and entry into the illuminated compartment was reinforced by food. In the second stage of training, the indicator light in the observing-response compartment was illuminated at the beginning of each trial; upon entry into the observing compartment, that indicator light was extinguished and the light in either the right or left reporting-response compartment was illuminated. Entry into the illuminated reporting-response compartment resulted in food reinforcement, whereas entry into the non-illuminated compartment resulted in a short timeout (3–5 s, house light off).

In the third stage of training, the indicator light in the observing-response compartment was illuminated at the beginning of each trial. Upon entry into the observing compartment, the indicator light was extinguished and a 100-ms duration noise burst was presented from either the right or left speaker. The noise stimuli were identical to those used in Experiment I and training was for a 180° speaker separation. Both reporting-response compartments were illuminated at the end of the noise. A reporting response on the side of the active

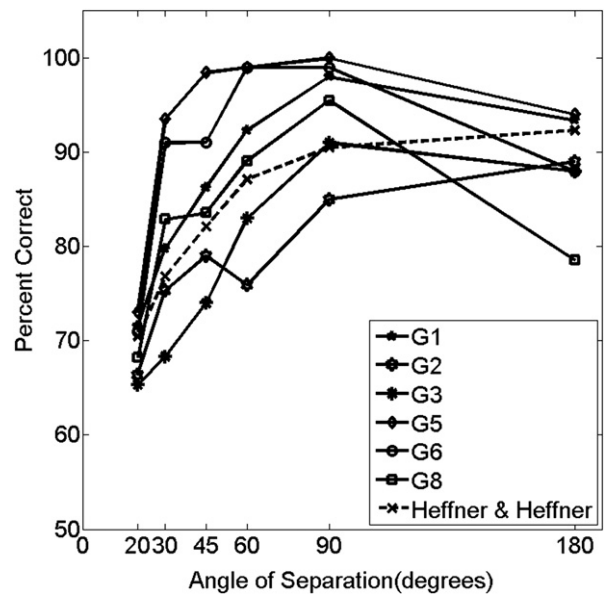


Fig. 3. Individual thresholds vs angle of separation for Experiment I. Six animals were tested in the round sound-localization apparatus (Fig. 1). The dashed line shows the mean results from Heffner and Heffner (1988b).

speaker was reinforced with food in that reporting compartment, whereas an incorrect reporting response resulted in a 5-s timeout.

In the final stage of training, the indicator light in the observing-response compartment was illuminated at the beginning of the trial. Upon entry into the observing compartment, a 100-ms duration noise was presented from either the right or left speaker. The animal was required to stay in the observing response compartment for 1 s, at which time both the right and the left reporting-response compartments were illuminated. Withdrawal from the observing-response compartment before 1 s had elapsed resulted in a dead period of 3 s, after which the observing-response compartment was re-illuminated to initiate another trial. An invalid reporting response, e.g. a response made before noise presentation or after an early withdrawal from the observing-response compartment, resulted in a 5-s timeout. A protected period of 4 s followed food reinforcement; this prevented activity near the reporting-response compartment associated with eating the reinforcement from resulting in a timeout. Following that period, the indicator light in the observing compartment was illuminated to begin the next trial.

Heffner and Heffner (1988b) used a corrective procedure to avoid bias towards one side; in that procedure, an incorrect trial on one side was followed by repeated trials on that side until the animals made a correct response, and the 'corrective' trials were not included in the final results. Problems with bias were not observed while training the animals in this study, and thus this corrective procedure was not implemented. Another difference between the procedures used in this study and those in Heffner and Heffner (1988b) that might have contributed to the difference in performance was that each animal was tested using a random sequence of speaker separations, which added uncertainty to the task; in the previous study, a sequentially decreasing set of speaker separations was used.

3. Results

3.1. Experiment I – localization in the round apparatus

Localization performance as a function of speaker separation for 6 gerbils is shown in Fig. 3, along with the group average from

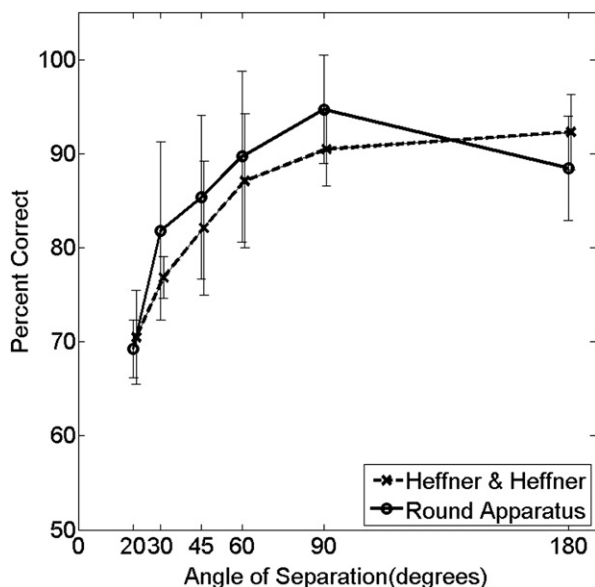


Fig. 4. Comparison of mean thresholds vs azimuthal separation (from Fig. 3) to mean results from Heffner and Heffner (1988b). Thresholds were not significantly different across the two sets of data. Error bars are plus/minus one standard deviation.

Heffner and Heffner (1988b). The mean and standard deviations of percent correct as a function of speaker separation are illustrated Fig. 4, with the means and standard deviations from Heffner and Heffner (1988b). Results shown are based on the best two sessions for each animal, for consistency with Heffner and Heffner (1988b). The minimum resolvable angle (MRA, angle of separation corresponding to 75% correct) was 25°. There were no significant differences in performance as a function of separation between the two groups of animals at any of the tested locations (Student's *t*-test). Thus, the performance in the round apparatus, for which the task involved direct approach to the target on each trial, was not superior to performance in the Heffner and Heffner study.

The use of 75% correct as a performance criterion was consistent with the studies of Heffner and Heffner (1988b) and Maier and Klump (2006). This criterion results in an estimate of sensitivity close to $d' = 1$ (Macmillan and Creelman, 2005) which is useful for comparisons to psychophysical results in humans (for which $d' = 1$ is the standard threshold criterion) and to physiological results, for which a $d' = 1$ criterion can be readily determined. The 75% correct point also falls near the steepest point of the psychometric function for a two-alternative task (for which chance performance is 50%); the estimate of a stimulus parameter associated with a particular performance level is best where the function is steepest. In a recent study of gerbil localization (Lesica et al., 2010), the 62.5% correct performance level was estimated (based on an argument that for the number of trials used, statistical significance could be established at this criterion). The gerbils were described as having “high acuity,” however, their MRAs based on the standard 75% correct criterion were consistent with our results as well as Heffner and Heffner (1988b) and Maier and Klump (2006).

One striking feature in the results from the round apparatus was a drop in performance for the 180° speaker separation for most animals. This drop in performance was presumably related to front–back confusions, which were possible in this apparatus. Although the animal's body was oriented toward the front of the test enclosure, the orientation of the head was not constrained at the beginning of each trial. Animals typically oriented their heads toward one speaker or the other (and in many cases switched between the two as they waited for the stimulus). Thus, in the case of the 180° speaker separation, some animals oriented their heads

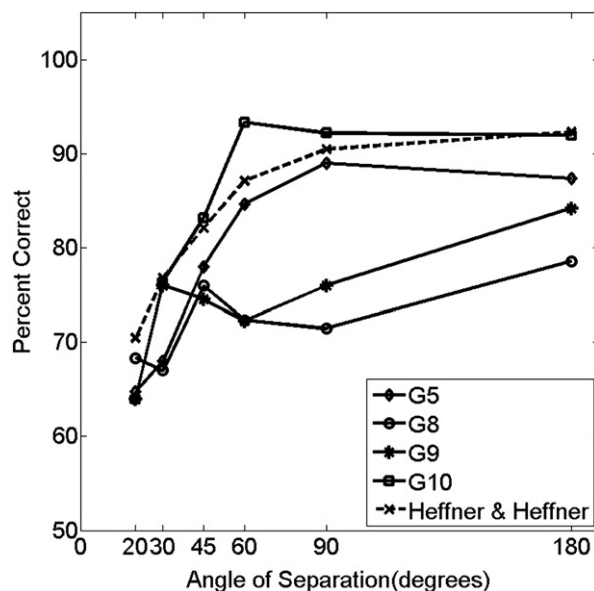


Fig. 5. Individual results for Experiment II. Four animals were tested in the apparatus modeled after that of Heffner and Heffner (1988b). The dashed line shows the mean results from Heffner and Heffner.

directly towards one speaker, but directly opposite the other speaker at the beginning of a trial, and thus could have experienced front–back confusions. The lack of control of the animal's head position at the beginning of each trial was a short-coming of the round apparatus. That and the fact that the animals did not show superior performance in this apparatus inspired Experiment II.

3.2. Experiment II – localization in the Heffner and Heffner apparatus

Two animals from the above group and two novice animals were tested in a setup that matched that used in the Heffner and Heffner (1988b) study. The estimates of localization ability for these animals (Fig. 5) were based on averages of the best two 50-trial blocks for each animal at each speaker separation; the results from Heffner and Heffner study are included for comparison. Two of the animals (G5 and G10) performed well on this task, with percent-correct scores similar to the group means from the Heffner and Heffner data. One of these animals had been previously tested in the round setup, and one was a novice. The other two animals (one experienced and one novice) had much more difficulty with the task. Nevertheless, the mean performance from the four animals in this study (Fig. 6) was significantly ($p < 0.05$) different from the results of the Heffner and Heffner study only at the 30° separation. The MRA based on the average of all four animals was 38°, which is substantially larger than that reported by Heffner and Heffner; however, the average MRA for the two animals that performed best at small separations in this apparatus was 29° (G9, G10; see Fig. 5), which is similar to that reported in the Heffner and Heffner study.

A possible reason for the differences in performance of individual animals across studies was that the present study did not use the early corrective procedure that was used in the Heffner and Heffner study (see above). It is possible that with sufficient training and the introduction of the corrective procedure, the animals that performed more poorly in this study would have improved their performance. Certainly, one could argue that G8 was capable of better performance, because this animal performed much better in the round apparatus (Fig. 1). In addition to the four animals shown

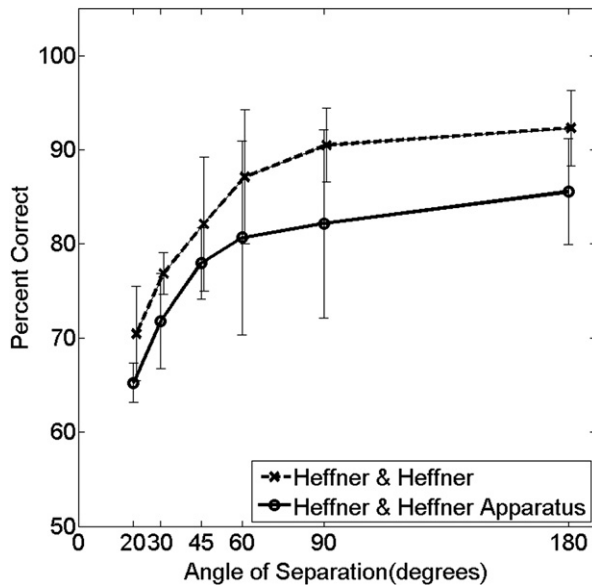


Fig. 6. Comparison of mean thresholds for Experiment II (from Fig. 5) to mean results from Heffner and Heffner (1988b). Thresholds were significantly different across the two sets of data only at the 30° separation. Error bars are plus/minus one standard deviation.

in Figs. 5 and 6, tests of G1, G2, and G3 (from Exp. I) were also attempted in Experiment II; however, these three animals all performed poorly and were not tested to completion. These animals were not included in the results above (Figs. 5 and 6) because of concern that their age (16–17 months) may have been a contributing factor; they are mentioned only because of the difficulty in training them in the Heffner and Heffner apparatus. However, there was no attempt to improve their performance using more extended training strategies.

The relatively poor performance of some animals in the Heffner and Heffner apparatus, as compared to their performance after similar training durations in the round apparatus, indicates that there may have been real differences between the tasks that affected performance. For example, the difference between the response mapping required in the two tasks may have contributed to the more variable performance near threshold in the Heffner and Heffner apparatus. In addition, a light was used to reinforce all reporting responses in the Heffner and Heffner apparatus, to match their paradigm, whereas an acoustic click was used in the round apparatus. Nevertheless, no significant differences in sound-localization ability were seen between the more readily learned task involving the direct approach (round apparatus) and the more difficult task that involved responding at 90° right or left, regardless of speaker position (Heffner and Heffner apparatus). Thus, the difference between the response maps of these tasks, as well as other details of the paradigms, apparently did not significantly influence estimates of the localization performance ability of the gerbil. In addition, suprathreshold performance in both experiments showed considerable variability.

4. Discussion

The relation between sound-localization ability and the physiological processes for coding and processing sound location information has been a topic of interest in the field of auditory neuroscience for decades. An important issue for the study of this relation is the quality of estimates of behavioral performance. Behavioral estimates for the ability to discriminate sound sources at

different locations are essential for providing a comparison to neural estimates of acoustic cue discrimination. The focus of this study was to examine the response map, which is a key aspect of the operant tasks used to study sound localization, in order to determine whether a task with a simpler response map could result in improved localization performance.

The results of this study suggest that the response maps used in the operant tasks considered here did not significantly influence localization performance, although response mapping may have influenced the time required for training. The simple response map made possible by the round setup (Experiment I, Fig. 1) allowed the animal to directly approach the speaker regardless of speaker location. Results for a task with this simple response map (25° MRA) were compared to those for a task in which the response was always to approach a response box located 90° to the left or to the right of the observing position, regardless of speaker location (Experiment II, Fig. 2). Results in this study for the task with the indirect response map (38° MRA for all 4 animals; 29° for the better two animals) were consistent with that reported by Heffner and Heffner (1988b, 27° MRA). A comparable result (23° MRA for broad-band noise presented in front of the animal) was reported more recently for gerbil localization ability in a Y-maze, for which the responses were made by walking down the arms of the maze, fixed at 45° angles to the right or left of the observing position, regardless of speaker position (Maier and Klump, 2006). The results of Lesica et al. (2010) show 75% correct performance at speaker separations ranging from approximately 20–60°.

The wideband noise stimuli used in this study purposefully contained more than one cue for sound localization, in an effort to obtain the best possible performance from the animals. Information based on both interaural time differences at low frequencies and interaural level differences at high frequencies was included in the wideband noise stimuli. Spectral cues for sound localization associated with the head-related transfer function, which occur at frequencies above 25 kHz for gerbil (Maki and Furukawa, 2005), were presumably weakly represented in the band-limited stimuli used in this study. The roles of individual cues have been explored in more detail in recent studies (Maier et al., 2008; Maier and Klump, 2006). It can be argued that changes in the average rates of neural responses in the medial and lateral superior olives are more than adequate to explain the observed performance based on interaural differences of time and level (see Discussion in Maier and Klump, 2006). However, differences in localization ability from species to species are not easily explained in terms of basic neural coding arguments. The response properties of superior olivary neurons do not change markedly across species; for example, neural thresholds for ITD of ~30 μs (Skottun et al., 2001; Shackleton et al., 2003; Lesica et al., 2010), and ILD thresholds of 1–4 dB (Sanes and Rubel, 1988; Tollin et al., 2008), are reported across species. Yet sound-localization performance varies considerably across species (Heffner, 1997). That is, although different species have been shown to have a wide range of sound-localization ability, with gerbils falling near the low end of the distribution for mammals, the sensitivity of single neurons for binaural cues does not vary considerably across species. Inferring sensitivity from single neurons is complicated by the fact that neural responses are strongly affected by stimulus parameters, such as sound level (Tollin, 2003), that are not necessarily related to sound location, but may co-vary with it. For example, Tsai et al. (2010) showed large changes in sensitivity of single LSO neurons based on overall sound level. In addition, neural sensitivity is influenced by dynamic cues, such as would be associated with source motion (Spitzer and Semple, 1995). Thus, one can speculate that the different sound-localization abilities across species may reflect different abilities to extract information from the responses of single neurons or

differences in the efficiency and strategies for combining information across neurons, for example pooling strategies (e.g. Hancock and Delgutte, 2004; Lesica et al., 2010). Further studies of the processing of sound localization cues at higher levels of the auditory pathway will provide more insight into the relationships between neural and behavioral responses related to sound location.

Acknowledgements

Dr. Rickye Heffner provided experimental data from the Heffner and Heffner (1988b) study and instructive comments related to operant training of the gerbils. Numerous helpful comments on the manuscript were provided by members of our Lab Writing Workshop. We gratefully acknowledge the care that our animals receive in the Laboratory Animal Resource facilities in the Institute for Sensory Research. This work was supported by NIDCD R01-01641.

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