Research Article

Near-Field Discrimination of Sound Source Distance in the Rabbit

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ABSTRACT

The acoustical cues and physiological processing mechanisms underlying the perception of the distance of sound sources are not well understood. To understand the relation between physiology and behavior, a first step is to use an animal model to study distance sensitivity. The goal of these experiments was to establish the capacity of the Dutch-belted rabbit to discriminate between sound sources at two distances. Trains of noise bursts were presented from speakers that were located either directly in front of the rabbit or at a 45 ° angle in azimuth. The reference speaker was positioned at distances of 20, 40, and 60 cm from the subject, and the more distant test speaker was systematically moved to determine the smallest difference in distance that could be reliably discriminated by the subject. Noise stimuli had one of three bandwidths: wideband (0.1–10 kHz), low-pass (0.1–3 kHz), or high-pass (3–10 kHz). The mean stimulus level was 60 dB sound pressure level (SPL) at the location of the rabbit's head, and the level was roved over a 12-dB range from trial to trial to reduce the availability of level cues. An operant one-interval two-alternative non-forced choice task was

used, with a blocked two-down-one-up tracking procedure to determine the distance discriminability. Rabbits were consistently able to discriminate two distances when they were sufficiently separated. Sensitivity was better when the reference distance was 60 cm at either azimuth (distance ratio=1.5) and was worse when the reference distance was 20 cm (distance ratio=2.4 at 0 ° and 1.75 at 45 °).

Keywords: sound localization, operant conditioning, auditory distance perception

INTRODUCTION

The bulk of human studies of auditory distance perception has focused on sound source distances in the far field (>~1 m). The general consensus is that distance perception is poor in anechoic environments but better and systematic in reverberant environments (reviewed by Zahorik et al. 2005). In reverberation, the relationship between perceived and physical distances is approximated by a straight line in a log-log plot of perceived distance vs. physical distance with a slope less than unity. Perceived distances are underestimated for farther distances and overestimated for closer distances. The crossover distance is often ~1 m but varies noticeably among listeners and in different stimulus conditions (Zahorik 2002a).

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Distance perception of a sound source in the near field (<1 m) is of particular interest because it is in this realm that critical decisions of fight or flight to threatening sounds must often be made (Cannon 1915) and where daily events such as personal conversations occur (Shinn-Cunningham et al. 2005). Neural support for distance sensitivity in the near field was reported by Graziano et al. (1999). They found that neurons in the ventral premotor cortex of the awake monkey increased their firing rate as the sound source became closer and closer at distances within its arm's length (i.e., personal space, near field). They reported that more than half the neurons were sensitive to distance, independent of the source level. Kopčo et al. (2012) using functional magnetic resonance imaging showed a distance-sensitive area in the putative posterior auditory-cortex "where" pathway of humans. Support for distance sensitivity in humans in the near field was provided by Brungart and his colleagues (1999), Zahorik (2002a, b), and Kopčo and Shinn-Cunningham (2011).

Distance perception has been studied in birds (e.g., Nelson and Stoddard 1998, Naguib et al. 2000) and bats (e.g., Valentine and Moss 1997, Suga 1995), mostly in the far field; however, there is a dearth of behavioral studies of distance perception in mammals. Such studies are needed to understand the neural substrates of distance sensitivity, which are only accessible in non-human species. The goal here is to provide the behavioral sensitivity to distance in rabbits, a common animal for neural studies of hearing. The rabbit's hearing encompasses the range of human hearing (Heffner and Masterton 1980). Its sensitivity in azimuth is $\sim 20^\circ$ (Gandy et al. 1995, Heffner 1997). Kuwada and colleagues (e.g., 1989, 2006, 2014, Stanford et al. 1992, Fitzpatrick et al. 1999) have made neural recordings in the superior olivary complex, dorsal nucleus of the lateral lemniscus, inferior colliculus, medial geniculate body, and auditory cortex of the awake rabbit, with a focus on processing of interaural time differences. The responses of these structures in the rabbit resemble those of the cat, guinea pig, and chinchilla. For all these reasons, and because recordings can be made in the awake state, the rabbit has proven to be a valuable model for auditory processing. The rabbit is crepuscular (i.e., most active during dawn and dusk) and its survival, at least in part, depends on its ability to localize an auditory source in distance (Popper and Fay 1997).

METHODS

Subjects

Three adult female Dutch-belted rabbits were studied. The rabbits were aged 10–11 months at onset of

testing, and the duration of testing was approximately 2 years for all three animals. The three rabbits were tested using wideband and low-pass stimuli. Only two were tested using high-pass stimuli after determining that one animal (R19) was not able to complete this task. It is possible that this animal had high-frequency hearing loss, but its thresholds for the wideband and low-pass stimuli were consistent with the other animals, so those results are reported here.

Rabbits were maintained at 80 % of their *ad libitum* weights and housed individually in the vivarium with access to fresh water. Daily behavioral testing sessions were approximately 400 trials ($1\frac{1}{2}$ to 2 h) in length. The daily pelleted ration (Purina Mills Lab Rabbit High Fiber test diet) was typically consumed as task reinforcements, and the diet was supplemented daily with Timothy hay. All procedures were approved by the University Committee on Animal Resources at the University of Rochester.

Behavioral Apparatus

The behavioral apparatus was inside an IAC sound-attenuated booth with inner walls of standard perforated metal ($2.13 \text{ m} \times 1.98 \text{ m} \times 2.57 \text{ m}$). The reverberation was later measured in another IAC booth of comparable size and found to be mildly reverberant (mean T60 for 0.125 to 4 kHz = 0.1 s). This is a conservative estimate because in the experimental booth the apparatus rested on a metal table. The hardware cloth test enclosure was 30.5 cm width $\times$ 45.7 cm length $\times$ 34.3 cm height. The wall of the enclosure facing the speakers had three 4-cm diameter response holes (Fig. 1). Responses were detected using infrared emitter/detector diode pairs (Radio Shack) mounted in the sides of the response holes. Speakers were mounted on motorized posts (Firgelli Automations, Model JC35PB24-110) that were used to randomize speaker heights from block to block during testing; the range of the vertical rove was 10 cm. The speaker further from the enclosure was mounted on a motor (Firgelli Automations) that varied the speaker distance between blocks of trials. A house light was on during test sessions, except during time-outs.

Stimuli

Sounds were generated using an acoustic system (Tucker-Davis Technologies, System III, Gainesville, FL, USA) under the control of MATLAB (The MathWorks, Natick, MA, USA). Stimuli were presented by Audax tweeter loudspeakers (1M025F7; Parts Express, Springboro, OH). An Ivie IE-35 (Springville, UT) handheld audio analyzer was used to measure the

FIG. 1. *Top:* Behavioral test setup for 0° azimuth speaker positions. *Bottom:* Setup for 45° azimuth speaker positions. The middle nose-poke hole was for the observing response (OR) that was made by the animal to initiate the acoustic stimulus on each trial.

sound pressure level. The analyzer was placed at the height of the rabbit's ears and at approximately the same distance from the cage front (6.5 cm) as the base of the animal's pinnae during a trial. The noise level was initially adjusted to a mean of 60 dB sound pressure level (SPL) (A weighting) in the test enclosure for both speakers and at all distances. The stimulus levels were roved over a 12-dB range from trial to trial to control for level cues because preliminary tests on other animals indicated a strong bias in responses based on stimulus level.

Sounds were presented in trains of 250-ms (50 % duty cycle) noise bursts until the animal responded (up to 5-s durations). Noise bursts were gated on and off abruptly. For each speaker position, animals were tested with stimuli at three bandwidths: wideband (0.1–10 kHz), low pass (0.1–3 kHz), or high pass (3–10 kHz).

Testing Procedure

An operant one-interval two-alternative choice task was used. Each trial of the final task consisted of an observing response (nose poke) in the center hole that initiated the acoustic stimulus. A reporting response (nose poke) was made to either the upper or lower hole to indicate if the speaker was the more distant or the nearer speaker. The response holes were aligned vertically to avoid bias to the left/right that was anticipated for testing at 45° azimuth (Fig. 1, lower panel). Correct responses were reinforced with a single pellet delivered to the dish behind the animal. Incorrect responses resulted in a lights-out time-out. Food reinforcement was delivered behind the animal to disassociate the position of the response hole with the food reward.

During initial training, the center nose poke hole was plugged. The sequence of training steps began

with magazine training, followed by reinforcement only for nose pokes made during noise bursts. The final stage of training required the animal to initiate each stimulus with an observing response (OR) that was a nose poke in the center hole, followed by a reporting response (RR) in either the upper hole (for stimuli from the near speaker) or in the lower hole (for stimuli from the far speaker). Stimuli were presented from one of the two speakers with equal probability. The stimulus was terminated when a RR was made. Correct RRs were reinforced with food pellets. Incorrect RRs initiated time-outs, during which the house light was extinguished for 5 s; the time-out timer was reset to 5 s after any poke made between stimuli. Bias [$\beta = 0.5 \times (Z\text{-score for hits} + Z\text{-score for false alarms})$] was monitored throughout each session and was controlled by the delivery of two pellets for the biased-against response type for a certain percentage of trials. This percentage was adjusted every 50 trials based on a running estimate of the animal's bias. Sessions were typically 1–2 h or 400 trials in length and were concluded when the daily allotment of food had been delivered or when 2 h had elapsed.

The near speaker remained stationary during testing for each distance, and the far-speaker position was varied depending upon previous performance. For speakers at 0° azimuth, three near-speaker distances were tested (20, 40, and 60 cm) for each stimulus bandwidth. Stimulus conditions were tested in different orders for each animal. After the completion of testing 0° azimuth, the apparatus was repositioned for testing at 45° azimuth. At 45° azimuth, two distances (20 and 60 cm) and three stimulus bandwidths were tested in different orders for each animal. Head position was monitored using a video camera positioned above the test enclosure over several sessions to verify that the head faced forward at the beginning of each trial, regardless of the speaker azimuth.

After each block of 10 trials, the percent correct for that block was computed; each block of 10 trials had 5 near and 5 far stimuli that were presented in a random sequence. A blocked two-down one-up algorithm controlled speaker position (Levitt 1971). Figure 2 is an example of this procedure for which the near speaker was fixed at 20 cm, the azimuth was set at 0°, and the noise bursts were high pass. If the percent correct exceeded 70.7 % for two consecutive blocks of 10 trials, the distance between the far and near speakers was decreased. If the percent correct for a block of 10 trials fell below 70.7 % correct, the distance between the speakers was increased. The far speaker was moved in equal logarithmic steps. The ratio of the far-speaker distance to the near-speaker distance is referred to as the distance ratio (DR). The

$\log_2$ DR step was changed in increments of 0.15 until a $\log_2$ DR of 1.5 was reached; then, the increment was decreased to 0.05. An automated motor was used to vary the distance of the far speaker, which was at a distance of 120 cm from the enclosure at the start of every session. A 10-cm vertical rove was used for the speakers to randomize their heights after each block of trials. To eliminate visual cues, such as vibration of the Mylar dome of the near speaker during the noise bursts, a piece of gauze was draped in front of the near speaker.

Tracks were only included in the final threshold estimate if they had standard deviations of $\log_2$ DR less than 0.3 and bias less than 0.3. The estimate of the discrimination threshold for each track was obtained from the last four reversals of $\log_2$ DR in the track. For the example in Figure 2, at the threshold for discrimination, the distance of the far speaker was approximately 56 cm and the fixed near speaker was at 20 cm. For this estimate, the distance ratio was 2.8, i.e., the far speaker was at a distance 2.8 times the near speaker when the rabbit could just reliably discriminate the two speakers. This condition (near speaker=20 cm, azimuth=0° and high-pass noise bursts) had the highest discrimination thresholds (see Figs. 3, 4). Final threshold estimates for each near-speaker position were based on the mean of the last five individual thresholds that were unbiased and consistent (i.e., the criterion standard deviation was applied to the track used for each threshold estimate). If a significant trend was observed across the five estimates (i.e., a slope statistically different from zero), suggesting an improvement associated with learning, testing continued until five consecutive thresholds were obtained without such a trend. The 95 % confidence intervals in Figures 3 and 4 were derived from the means and standard deviations across all animals tested in each condition. Because of the small number of subjects, the data sets were not appropriate for analysis using either parametric or non-parametric statistics, given the statistical assumptions required. As a result, differences in thresholds between conditions are described on the basis of non-overlapping confidence intervals.

RESULTS

Behavioral results were based on thresholds estimated for speaker separation discrimination at 0 and 45° azimuths. Thresholds for distance discrimination are shown in terms of absolute distance of the far speaker (Fig. 3), and in DR (Fig. 4), as a function of near-speaker location. Each threshold for an individual animal represents the mean of five estimates (bars

FIG. 2. Example of a two-down one-up (2D1U) track used to estimate the threshold for distance discrimination. The near speaker, in this example, was fixed at 20 cm; the azimuth was set at 0°; and the noise bursts were high pass. Reversals of the track direction are indicated by circles. The mean of $\log_2$ DR of the last four reversals was used to compute the confidence interval for each track. Each track consisted of many blocks (30 in this example), with each block consisting of 10 trials. Within each block, half of the trials were from each speaker, presented in random sequence.

indicated the 95 % confidence intervals of the means). Mean thresholds were estimated from the pooled set of 15 thresholds (for three rabbits) or 10 thresholds (for two rabbits). In Figure 3, the means and 95 % confidence intervals of the absolute distances of the far speaker are generally consistent across animals, and confidence intervals are non-overlapping for different speaker distances in each stimulus condition.

Figure 4 shows the same threshold estimates as in Figure 3, but in terms of the DR, a form of the Weber fraction (i.e., $(D+\Delta D)/D=1+\Delta D/D$). This plot allows the visual determination of how well the results are described by Weber's Law, which predicts that distance-discrimination thresholds should be proportional to speaker distance or that DR should be constant across different near-speaker distances. Figure 4 shows clearly that proportional thresholds are largest for the nearest speaker distance tested (20 cm) and that thresholds were similar for the 40- and 60-cm distances. The difference between DR at the near distance and the two farther distances was most pronounced for the high-pass condition.

At 45° azimuth and 20-cm reference distance (Fig. 4, right panels), distance discrimination improved relative to the 0°, 20-cm conditions for all three frequency bands. When the reference distance was 60 cm, however, there was no advantage of the 45° azimuth over the 0° azimuth. Regarding the effect of reference distance, the 45°, 20-cm performance

was only marginally worse than the 45°, 60-cm case for the low-pass and wideband noise bursts. However, similar to the 0° azimuth condition, the difference between the 20 and 60 cm references was larger for the high-pass noise bursts.

DISCUSSION

The main findings of this study are that the rabbits were able to most accurately discriminate distance when the near-speaker reference distance was 40 or 60 cm and were worse when the near-speaker distance was 20 cm, particularly at 0° azimuth. At 20-cm reference distance, distance discrimination was better at 45° azimuth than at 0°. At both azimuths, distance discrimination at the closest reference distance (20 cm) was better for low-pass and wideband noise than for high-pass noise.

Most studies of distance perception in humans asked the listeners to directly estimate the distance of a sound source. Such a task is not possible in animals and that is why the measurement of distance discrimination was used in this study. Zahorik (personal communication) derived estimates of human listeners' distance-discrimination thresholds from observations made in a moderately reverberant (mean T60 for 0.2 to 16 kHz=0.7 s) auditorium (Zahorik 2002a) following the logic described in Zahorik (2002b, pp. 2115–2117). For a d' of 1.09, which corresponds to 70.7 % correct in a single-interval two-alternative forced choice task (Macmillan and Creelman 2005), the estimated human threshold DRs for wideband noise stimulation at 0° were 2.9, 2.2, and 2.3 for reference distances of 30, 43, and 61 cm, respectively. These estimates are similar in pattern (i.e., worst at the closest reference distance) but overall slightly less sensitive than the corresponding rabbit data (DR=2.4, 1.6, and 1.5 for 20, 40, and 60 cm, respectively, for 0° azimuth). The lower distance sensitivity in humans may be partly due to the fact that listeners were tested in a distance-estimation task rather than the discrimination task used for the rabbit. Another difference between the experiments was the use of trains of noise bursts up to 5 s in duration for the rabbits. This potentially allowed head movements; however, no systematic head movements were observed, and for most trials, the animals responded briskly and the stimulus was terminated.

Human distance-discrimination thresholds were also derived from the distance perception responses reported by Brungart (1999) for cases in which the stimulus level was roved. These estimates were also based on the logic described by Zahorik (2002b) but relied on estimates of response standard deviation

FIG. 3. Mean distance-discrimination thresholds for all tested conditions. *Left:* Speakers at 0° azimuth; *Right:* speakers at 45° azimuth. *Top:* Wideband stimuli (0.1–10 kHz); *Middle:* Low-pass stimuli (0.1–3 kHz); *Bottom:* High-pass stimuli (3–10 kHz). Mean and

95 % confidence interval of the mean ($n=5$ estimates) for each individual rabbit (*open symbols*) as well as the mean and 95 % confidence interval collapsed across rabbits ($n=10$ or 15; *solid squares*) are plotted for each condition.

derived from reported values of slope and correlation between log-transformed source distances and responses (see Fig. 9 in Brungart 1999) and an estimated source distance standard deviation of 0.96 $\log_2$ cm (see Fig. 7 in Brungart 1999). For $d'=1.09$, 70.7 % correct, the average threshold DR estimates were 6.4 and 2.7 for 0 and 45° azimuth, respectively, over the range of source distances studied (10 to 100 cm). These estimated human sensitivities were again lower than those for the rabbit, where DR for wideband stimulation when averaged across distance (20–60 cm) was 2.2 and 1.6 for 0 and 45°, respectively. The distance-discrimination performance was better at 45° azimuth in both rabbits and humans, although greater improvement was observed in humans.

Brungart's findings that distance perception in humans was better for low-pass and wideband noise bursts are also consistent with the results for rabbit, for which better distance-discrimination thresholds were estimated for low-pass and wideband noise bursts, especially at the nearest distance.

One difference between the studies of Zahorik (2002a) and Brungart (1999) is the acoustic environment: moderately reverberant ($T60=0.7$ s) in the former and anechoic in the latter. Distance discrimination was better in the moderately reverberant environment ($DR=2.4$, averaged over 30–61 cm at 0°) than in the anechoic environment ($DR=6.4$ at 0°). This is consistent with the concept that distance localization is facilitated by reverberation. The distance sensitivity in

FIG. 4. Mean distance-discrimination thresholds plotted as distance ratio (far-speaker distance at threshold divided by fixed near-speaker distance). Same format as Figure 3. Error bars are 95 % confidence intervals, as in Figure 3.

an anechoic environment was surprising because many studies report poor distance perception in such environments (Mereshon et al. 1989, Nielsen 1993). Shinn-Cunningham et al. (2000) using near-field virtual stimuli and roved stimulus levels reported that distance perception in anechoic conditions was below chance levels and, even with feedback, was below that reported by Brungart (1999). Shinn-Cunningham et al. (2000) also showed that distance perception was much improved in reverberation. The discrepancy between the two studies in anechoic environments may be explained by the presence of a person who manipulated the position of the sound source in the Brungart (1999) study. The person stood next to and slightly below the subject in order to manipulate the spatial position of the sound source that was attached to the end of a rod and thus could have created inadvertent reverberations. The

Shinn-Cunningham et al. (2000) study avoided this problem because virtual sound source methods were used.

Brungart (1999) attributed the better performance for sound off the midline to increasing interaural level difference (ILD) cues at low frequencies with decreasing distance (humans: Brungart and Rabinowitz 1999, Kuwada et al. 2010a, Kuwada et al. 2010b; barn owl: Kim et al. 2008; rabbits: Kim et al. 2010; chinchilla: Jones et al. 2013). However, several studies (Shinn-Cunningham et al. 2000, Kopčo and Shinn-Cunningham 2011, Kopčo et al. 2012) showed that distance perception is dominated by reverberant cues (i.e., direct-to-reverberant energy (D/R)) and that contribution of ILD cues was minimal. These findings are supported by a human neural-imaging study that found that reverberant cues (i.e., D/R), not ILD, play a dominant role in neural distance sensitivity (Kopčo et al. 2012).

CONCLUSIONS

Rabbits performed a distance-discrimination task for trains of noise bursts presented in the near field. Relative distance-discrimination thresholds were consistent across stimulus bandwidths and for 0 and 45 ° azimuths for near-speaker reference distances of 40 and 60 cm, consistent with Weber's Law. In contrast, relative distance-discrimination thresholds were higher, across stimulus bandwidths and azimuths, when the fixed reference speaker was nearer (20 cm). Trends in discrimination thresholds in the rabbit as a function of near-speaker distance were similar to those inferred from distance-estimation experiments in human listeners.

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