Evidence for spatial representation of object shape by echolocating bats (*Eptesicus fuscus*)

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Big brown bats were trained in a two-choice task to locate a two-cylinder dipole object with a constant 5 cm spacing in the presence of either a one-cylinder monopole or another two-cylinder dipole with a shorter spacing. For the dipole versus monopole task, the objects were either stationary or in motion during each trial. The dipole and monopole objects varied from trial to trial in the left-right position while also roving in range (10–40 cm), cross range separation (15–40 cm), and dipole aspect angle (0°–90°). These manipulations prevented any single feature of the acoustic stimuli from being a stable indicator of which object was the correct choice. After accounting for effects of masking between echoes from pairs of cylinders at similar distances, the bats discriminated the 5 cm dipole from both the monopole and dipole alternatives with performance independent of aspect angle, implying a distal, spatial object representation rather than a proximal, acoustic object representation. © 2008 Acoustical Society of America. [DOI: 10.1121/1.2912450]

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I. INTRODUCTION

Insectivorous bats use an active mode of sound perception called *echolocation* (Griffin, 1958). They emit high-frequency sounds and perceive objects in their environment from the echoes that return to their ears. The sonar broadcasts of most bats are wideband signals covering frequencies of roughly 20–150 kHz (varying across species; Neuweiler, 2000). For example, the big brown bat (*Eptesicus fuscus*) emits frequency-modulated (FM) biosonar sounds with frequencies from 20 to 100 kHz arranged in several downward-sweeping harmonics (Hartley, 1992; Saillant *et al.*, 2007; Surlykke and Moss, 2000). These bats use echoes to navigate, to find prey, and to avoid obstacles.

Behavioral tests of object discrimination have focused on how bats employ acoustic parameters such as echo delay, echo amplitude, and echo spectrum to discriminate among objects that vary in size, shape, and distance from the bat (Grinnell, 1995; Moss and Schnitzler, 1995; Neuweiler, 2000; Simmons *et al.*, 1995). Additionally, neuroethological studies have explored how these acoustic parameters are encoded in the ear and auditory nervous system of bats (Neuweiler, 2000; Pollak and Casseday, 1989; Simmons *et al.*, 1996). However, there has been only a limited examination of the nature of echolocating bats' perception from a psychological perspective (Simmons, 1989). Specifically, we are interested in the nature of bats' representations. A cognitive representation is an internal model of a past experience (e.g., an object) that is used to guide future action and must be inferred from an organism's behavior (i.e., it cannot be investigated by examining the nervous system).

An organism's representation of objects in its environment may correspond to the parameters of the object itself (the *distal* stimulus) or to the parameters of the sensory experiences produced by the object (the *proximal* stimulus). For example, a person listening to a ball bouncing on the floor in another room could form a representation of the

characteristics of the sounds produced by the ball, such as the loudness, duration, and repetition rate of the sounds. Alternatively, the person could form a representation of the characteristics of the ball itself, such as its shape, size, and structure. Similarly, echolocating bats' representations could contain the proximal stimulus or the distal stimulus. The proximal stimuli are the echoes that return to the bats' ears after sending out sonar signals. The bats could form a representation that would contain merely a list of echo acoustic features (e.g., amplitude, frequency, delay). In contrast, the bats could represent the distal stimulus, which would contain the size, distance, and spatial dimensions of the object.

Distal object representations are advantageous. For instance, they allow an organism to link different perceptual experiences of the same object. The same object representation could be accessed whether the object was observed visually or via echolocation. In addition, a distal object representation would allow an organism to identify an aspect-dependent object from different orientations relative to the object. Many objects that bats need to identify, such as prey animals, have an appearance that is aspect-dependent—that is, the object presents different-sized or different-shaped surfaces from different orientations. Consequently, the echoes the targets reflect depend on the aspect angle at the instant individual incident sounds impinge on the object to form echoes. The acoustic features of echoes returning from aspect-dependent targets vary greatly with the target's orientation with respect to the echolocating animal (e.g., Moss and Zagaeski, 1994).

The purpose of this study was to determine whether bats form proximal or distal object representations. Echolocating bats were trained to discriminate between two objects presented on flat circular surfaces located to the bat's left and right. Both objects were presented together on each trial, so the bats faced a simultaneous-discrimination two-choice test. Within the limits set by randomly introduced variations in the relative distance to each object, echoes from both objects

reached the bat at about the same time. The bat's task was to decide which of these objects consisted of a pair of cylinders separated by 5 cm (referred to as the *dipole target*) and to move toward that object to receive a food reward. In the first experiments (experiments 1A and 1B), the other object—the unrewarded stimulus—consisted of just one cylinder (referred to as the *monopole target*). The dipole target was presented at different aspect angles from one trial to the next. Both the dipole and the monopole were also roved to different distances and different horizontal directions from trial to trial, so their specific positions and overall echo strengths could not serve as reliable cues.

In the second experiment, both the positive and the negative stimuli were dipoles. The negative stimulus had a spacing of 1.0, 1.5, 2.0, 2.5, or 3.0 cm between the cylinders (versus the 5 cm spacing for the positive stimulus). The 5 cm dipole versus shorter dipole experiment is likely to be more difficult for the bats because there are two reflecting parts to each target, so the average strength of the echoes will be the same, and both objects now contain two parts, so the simple two versus one cue is no longer present. By varying the distance, direction, and aspect angle of both dipoles from trial to trial, as well as the spacing of the shorter dipole, conditions were created for masking between reflections from individual parts of the targets at the same time at the bat's ears, thus lowering the bat's performance to the region of greatest sensitivity between 60% and 85% correct responses.

Taking the dipole versus monopole and dipole versus dipole experiments together and roving the targets to different locations and orientations between trials prevented any single feature of the acoustic stimuli from being a stable indicator of which target was the correct choice. The bat had to recognize the dipole with the 5 cm spacing without using any of the extraneous features. By reconstructing the locations of the various reflecting parts of each target on each trial, we could determine which acoustic or object features did affect the bat's performance and, thus, whether the bats were likely to have used proximal or distal object representations.

II. EXPERIMENT 1: MONOPOLE TARGET VERSUS DIPOLE TARGET

A. Method

1. Animal subjects

Five adult big brown bats, *Eptesicus fuscus*—two females (“Frodo” and “Astro”) and three males (“Buddy,” “Chris,” and “Patrick”)—were used in this experiment (for information about this species, see Kurta and Baker, 1990). They were obtained from colonies in the attics of houses in Rhode Island. The animals were kept in individual aluminum mesh cages in a temperature-controlled (72°F) room with relative humidity maintained between 60% and 70%. The light-dark cycle of the room was 12–12 h, with lights on at 10:30 p.m. and lights off at 10:30 a.m. This cycle was implemented to enable the bats to be active during the daytime. The bats had continual access to vitamin-infused water (Poly-Vi-Sol drops) in their cages and were fed the majority

of their mealworm diet during the experiments. The weights of the bats were recorded daily, and mealworm intake was adjusted according to the measured weights. During the course of experimentation, the bats' weights were kept roughly between 14 and 18 g. Notably, the big brown bats do not require extensive food deprivation to render them sensitive to food reward; bats at normal body weights in this range will respond to food without having to undergo deprivation beforehand.

2. Stimuli

Each bat was trained in a two-alternative forced choice procedure to discriminate between a dipole target consisting of two cylinders and a monopole target consisting of just one cylinder. The dipole target was always the positive stimulus. In the test condition, the cylinders making up the targets were identical; they each had a diameter of 1.59 cm and a height of 1.27 cm. They were made of a hard black plastic. The single cylinder for the monopole and the two cylinders for the dipole were mounted on thin strips of clear polyethylene (0.1 mm thick) to serve as a base and to keep the cylinders in the dipole at a fixed separation of 5.0 cm (measured from the center of the first cylinder to the center of the second cylinder). The monopole was centered on a polyethylene strip (1.91 cm × 2.54 cm) and the dipole targets were mounted on polyethylene strips (7.3 cm × 2.54 cm) such that the cylinders were 0.32 cm from the left and right edges of the strips. The targets were spray painted flat black and were presented on flat black surfaces located to the bat's left and right.

3. Experimental setup and procedure

Figure 1 shows the experimental setup. The bat was trained to sit on an elevated Y-shaped platform and broadcast its sonar sounds to the left and right to discriminate the dipole target from the monopole target. The bat was rewarded with a piece of mealworm offered in forceps following the completion of each correct response, which consisted of crawling forward onto the arm of the platform that faced the dipole target (see arrow in Fig. 1). An incorrect response consisted of crawling onto the arm of the platform that faced the monopole target and resulted in the trainer making a “shh” sound and delivering no mealworm reward. Prior experience showed that the “shh” served as a signal that the bat had made an error and it was not intrinsically aversive. Use of this cuing sound greatly speeds up training.

The experiment took place in a dark experimental chamber (5.2 m long × 3.4 m wide × 2.4 m high). The Y-shaped platform (15.5 cm in length and 20.0 cm in width) was mounted on a heavy Brunson optical tooling stand with a tripod base. A plastic dish to hold the mealworms ready for reinforcement was mounted on the same stand 30.0 cm below the platform and out of the bats' visual range. A dim light consisting of a cluster of three light emitting diodes (LEDs) was mounted above the mealworm dish, so the experimenter could see the mealworms in the dark. A ceiling mounted spotlight weakly illuminated the center of the platform (covering the bat but not the targets), so the experi-

FIG. 1. Experimental setup and design of stimuli for experiments: experiment 1A, dipole versus monopole stationary; experiment 1B, dipole versus monopole moving; experiment 2, dipole versus dipole stationary. The positive stimulus is the 5 cm dipole target, and the bat's response is to move forward onto the arm of the Y-shaped platform facing this target to receive its food reward. The bat's broadcast beam is wide enough to encompass both targets even when the bat's head is aimed at either one. In experiment 1B, the disks rotate (the left disk rotates clockwise; the right disk rotates counterclockwise) to bring the targets toward the bat during each trial. In experiment 2, the positive dipole cylinders were separated by 5 cm, whereas the negative dipole cylinders were closer together (1.0, 1.5, 2.0, 2.5, or 3.0 cm separation).

menter could see the bat but the bat was unlikely to be able to see the targets, which were flat black on a flat black surface. The stimuli were placed on two Plexiglas disks (diameter=91.5 cm, thickness=0.5 cm) controlled by a pulley system driven by a motor (Minarik Electric Co. model SH-14) that allowed the disks to rotate at various speeds. The Plexiglas disks were approximately 4 cm below the bottom of the right and left arms of the Y-shaped platform.

A downward facing black and white charge coupled device camera (DSP, Inc. model 15CB221) was mounted on the ceiling approximately 125 cm above the rotating disks. On each side of the camera were two IR lights (each an array of infrared LEDs 16.0 cm in length $\times$ 12.0 cm in width) that automatically turned on when the illumination in the room was low and trials were about to be conducted for a bat. Two Titley Electronic Ltd. ultrasonic microphones were located to the bat's left and right and 150 cm from the bats' observing position at the center of the platform. These microphones allowed for high-quality ultrasonic recordings to be made of the bat's signals during trials. Additionally, a mini-2 heterodyning bat detector (Ultra Sound Advice Ltd.) tuned to 28–29 kHz was mounted on a stand located 150 cm from the center of the platform and in front of the bat. The bat detector translated the bats' ultrasonic sounds down to the audio range, so the experimenter could listen to the bats' sonar sounds during trials via the auditory output of the bat detector. The low-frequency auditory output of the bat detector was not aversive to the bats, as there was no difference in their performance when it was turned on or off. All experimental trials were recorded on a digital video cassette recorder (Sony model GV-D800 NTSC "Video Walkman") by using Fujifilm Hi8 MP P6-120 digital video tapes. The bat detector's audio-frequency signals were stored on the sound track of this video tape to mark the time of occurrence of echolocation sounds. A Sony digital instrumentation/video recorder (model SIR-1000 W) was used to capture high-fidelity recordings of the ultrasonic sounds along with the video stream to record representative trials.

Two experimenters, a bat trainer and a recorder, were present for each test trial. At the beginning of each trial, the bat would crawl from the trainer's hand onto the back of the

Y-shaped platform. Then, the bat would emit sonar signals for approximately 1–10 s and then walk forward toward one arm of the Y-shaped platform. When the bat reached the end of the arm, if it was correct (facing the dipole target), the trainer would then deliver the mealworm reward by presenting the mealworm piece in the forceps just in front of the bat's mouth. After the bat grasped the mealworm at the conclusion of a correct trial (or after the trainer said "shh" at the conclusion of an incorrect trial), the trainer would pick up the bat and hold it while it ate the mealworm for an intertrial interval of about 5 s. During this intertrial interval, the recorder would record the bat's choice on a list of trial alternations from left to right according to a pseudorandom schedule (Gellermann, 1933) and then reposition the targets for the next trial. The trainer shielded the bat from the movements of the recorder during the intertrial interval to avoid inadvertent cuing.

The bats were tested 5–6 days per week. On test days, each bat was run for a total number of trials to attain a predetermined number of correct, rewarded trials that was determined by the quantity of mealworms it could eat on that day to maintain its current body weight. Each bat typically worked through 30–60 trials per day. The first trial of the day was prompted, such that the mealworm was held in front of the arm of the platform with the correct target (the dipole). If during the test session the bat got three incorrect choices in a row, the next trial was also prompted. On all other trials, the mealworm was held out of view, so that the bat had to use its sonar sounds to discriminate between the targets. Prompted trials were not included in the data.

(a) *Pretraining.* Although during testing the cylinders in the monopole and dipole targets were the same in height, which is 1.27 cm, during the pretraining phase before testing, the monopole and dipole differed in size, so that the monopole was always shorter than the dipole. This added a size difference and thus a reliable echo amplitude difference to the monopole versus dipole stimuli that facilitated training the bats by a fading procedure of reducing the size difference. Figure 2(a) is a diagram of the different combinations of cylinders used for pretraining the bats. There were two different sets of training stimuli used in two different pre-

FIG. 2. (A) Arrangement of stimuli in two sequences for pretraining to bring bats to discriminate monopole and dipole with the same cylinder height (cylinder dimensions and spacing in cm). Three bats learned the test task with progressively increasing height of monopole cylinder (left panels; pretraining stages 1–5 culminating in the test task with 1.27-cm-high cylinders). Two bats learned the test task with progressively decreasing heights of dipole cylinders (right panels; pretraining stages 1–5 culminating in the same test task with 1.27-cm-high cylinders). Decibel values give target strengths of the monopole and dipole targets relative to a single 1.27-cm-high test cylinder. (* denotes an average 3 dB increase in dipole target strength relative to test-sized 1.27-cm-high monopole for most aspect angles.) (B) Mean performance of three bats in ascending pretraining sequence (light gray bars) and two bats in descending pretraining sequence (dark gray bars).

training regimes. Three bats (Buddy, Frodo, Chris) received the “ascending monopole” pretraining set, in which the cylinders in the dipole target were kept at their intended height of 1.27 cm, while the height of the cylinder in the monopole target started very short, which was at only 0.32 cm, and was increased in several steps to arrive at 1.27 cm [left side of Fig. 2(a)]. The other two bats (Patrick, Astro) received the “descending dipole” pretraining set, in which the monopole cylinder was kept at the intended height of 1.27 cm, while the cylinders in the dipole target started much higher, which were at 2.54 cm, and were decreased in several steps to arrive at 1.27 cm [right side of Fig. 2(a)]. For both pretraining sets, each bat completed a minimum of 200 trials on each target pairing and was made to achieve a mean of approximately 75%–95% correct responses (reaching asymptotic performance) before moving to the next pair in the pretraining series [in Fig. 2(a), starting with pair 1 and ending with pair 6].

(b) *Experiment 1A: Stationary targets.* In experiment 1A, the disks that the dipole and monopole test stimuli were placed on [see Fig. 1(a)] did not rotate during each trial. The targets were placed in different positions between trials, but they were stationary during individual test trials while the bat made its choice [Fig. 1(a)]. The targets were repositioned during each intertrial interval in three ways: (1) left/right position, (2) distance from the Y-shaped platform, and (3)

dipole orientation with respect to the platform [examples shown in Fig. 3(a)]. First, the dipole target appeared on either the left or right disk as determined by a pseudorandom Gellermann series (Gellermann, 1933). Second, the dipole and monopole were placed at varying distances approximately 10–40 cm from the end of the arms on the Y-shaped platform. This resulted in three situations: the monopole was closer to the bat than the dipole [Fig. 3(A1), top], the dipole was closer to the bat than the monopole [Fig. 3(A2), middle], or the monopole and the dipole were approximately equidistant from the bat [Fig. 3(A3), bottom]. There were no three distinct positions for the targets, rather, the monopole and dipole were placed anywhere on a continuum of locations ranging from 10 to 40 cm from the platform. The cross range (left to right) distance between the dipole and monopole varied from roughly 15 to 40 cm from trial to trial. This varied the angular separation of the targets from the bat’s position. Third, the orientation, or aspect angle, of the dipole was varied so that it could be in any possible position from 0° to 90° in either direction [see Fig. 3(a)]. The orientation in which the second cylinder of the dipole was directly behind the first cylinder was called 0°, and the orientation in which the two cylinders were side by side was called 90°. The positions, distances, angular separations, and orientation of the targets were semirandomly (spontaneously) determined by the recorder and altered between trials by using a small,

FIG. 3. (A) Three sample test trial configurations of the dipole and monopole for experiment 1A. The circles represent the disks (stimuli are shown larger than they actually were compared to the size of the disks). The Y-shaped platform with the bat is shown in front of the disks. At the top, the monopole is in front of the dipole and the dipole is oriented at approximately 5°. In the middle, the dipole is in front of the monopole and the dipole is oriented at 45°. At the bottom, the monopole and dipole are equidistant from the bat and the dipole is oriented at 45°. (B) Overlay of all positions for cylinders in the monopole and the dipole targets from experiment 1A. (C) Overlay of all positions for cylinders in the two dipole targets from experiment 2. The point (0,0) is the position of the bat's head. Each point represents the center of the each cylinder. The different cylinders (e.g., monopole, dipole near, dipole far) are plotted in different colors and overlaid. Plots B and C show that the target position varied from trial to trial by amounts that were, on average, several times larger than the target dimensions.

handheld LED flashlight while the trainer was holding the bat. The large quantity of test trials run for each bat ensured that all possible distances and orientations were included. The actual positions of the cylinders with respect to each other and to the bat were determined by digitizing the video records of all trials [see Fig. 3(b)]. Each of the five bats run in experiment 1A completed a minimum of 1000 trials.

(c) *Experiment 1B: Moving targets.* In experiment 1B, the large Plexiglas disks that the monopole and dipole stimuli were placed on rotated during the trials [see Fig. 1(b)]. The stimuli and the procedure were otherwise the same as in experiment 1A in that the left/right position, distance from the platform, angular separation, and orientation of the dipole target were changed during intertrial intervals. At the beginning of each trial, the dipole and monopole targets would be placed approximately 65 cm from the back of the Y-shaped platform, which is nearer the tops of the disks in Fig. 1(b) than they would have been placed for experiment 1A. During the ensuing trial, the disks would rotate inward (left disk would rotate clockwise; right disk would rotate counterclockwise), carrying the targets toward the bat just placed on the platform. As in experiment 1A, the bat would emit sonar sounds for 1–5 s and then walk down one of the arms of the platform. If the bat did not make a choice before the stimuli rotated past the platform (at a distance of about 3–6 cm from the ends of the arms), that trial was not counted as an incorrect choice. Instead, the bat was picked up and the same trial was restarted. It took about 5 s for the stimuli to reach the end of the platform as the disks rotated, but the bats made their choices before the stimuli rotated past the platform on about 85% of all trials. Two of the five bats (Chris and Astro) participated in experiment 1B. (The other three bats directly went to experiment 2.) Chris completed 1378 trials and Astro completed 693 trials with the moving stimuli.

4. Data analysis

Videotapes of all the test sessions were analyzed to determine the bats' performance in the first experiment. First, a single video frame representing the bats' choice point for each test trial was clipped from the videotape of the daily test session and then all the frames for a given bat on a given day were put together and saved in chronological order as a single video (avi) file by using PINNACLE STUDIO 9 (v 9.4.3, Pinnacle Systems Inc., 2004). The individual choice-point frame was chosen to capture the moment at which the bat started rapidly moving forward toward its final destination (either the correct arm or the incorrect arm of the platform). The bats often made their decision in the center of the platform but sometimes would walk toward one arm then change their direction and walk down the other arm. The frame that was clipped represented the bat's last turn toward its chosen target regardless of where the bat was on the platform.

The video file containing the clipped images from all the trials in a day's session was then imported into PEAK MOTUS (v 8.2, Peak Performance Technologies Inc., 2004) for analysis. In this program, six different spatial reference points were located and digitized for each test trial: (1) the bat's head (defined as the tip of the nose), (2) the left corner of the platform, (3) the right corner of the platform, (4) the center of the monopole cylinder, and [(5) and (6)] the center of each of the dipole cylinders. For each trial, the location of these points in the corresponding video image was used to calculate the distance from the bat's head to each of the cylinders and also to calculate the orientation of the dipole target.

5. Echo measurements

Echoes reflected by each of the targets were recorded using an "artificial bat" consisting of two Bruel & Kjaer model 4136 ($\frac{1}{4}$ in.) condenser microphones separated by 3 cm to record the echoes and a centrally located custom-

built condenser loudspeaker to broadcast the test sounds [see Fig. 8(B) for the arrangement of the microphones and loudspeaker in relation to the target and the disk on which the target was rotated to different aspect angles]. The test signal consisted of a 1-ms-long FM sweep from 110 to 20 kHz that was generated by a National Instruments PCI-6111e digital-to-analog board in a Pentium-III computer. Echoes picked up by the microphones were amplified ($1000\times$) and band limited to 15–100 kHz (Wavetek-Rockland variable bandpass filters) and digitized at a sampling rate of 500 kHz in a National Instruments PCI-6111e two-channel analog-to-digital converter board. Custom software written in LABVIEW and MATLAB provided for windowing the data and averaging the echoes reflected from each of the targets for 20 repetitions of the test signal.

To make the dipole target echo measurements, the dipole target was placed on the center of a Plexiglas rotating disk 30 cm away from the artificial bat [Fig. 8(b)]. The target was first oriented at 0° with respect to the artificial bat and ensounded for 20 repetitions of the test signal. (Each such data-collection procedure was repeated two times to check for possible acoustic transients.) Then, the circular table holding the target was rotated 2° clockwise and the same echo-measurement procedure was repeated. Following each recording of echoes, the target was again rotated 2° clockwise until echoes had been recorded from target aspect angles from 0° to 94° in increments of 2° . This provided a set of echoes that encompassed all possible orientations of the dipole. The monopole target was measured using the same setup and procedure as the dipole target, except that instead of rotating the monopole, it was measured at varying distances from the artificial bat, including 20, 25, 30, 35, and 40 cm. The set of pretraining stimuli was measured 30 cm away from the artificial bat. Individual cylinders reflected strong, short-duration specular echoes, and the peak-to-peak amplitudes of these primary reflections proved to be adequate to characterize the relative target strength for different-sized cylinders.

B. Results

1. Pretraining trials

Figure 4(a) plots the results from echo measurements of the various cylinders with different heights used in pretraining [see Fig. 2(a)]. The sequence of stimuli used in the two pretraining regimes—monopole ascending height and dipole descending height [Fig. 2(a)]—is marked on the graph in Fig. 4(a). During pretraining, the negative stimulus (monopole) always had a lower target strength than the positive stimulus (dipole), first, because the dipole returned two reflections for the monopole's one reflection and, second, because the heights of the cylinders always favored the dipole with several decibels of additional target strength during either of the pretraining approaches to the test stimulus with equal cylinder heights. As expected, differences in peak-to-peak echo amplitude remained a reliable cue during the pretraining trials, with the higher amplitude echoes always from the positive stimulus.

FIG. 4. (A) Graph showing peak-to-peak amplitudes of echoes recorded with two microphones from cylinders of different heights in decibels relative to peak-to-peak amplitude of echoes from 1.27-cm-high test cylinder (target distances are 30 cm; see Fig. 2 for relationship to pretraining sequences). (B) Graph showing the relationship between the target distance and relative echo strength for a 1.27-cm-high cylinder.

Figure 2(b) displays the bats' performance on the pretraining trials for the two pretraining regimes illustrated in Fig. 2(a). In general, their pretraining performance was related to the difference in height between the monopole and the dipole targets and, thus, the difference in echo strength [Fig. 4(a)]. The bats' performance was high when the difference in height between the monopole and dipole was large (stages 1–3 of either pretraining series) and lower when there was no difference in height between the dipole and the monopole [i.e., the test condition in Fig. 2(b)]. Most importantly, there was no significant difference in performance between the bats in the ascending monopole and the descending dipole pretraining regimes when they reached the final test stimuli [$t(121)=1.93$, $p>0.05$], so the data from the two groups of bats were pooled for subsequent analyses of performance.

2. Experiment 1A: Stationary targets

Figure 3(b) shows the locations of the individual cylinders in the dipole and the monopole targets on all trials of experiment 1A. Target distances roughly varied over a 2:1 range, mostly from 15 cm to almost 40 cm. Differences in range between the dipole and the monopole mostly varied over ± 10 cm (see below). The angular separation of the targets varied from about 25° to 120° relative to the bat's location. Because the individual cylinders were presented at different distances from the bat, the amplitude of reflections at

FIG. 5. (A) Performance as a function of dipole aspect angle for experiment 1A (mean performance of all five bats is shown; error bars show standard deviations). The dipole could be rotated either clockwise (e.g., $+40^\circ$) or counterclockwise (e.g., -40°), but these two categories are plotted together (shown as 40°). Chance performance is 50% correct. The average performance of the bats was significantly above chance for every dipole orientation (summed binomial test, $p < 0.001$). (B) Target strength of the dipole relative to the monopole for different aspect angles.

the bat's ears necessarily differed, too. Figure 4(b) shows the strength of echoes reaching the microphones from a single test cylinder at different distances. Approximately 90% of all trials in experiment 1A involved individual cylinders at distances of 25–40 cm, and the plot in Fig. 4(b) depicts the relationship between the distance and the strength of echoes acting as stimuli. Note that the spread of differences in echo amplitude as a function of distance in Fig. 4(b) is comparable to the spread of amplitudes as a function of cylinder height during the pretraining series in Fig. 4(a).

The bats were able to discriminate between the monopole and the dipole across all orientations of the dipole, as shown in Fig. 5(a). From the bat's position, by considering the dipole as a single object, 0° corresponds to an end-on view, while 90° corresponds to a side-on view. The mean choice accuracy of the five bats was significantly above chance for all dipole orientations (summed binomial test, $p < 0.001$). The performance of individual bats is shown in Table I. Choice accuracy was above chance for all dipole orientations for three of the bats (Frodo, Chris, and Patrick). The other two bats' (Buddy and Astro) performance was above chance for all orientations except 80° . The bar graph in Fig. 5(a) shows only a moderate dependence of the bats' performance on the orientation of the dipole target, with differences between bats equaling or exceeding differences between orientations (see Table I). The highest mean performance was at the 30° orientation and the lowest mean performance was at the 80° orientation.

TABLE I. Performance accuracy as a function of dipole aspect angle for each of the five bats in experiment 1A. (The number of trials completed for each bat in each orientation is shown in italics under the accuracy value. Values with an asterisk are not significantly different from chance. All other values are significant at $p < 0.001$.)

Dipole orientation (deg)	Bat					<i>M</i> (Total)
	Buddy	Frodo	Chris	Patrick	Astro	
0	80.3% (61)	79.7% (64)	76.6% (47)	82.2% (45)	76.7% (60)	79.1% (277)
10	68.4% (117)	77.4% (133)	77.3% (128)	84.7% (85)	73.9% (138)	75.9% (601)
20	74.5% (153)	83.0% (88)	78.2% (87)	84.1% (69)	72.8% (103)	77.6% (500)
30	79.3% (179)	79.6% (98)	84.5% (103)	89.1% (137)	76.2% (126)	81.6% (643)
40	78.9% (208)	73.6% (140)	83.6% (134)	83.8% (105)	75.0% (128)	78.7% (715)
50	78.8% (184)	73.8% (122)	74.2% (124)	84.3% (127)	79.2% (130)	78.2% (687)
60	79.1% (158)	71.8% (117)	80.4% (102)	78.4% (116)	68.3% (123)	75.6% (616)
70	72.0% (118)	68.4% (79)	72.2% (72)	77.6% (67)	70.6% (92)	72.0% (428)
80	*58.4% (77)	73.1% (78)	78.4% (51)	73.4% (64)	*61.8% (68)	68.3% (338)
90	75.5% (94)	66.3% (101)	67.0% (88)	75.6% (119)	69.5% (82)	71.1% (484)
<i>M</i> /Total	75.6% (1349)	74.5% (1020)	77.7% (936)	81.8% (934)	72.9% (1050)	76.3% (5289)

3. Experiment 1B: Moving targets

The two bats used in this experimental condition (Astro and Chris) continued to discriminate between the monopole and the dipole when the disks supporting the targets were rotating during the test trials [see Fig. 1(b)]. Both bats' mean choice accuracy in experiment 1B for moving targets was significantly above chance (summed binomial test, $p < 0.001$). Astro's performance for stationary targets was not significantly different than its performance for moving targets [stationary: 72.9% on 1050 trials, moving: 69.3% on 655 trials; $t(33) = 1.66$, $p > 0.05$]. Chris' performance for stationary targets was significantly higher than its performance for moving targets [stationary: 77.7% on 936 trials, moving: 73.8% on 1378 trials; $t(62) = 2.39$, $p < 0.05$].

C. Discussion

Figure 5(b) shows the target strength of the dipole target relative to the monopole target at the same distance but different aspect angles. At an aspect angle of 0° , the two cylinders are located one behind the other, and their reflections arrive $290 \mu\text{s}$ apart. At an aspect angle of 90° , the two cylinders are side by side, and their reflections arrive at approximately the same time (time difference of $0 \mu\text{s}$, give or take the effect of the bat's head movements). If the bats were using echo amplitude to perform the task, the best performance should have been sharply highest at the 90° orientation since that is where the difference in amplitude between the dipole and monopole echoes is largest. Instead, the profile of performance at different dipole aspect angles does not resemble the profile of echo amplitude differences at different aspect angles.

The plot in Fig. 5(a) shows reduced performance at some dipole orientations relative to others, but the relation is not monotonic, as would be expected if the presence of two cylinders is more difficult to detect when the aspect angle is at one extreme (0°) or the other (90°). The bats' performance is somewhat lower at both extremes of the dipole angle range, at 0° – 5° and at 75° – 90° , than at intermediate angles. It might be expected that dipole aspect angles that provide for a greater separation of the cylinders ($< 60^\circ$) would be easier to detect, but performance is highest for angles around 30° – 40° and gradually lower for both higher and lower angles. It thus does not seem as though the aspect angle is behaving as the critical feature of the dipole that determines its discriminability from the monopole.

There are other relations among the reflecting points—the cylinders—making up the targets that could have caused the effect shown in Fig. 5(b) without the aspect angle itself being directly responsible. Besides the dipole orientation itself, the most important additional feature of the stimulus ensemble is the placement of the monopole and dipole targets relative to each other and to the bat. Although the monopole and dipole targets are separated from each other in *direction* because they individually appear on the bats left and right, many of the trial-to-trial positions involve them being at the same *distance* from the bat. As shown in Fig. 3(b), these directions and distances vary over a large range across all trials in experiment 1A, but how does the bats' perfor-

mance vary when the trials are sorted into different groups according to the relative distances of the cylinders? Figure 6(a) shows that the near cylinder of the dipole was closer to the bat than the monopole on slightly over half of the trials (black circle data points). On average, the near cylinder of the dipole was about 1 cm closer to the bat than the single cylinder of the monopole, but the spread of differences is large, over a span of ± 6 cm on the majority of trials. On average, the far cylinder of the dipole was 2–3 cm farther away than the monopole on the majority of the trials (gray triangle data points), but, again, the spread of differences is large. In fact, there were several hundred trials where the far cylinder of the dipole was closer even than the monopole. Figure 6(a) also shows the distribution of differences in distance to two cylinders of the dipole (white square data points). Of course, the near cylinder of the dipole was closer to the bat than the far cylinder by definition, but the aspect angle varied over the entire 0° – 90° span, so there were nearly 600 trials with both cylinders at the same distance [0 cm in Fig. 6(a)].

The performance of the bats as a function of the distance to each cylinder in the dipole target with respect to the monopole target or the cylinders in the dipole target with respect to each other is shown in Fig. 6(b). Across trials, the errors made by the bats in experiment 1A proved to be uniformly related to the relative distances from the bat to the individual cylinders. Whenever the trial-to-trial shifts in the locations of the monopole and dipole targets resulted in the monopole being at about the same distance [target range = 0 in Fig. 6(b)] as either of the two cylinders of the dipole [e.g., see Fig. 3(a)], the bats' performance declined. Similarly, whenever either of the cylinders of the dipole were located at about the same distance [which occurred when the aspect angle approached 75° – 90° , see Fig. 5(a)], the bats' performance declined. In all three cases, the echoes from one of the cylinders arrived at about the same delay as the echoes from the other cylinder, and a masking effect could have occurred due to a simultaneous reception of two reflections that had to be distinguished for a successful identification of the dipole versus monopole. Figure 7 illustrates the origin of this masking effect. In the diagram, going from Fig. 7(a) to Fig. 7(e), the dipole target rotates from an aspect angle of 0° (end-on view) to an angle of nearly 90° (side-on view). Each cylinder in the dipole, as well as the cylinder in the monopole, creates a trace in the bat's perception that is represented by the gray distribution located below either of the dipole cylinders or above the monopole cylinder. If these traces are separated along the horizontal echo delay or target range axis in the diagram, they are separable to the bat, so that each of the cylinders is perceived to be at its corresponding location on the horizontal axis. However, if any two of the cylinders are located at about the same distance from the bat, then their echoes arrive at about the same delay, and the gray distributions that depict those cylinders in the bat's perception overlap with each other and appear less distinguishable. The masking effect is absent in Figs. 7(a) and 7(b) but it is very strong in Fig. 7(c) and moderately strong in Figs. 7(d) and 7(e). Note that there can be interference between the monopole and either of the dipole cylinders or between the two

FIG. 6. (A) Distribution of relative distances to each of the cylinders in experiment 1A for all trials of five bats. Curves show distances from the monopole to the near and far cylinders of the dipole and distances from the near to the far dipole cylinders. (B) Plots of mean performance of five bats separately sorted by trials and aligned according to the relative distance of each cylinder. (C) Distribution of overall echo strengths for echoes from the dipole relative to the monopole. (* assumes random aspect angle with an average 3 dB increase in echo strength.) (D) Plot of mean performance of five bats in experiment 1A for various differences in overall echo strength (black circles) for comparison with performance in echo intensity discrimination (white triangles; Simmons and Vernon, 1971).

dipole cylinders themselves. The occurrence of this masking is visible in the bat's performance whenever one of the cylinders is aligned at the same distance as either of the other cylinders. The curves in Fig. 6(b) are aligned to the same scale of differences in distance between pairs of cylinders. Their superimposition reveals that the masking effects among the three cylinders are of equivalent strengths. That is, the cylinders were roughly equal to each other in their perceptual salience and thus their potential for reducing performance when their reflections were simultaneous, as opposed to when their reflections arrived at somewhat different delays (as explained in Fig. 7). In Fig. 6(b), the range of differences in performance from about 85% correct responses down to 67% correct responses, depending on the alignment of the cylinders in distance, is about the same as the range of differences in performance in Fig. 5(a) as a function of dipole aspect angle, from 82% correct responses at 30° to 70% correct responses at 90°. This finding suggests that the apparent dependence of the bats' performance on aspect angle *as such* may instead be caused by the range differences between the near and far dipole cylinders relative to the bat. However, the decline in performance for aspect angles at 0°–5° in Fig. 5(a) cannot be related to simultaneity and masking of reflections from the two cylinders in the dipole because, at these angles, the dipole cylinders are about

5 cm apart from the bat's view, so their reflections arrive at or near the maximum separation of 290 μ s.

Besides the direct effect that the presence of two cylinders has on the amplitude of echoes from the dipole relative to the monopole [average difference of 3 dB; see Fig. 5(b)], the dipole's spread along the range axis ensures that, on average, the nearer cylinder of the dipole will be closer to the bat than the farther cylinder, although the distribution of relative distances is broad [see Fig. 6(a)]. Apart from creating conditions for masking when the cylinders are at the same distance [Figs. 6(b) and 7], the nearer cylinder of the dipole will, on average, return a stronger reflection than the single cylinder of the monopole just because that cylinder is nearer on many trials. Therefore, its reflections undergo less spreading losses and atmospheric absorption. Figure 4(b) shows the relation between the cylinder distance and echo strength to serve as a model for estimating the strength of echoes on test trials in the experiment from the locations of the cylinders in the video reconstructions of their positions relative to the bat. From these reconstructions, Fig. 6(c) plots the relative amplitude of echoes from the dipole and the monopole targets. These estimates of echo strength are based on measurements of the amplitude of echoes from cylinders at different distances in Fig. 4(b) and assuming an additional mean difference of 3 dB due to the presence of two cylinders in the

FIG. 7. Potential masking effects to be expected whenever one of the target's cylinders is aligned at the same distance from the bat as another of the cylinders. Then their echoes arrive at the same time to create mutual masking. Gray peaks represent zone of masking for each cylinder. The dipole also rotates to different aspect angles in each drawing. (A) Monopole and dipole cylinders are all located at different distances for no masking. Note that the dipole is at 0° , and the echo from the second dipole cylinder is partly occluded by the first cylinder. (B) Monopole cylinder is closer to the first dipole cylinder but masking is still largely absent. (C) Monopole cylinder is aligned at the same range as the first dipole cylinder, and strong masking occurs. The second dipole cylinder is further away and is thus unaffected, but masking of the first cylinder is sufficient by itself to conceal the dipole. (D) Monopole cylinder is aligned at a similar range to both dipole cylinders and a very strong masking occurs. The dipole aspect angle also brings both dipole cylinders into positions to mask each other. In this condition, mutual masking affects all three cylinders. (E) Monopole cylinder is farther away than either dipole cylinder, but the dipole cylinders are at a similar range and they mask each other.

dipole rather than one cylinder. For most trials in Fig. 6(c), the echoes from the dipole were 2–5 dB stronger than the echoes from the monopole due to the relative distances, although for an appreciable number of trials, the range was –1 to 8 dB. Moreover, there are about 400 trials where the echoes from the two targets were of equal strength.

Figure 6(d) plots the performance of the bats with data regrouped according to the relative strength of echoes from the dipole versus the monopole. On this scale of echo strengths, the bats' performance (black circle data points) extends from about 80% to 85% correct responses down to about 70% correct responses. Figure 6(d) also plots the only data from an experiment that directly tested echo amplitude discrimination by big brown bats (white triangle data points; from Simmons and Vernon, 1971). The curve for echo amplitude discrimination is very steep for small amplitude

changes, rising from chance near 50% correct responses for 0 dB difference to 80% correct responses for 3 dB difference. In contrast, the curve showing the performance of the bats in experiment 1A as a function of differences in the strength of echoes from the dipole and monopole targets at different distances is very shallow over this same range of amplitude differences. Most notably, when the dipole versus monopole echo amplitude difference ranges from 3 dB down to 0 dB in Fig. 6(d), the bats' performance stabilizes and does not fall below 70% correct responses, whereas performance rapidly falls to 50% correct responses in the echo intensity discrimination experiment. By using the binomial distribution, the probability that 70% correct responses would occur by chance is ≤ 0.01 . The divergence of the two curves in Fig. 6(d) over this 3–0 dB range indicates that the bats did not distinguish the dipole target from the monopole target as an echo amplitude discrimination task, which is a conclusion reinforced by the difference between echo strength as a function of aspect angle [Fig. 5(b)] and the bats' performance as a function of aspect angle [Fig. 5(a)]. In neither analysis does echo amplitude betray an effect on performance compared to the definite effect shown by the congruence of the curves in Fig. 6(b). Except for the anomalous decline in performance for aspect angles of 0° – 5° [Fig. 5(a)], the masking effect of one cylinder on another appears to dominate the bats' performance and is responsible for the apparent dependence of performance on aspect angle.

Figure 8 shows the results of echo measurements for the monopole target and the dipole target at different orientations but the same overall distance. Figure 8(b) is a diagram of the echo-measurement procedure, showing the placement of the target in relation to the loudspeaker and the two microphones. These echoes are illustrated by their spectrograms. The spectrogram for the reflection from the monopole in Fig. 8(a) is virtually identical to the spectrogram of the broadcast signal because the monopole echo is completely dominated by the specular return from the front face of the cylinder. This spectrogram shows the first harmonic of the test signal sweeping from 100 kHz down to 20 kHz and the weaker second harmonic sweeping from near 130 kHz down to 40 kHz. (This second harmonic is caused by distortion of the loudspeaker when it is driven to generate a FM signal with a sound pressure of 100 dB sound pressure level (SPL) at a distance of 10 cm.) There is a single, sharply defined sweep for each harmonic in the echo returned from the monopole. Figure 8(d) shows spectrograms for echoes from the dipole at orientations from 0° to 90° in 10° steps. The corresponding target outlines in Fig. 8(c) show the incident and reflected sounds in relation to the locations of the two cylinders at these aspect angles. In Fig. 8(d), at aspect angles of 0° and 10° , the dipole target returns reflections whose spectrograms resemble the spectrogram from the monopole [Fig. 8(a)] in that each spectrogram contains a single prominent FM sweep for the first harmonic and a second single sweep for the second harmonic. In Fig. 8(d), as the dipole aspect angle opens more, at 20° , 30° , 40° , and 50° , there are two different sweeps for the first harmonic and the second harmonic in the spectrograms. At these aspect angles, the range separation of the cylinders is large enough [Fig. 8(c)] for

FIG. 8. Spectrograms of echoes from monopole and dipole targets. (A) Spectrogram of monopole echo. (The transmitted sound has an identical spectrogram.) The signal contains two frequency sweeps, a first harmonic sweeping down from 100 to 23 kHz and a second harmonic sweeping down from about 130 to 45 kHz. The arrows show the direction of transmitted sound and echoes. (B) Diagram showing setup for broadcasting sounds and recording echoes from two microphones (see Sec. II A). (C) Aspect angles of dipole target. (D) Spectrograms of echoes from the dipole target at different aspect angles (see text for details). The dashed lines in the spectrograms for 0° and 10° aspect angles show where the echo for the second cylinder would be if it was not occluded by the first cylinder.

each harmonic to be separately registered from each cylinder. However, at an aspect angle of 60°, the two cylinders are near enough in range that the sweeps in the spectrogram begin to merge. Finally, at aspect angles of 70°, 80°, and 90°, the spectrograms in Fig. 8(d) show overlap between the FM sweeps reflected by the two cylinders, which are now very close together in range [Fig. 8(c)]. From Fig. 8(d), the spectrograms for the echoes of the monopole and the dipole at different orientations show a shift in the nature of the information that reveals whether the target is a dipole or a monopole. It is unknown whether the spectrograms themselves give a direct representation of the acoustic information processed by the bats, but we are assuming that similar effects appear in whatever acoustic information is used by the bats.

No single acoustic feature in the time domain or the frequency domain would allow the bats to distinguish between the dipole and monopole targets from these spectrograms. At angles of 0° and 10°, the dipole's second cylinder is located behind the first cylinder and its echoes are partly occluded [dashed lines in Fig. 8(d) show expected locations of the second-cylinder echo, which is too weak to emerge in these two spectrograms]. At angles of 20°–60°, the echoes from both cylinders are strong and well separated in the spectrograms. At angles of 70°–90°, the spectrograms of the echoes from the two cylinders merge together into a single

spectrogram that has a series of interference peaks and notches running along its ridges. This occurs when the time separation of the echoes becomes smaller than the horizontal width of the spectrogram ridge (spectrogram integration time). Thus, by using the criterion of two recognizable sweep traces for each harmonic, at 0°–10° and also at 90°, it is harder to determine that there are two cylinders in the dipole, while at 20°–80°, it is easier. In contrast, by using the criterion of ripples caused by the overlap of sweeps in the spectrogram, it is easier to determine which target is the dipole at 70°–80° than at other angles. Because the acoustic information for revealing the presence of two cylinders is different at 20°–60° (time domain cue of separable echoes) than that at 70°–80° (frequency domain cue of ripple pattern of interference), the bat may instead perceive the objects in a different format, which is one that combines the dual dimensions of the proximal, acoustic representation into a unitary distal representation that is more nearly spatial in nature. Use of spatially dimensioned perceptions would account for the independence of the bats' performance of the dipole aspect angle beyond the effects of masking between the individual cylinders in the targets. Further behavioral experiments are needed to shed light on this possibility.

III. EXPERIMENT 2: DIPOLE TARGET VERSUS DIPOLE TARGET

The stimuli for the dipole versus monopole experiments (1A and 1B) were intrinsically asymmetrical in several respects. Whether the bats perceived the overall echo strength or the number of reflecting sources, the dipole should, for the most part, be readily distinguished from the monopole. The analysis of results described above dissociated the bats' performance in experiment 1A from echo strength or from any one acoustic feature such as spectral ripples from interference or separate sweeps in spectrograms. Instead, this analysis tied the bats' performance to perception of the pair of cylinders, implying that the dipole was identified as having two reflecting parts and the monopole as having only one part. Variations in performance during experiment 1A appear to be caused by masking that occurs whenever any two of the three cylinders are located at about the same distance from the bat, so that their reflections coincided in time—which is a condition that has been demonstrated to cause masking in previous studies (Simmons *et al.*, 1989). However, the essential spatial asymmetry of the targets still remains with regard to the number of cylinders. To remove this asymmetry, experiment 2 replaced the monopole target with a new dipole target that differed only in having a shorter spacing between the cylinders. This transformed the bat's task from discriminating between targets that differed in type to discriminating between two similar dipole objects that differed only in one dimension, which is their length or dipole spacing. As in experiment 1, the targets were shifted in aspect angle, direction, range, and cross range separation from one trial to the next, which prevented any one acoustic cue or spatial location from serving as an indicator of the presence of the positive dipole on the bat's left or right.

A. Method

1. Animal subjects

Three of the same bats (Buddy, Frodo, and Patrick) from experiment 1 were tested.

2. Stimuli

The same dipole target from experiment 1 (two 1.59-cm-diameter cylinders separated by 5.0 cm) was the rewarded stimulus (positive dipole). There were five additional dipole targets used as negative, or unrewarded, stimuli. They were identical to the positive dipole target except for the spatial separation between the two cylinders within each target, which was 1.0, 1.5, 2.0, 2.5, or 3.0 cm at different stages of experiment 2. Each of these negative dipole targets was paired with the standard 5.0 cm dipole target in succession, starting with the shortest (1.0 cm) and ending with the longest (3.0 cm). The same negative dipole target was used for all the trials within each daily session (20–50 trials per session, where the number of trials depended on the quantity of mealworms each bat could eat on that day to maintain its current body weight). Negative dipole targets were changed between blocks of sessions. Individual bats completed a minimum of 400 trials for each negative dipole target (five to six sessions per week).

3. Experimental setup and procedure

Figure 1(c) shows the positive dipole versus negative dipole task. For each bat, experiment 2 immediately began after experiment 1 ended. During each trial, while the bat sat on the Y-shaped platform and examined the objects to make its choice, the targets remained stationary. Then, during each intertrial interval, the targets were repositioned in three ways: (1) the positive dipole appeared on the left or right as determined by a pseudorandom Gellerman sequence, (2) the positive and negative dipole targets were placed at variable distances from the bat on the platform, and (3) the orientations, or aspect angles, of both the positive and negative dipole targets were randomly changed (independently of one another). The distance of the dipole targets from the platform and the orientation of both dipole targets on each trial were spontaneously determined by the recorder.

The general setup for experiment 2 was the same as experiment 1, but the procedure was different in that the trials were run fully double blind to control for inadvertent cuing (the trainer was unaware whether the positive stimulus appeared on the left or right side until after the bat has made its choice). This precaution was taken because the targets now differed very little in structure, shape, or target strength, leaving the procedure especially sensitive to potential cues originating from the experimenters themselves. Two experimenters, a bat trainer and a recorder, were present for each test trial. At the beginning of each trial, the trainer, which was holding the bat, would be faced away from the platform. The recorder would place the stimuli in front of the Y-shaped platform. Once the stimuli were in position, the trainer then turned to face the Y-shaped platform and the bat crawled from the trainer's hand to the back of the platform. Since there were no visible lights on in the room (with the exception of the weak LED lights under the platform), the trainer was unable to see the stimuli. The bat would emit sonar signals for approximately 1–10 s and then walk forward toward one arm of the Y-shaped platform. When the bat reached the end of the arm, if it was correct (facing the dipole target), the recorder would tap the trainer on the shoulder. The trainer would then deliver the mealworm reward by presenting the mealworm piece in the forceps just in front of the bat's mouth, and then pick up the bat. If the bat was incorrect, the recorder would say “shh,” which prompted the trainer to pick up the bat without delivering the mealworm reward. At the conclusion of the trial, the trainer turned away from the platform for an intertrial interval of about 5 s as the recorder recorded the trial and repositioned the stimuli for the next trial.

4. Data analysis

Videotapes of all test sessions with the 2.0, 2.5, and 3.0 cm negative dipole targets were analyzed for each bat (except for Frodo). For Frodo, 21 out of 47 sessions with the 2.0 cm target and 4 out of 51 sessions with the 3.0 cm target were not analyzed due to video errors. Videotapes of the test sessions were analyzed in the same manner as in experiment 1, except that a new digitization point was added for the second cylinder in the negative dipole.

TABLE II. Performance accuracy as a function of stimulus condition (negative dipole spatial separation) for each of the three bats in experiment 2. (The number of trials completed for each bat in each condition shown in italics under the accuracy value. Buddy did not complete the 2.5 or 3.0 cm negative dipole stimulus conditions.)

Negative dipole (cm)	Bat			<i>M</i> (Total)
	Buddy	Frodo	Patrick	
1.0	73.3% (438)	71.5% (1302)	75.8% (1132)	73.5% (2872)
1.5	75.2% (1231)	75.7% (1413)	75.5% (1098)	75.5% (3742)
2.0	67.8% (574)	77.1% (1994)	71.4% (511)	72.1% (3079)
2.5	NA	71.8% (2143)	71.1% (570)	71.4% (2713)
3.0	NA	63.2% (549)	59.8% (433)	61.5% (982)
<i>M</i> /Total	72.1% (2243)	71.9% (7401)	70.7% (3744)	70.8% (13388)

5. Echo measurements

Echo measurements of the five negative dipole targets were made using the same setup and procedure as those in experiment 1.

B. Results

Two bats (Frodo and Patrick) completed test sessions with all five negative targets (1.0, 1.5, 2.0, 2.5, and 3.0 cm dipoles), while a third bat (Buddy) completed test sessions with three of the targets (1.0, 1.5, and 2.0 cm dipoles). Figure 3(c) shows the locations of the individual cylinders in the positive and negative dipole targets on all trials of experiment 2. Target distances varied by about 2:1 in range, mostly from 15 cm to almost 45 cm. Differences in range between the cylinders in the dipoles mostly varied over ± 15 cm (see below). The angular separation of the targets varied from about 30° to 120° relative to the bat's location. As in experiment 1A, because the individual cylinders were presented at different distances from the bat, the amplitude of reflections at the bat's ears necessarily differed [see Fig. 4(b)].

The three bats were all able to discriminate between the positive dipole and each negative dipole, as shown in Table II. Performance (percent correct responses) for the three bats was significantly above chance (50%) for all tested combinations of the positive dipole versus the negative dipole (summed binomial test, $p < 0.001$). The bats' performance progressively declined as the spatial separation of the cylinders in the smaller (negative) dipole approached the spatial separation of the cylinders in the larger (positive) dipole. The highest mean performance was for the 5 cm positive dipole versus the 1.5 cm negative dipole (75.5%), and the lowest mean performance was for the 5 cm positive dipole versus the 3.0 cm negative dipole (61.5%). Across bats and conditions, performance in experiment 1A (76.3% correct responses from Table I) was slightly higher than that in experiment 2 (70.8% correct responses from Table II).

FIG. 9. (A) Graph of the performance of three bats as a function of positive dipole aspect angle in experiment 2. (B) Graph of the performance of the three bats as a function of negative dipole aspect angle in experiment 2. In plots A and B, no data are shown for the 0° orientation because there were less than 100 trials in that category. (C) Graph of performance as a function of the difference in the extent of the dipoles along the range axis in experiment 2. The absolute value of the range difference between the cylinders in the negative dipole stimulus was subtracted from the absolute value of the range difference in the positive dipole stimulus. The error bars show standard deviations.

Aside from the discriminability of the whole series of dipoles, which is established by the data in Table II, further considerations involve the relative distances to individual cylinders or the aspect angles of the dipoles with respect to simultaneity of reflections from the cylinders and consequent masking, as illustrated in Fig. 6(b) for experiment 1A. The data for all five negative dipoles were combined for these analyses of experiment 2, as discussed below.

C. Discussion

Figure 9 shows the bats' performance as a function of the orientation of the positive dipole [Fig. 9(a)] and the negative dipoles [Fig. 9(b)]. The bats' mean performance was significantly above chance for all orientations of the targets (summed binomial test, $p < 0.001$). For the positive dipole, in Fig. 9(a), the bats' highest mean performance was for the 30° aspect angle (81.6%), and the lowest mean performance was for the 90° aspect angle (59.5%). This is the same pattern of performance as that obtained in experiment 1A [Fig. 5(a)]. In contrast, for the negative dipoles, in Fig. 9(b), the bats' highest mean performance was for the 70° aspect angle (81.3%), while the lowest mean performance was for the 30° aspect angle (65.5%).

The presence of two cylinders in each dipole creates an additional feature related to the targets' aspect angles. This is the relative size of each dipole along the range axis. At different orientations, the difference in distance or range between the near and far cylinders in each dipole is the target's range extent. The positive dipole has range extents from 0 to 5 cm as its aspect angle changes from 90° down to 0° .

The negative dipoles all have range extents of 0 cm at an aspect angle of 90° and range extents from 1.5 to 3 cm at an aspect angle of 0° according to their cylinder spacing. Figure 9(c) shows the mean performance (percent correct responses) for all three bats as a function of the difference in range extent between the positive dipole and all five negative dipoles at different combinations of aspect angles (see Fig. 9 caption). The bat's performance is highest when the positive dipole has the largest range extent relative to the negative dipole, while performance is lowest when the negative dipole has the largest range extent relative to the positive dipole. Moreover, this relation is linear and covers the entire span of performance from 83% correct responses, which is near the highest level achieved by any bat in experiment 2 (see Table II), down to near chance at 55% correct responses. The bats behaved as though they discriminated the dipoles by primarily choosing whichever target had the larger extent in range regardless of whether this was in fact the correct (5 cm) dipole. However, in Fig. 9(c), at a relative range extent of 0 cm (positive and negative dipoles oriented so that they have the same range extent), when the two dipole targets were of the same "size" along the single dimension of the range axis, the bats' performance of 64% correct responses was still significantly different from chance ($p < 0.05$). In this condition, from the bat's vantage point, the longer (5.0 cm) dipole had a larger left-right or cross range disparity than the smaller dipole (1.5–3.0 cm). The bats thus did not solely rely on range extent to find the larger dipole; rather, they perceived that the larger dipole had a longer dipole spacing or vector length in the range/cross range plane. This is equivalent to correctly perceiving the relative dipole lengths at different aspect angles. The ability of the bats to select the longer dipole when only their relative cross range extents are available as a cue definitely invokes a binaural dimension to the perception of the dipoles. It strongly points to a spatial representation for the dipoles, but it does not prove it.

As in experiment 1A, the errors made by the bats were related to the relative distances from the bat to the individual cylinders in the dipole targets and, thus, to the potential masking effect generated by the simultaneous reception of reflections from different cylinders. However, the addition of the fourth cylinder to make the negative target a dipole, too, increased the likelihood that for the majority of trials, some degree of masking always occurred. Overall, the bats' performance in discriminating between the dipoles in experiment 2 was slightly lower than the performance in discriminating the dipole from the monopole in experiment 1A (compare the total mean of 76.3% from Table I to the total mean of 70.8% from Table II). This could be a consequence of the increased similarity of the targets in experiment 2 (both objects were dipoles), with its attendant increase in the difficulty of the task. It could also be a consequence of a decrease in the likelihood that one of the cylinders in the positive target will be nearer than either cylinder in the negative target or to an increase in the level of masking prevailing across trials because there is now an additional cylinder present. With respect to masking, on average, one of the cylinders in the positive dipole now has an increased chance of being aligned

FIG. 10. (A) Distribution of distances to the near and far cylinders in the positive dipole (5 cm spacing) relative to the distance of the near cylinder in the negative dipole in experiment 2 for all trials of three bats. (B) Plots of mean performance of three bats separately sorted by trials according to the distance of the near and far cylinders in the positive dipole and of the far cylinder in the negative dipole relative to the distance to the near cylinder in the negative dipole. (C) Distribution of overall echo strengths for echoes from the positive dipole relative to the negative. (* assumes random aspect angle with an average 3 dB increase in echo strength from dipole.) (D) Plot of mean performance of three bats in experiment 2 for differences in overall echo strength.

in range with one of the cylinders in the negative dipole. Figure 10(a) shows that the near cylinder of the positive dipole was closer to the bat than the near cylinder of the negative dipole on slightly more than 50% of the trials, while the far cylinder of the positive dipole was closer to the bat than the near cylinder of the negative dipole on slightly less than 50% of the trials. However, the spread of relative distances to the near and far cylinders of both dipoles still allowed either target to be presented nearer to the bat on many trials. This provided the scope for the near and far cylinders of both dipoles to coincide in range often enough to test for the presence of masking due to the simultaneous reception of their reflections. Figure 10(b) shows that whenever the near cylinder of the positive dipole was at about the same distance from the bat as the near cylinder of the negative dipole (black circle data points), the bats' performance declined. This effect is similar to that for the cylinders in the dipole and monopole targets in experiment 1A: The curve in Fig. 10(b) comparing the relative distances of the near cylinders of both dipoles in experiment 2 has a shape and level that are similar to those of the curves in Fig. 6(b) comparing the relative distances of the near or far cylinders in the dipole relative to the monopole in experiment 1A. Thus, mutual masking of reflections from the near cylinders of the dipoles may have been a factor in lowering the bats' performance. However, in experiment 1, all three combinations of cylinder overlap and masking have about the same effect [range of performance for the three curves in Fig. 6(b) is from 85% down to 68% correct responses]. In experiment 2, only the curve for the near cylinders in both dipoles has this same range and shape [black circle data points range from 84% down to 64% in Fig. 10(b)]. In Fig. 10(b), in the curve comparing the far cylinder in the positive dipole with the near cylinder in the negative dipole (white triangle data points),

FIG. 11. Spectrograms of the six different dipole echoes (1.0–5.0 cm). The top row of the plots shows spectrograms of echoes for the five spacings of the negative dipole and for the positive dipole (rightmost spectrogram) at an aspect angle of 44°. The bottom row of the plots shows spectrograms for echoes from the six dipoles at different aspect angles.

the bats' performance is lower overall, ranging from 78% to 68% with no corresponding relation to the relative distances of the cylinders. The level of performance shown in this curve may be lowered overall due to the increased likelihood of masking from the other cylinders in both dipoles at various aspect angles, which would obscure any clear relationship to only one of the cylinders in the negative target.

In experiment 2, the echo strength of the positive dipole exceeded the echo strength of the negative dipole on slightly more than half of the trials, which is shown in Fig. 10(c). There is thus little scope for the bats to use just the echo strength to find the positive dipole. If the bats were relying on echo strength to discriminate between the dipoles regardless of which target had the larger (5 cm) spacing, their performance should have been above chance level (50% correct) when the echo strength of the positive dipole exceeded that of the negative dipole and below chance when the echo strength of the negative dipole exceeded that of the positive dipole. In effect, the bats' choices should reverse from the positive to the negative stimulus according to the echo strength. Instead, as shown in Fig. 10(d), the bats' performance remained above chance for differences in echo amplitude from –5 to 5 dB.

As in the case of the dipole versus monopole task of experiment 1 [see Fig. 8(d)], the bats' performance in the dipole versus dipole task of experiment 2 cannot be entirely explained by relying on any single feature of echoes or their spectrograms because the nature of the information the echoes contain varies with the aspect angle of the dipole. This occurs because the relative distances to the cylinders comprising the dipoles change with the aspect angle. The resulting changes in the time separation of their reflections is manifested as a change in the relative importance of the time axis or the frequency axis for spectrograms of the echoes [see Fig. 8(c)]. The top row of the spectrograms in Fig. 11 shows echoes for the five negative dipoles (spacing from 1.0 to 3.0 cm) and the positive dipole at an aspect angle of 44°. At this oblique angle, the cylinders are far enough apart in distance that the longer 5 cm positive dipole target yields two distinct frequency sweeps for the first and second harmonics of the sound in the spectrogram [see Fig. 8(d)]. At

this same angle, the cylinders in all five of the negative dipoles are close enough together in distance that their reflections merge to appear as a single sweep for each harmonic in the spectrogram, with the rippling pattern characteristic of overlap and interference. However, if the aspect angle of the positive dipole increases past 50°, the two sweeps in its echoes merge together so that the spectrograms resemble the echoes from the shorter dipoles in Fig. 11. [To see this effect for the positive dipole at different aspect angles, compare the spectrogram for 50° with the spectrograms for 60°, 70°, and 80° in Fig. 8(d)]. Because the bats can distinguish the positive dipole from the negative dipoles at all the different aspect angles, they cannot be using just the separation of the sweeps for the positive dipole and the merging of the sweeps for the negative dipoles. The bottom row of the plots in Fig. 11 shows spectrograms for echoes from the six dipoles at different aspect angles for each target. These angles were chosen to illustrate how the spectrograms can appear the same for each target by selecting conditions where the difference in the arrival time of the reflections from the cylinders is the same.

IV. GENERAL DISCUSSION

By taking the dipole versus monopole (experiment 1) and dipole versus dipole (experiment 2) results together, big brown bats are capable of recognizing the dipole target with the 5 cm spacing in the presence of several competing influences that act to reduce the bat's performance. These influences are not present with the same strength in every trial due to the roving positions and aspect angles of the targets. Roving the targets to different locations and orientations between trials prevented any single feature of the acoustic stimuli from being a stable indicator of which target was the correct choice. The bat had to recognize the dipole with the 5 cm spacing without using any of the extraneous features. There is also uncertainty introduced by the roving itself, which causes the level of performance to decrease across all trials. First, in both the dipole versus monopole and dipole versus dipole experiments, alignment of the cylinders in one target with one of the cylinders in the other target creates a

masking effect because the reflections from these cylinders coincide in arrival time [Figs. 6(b) and 10(b)]. When cylinders do not align in range, masking does not occur and performance is higher. Masking interacts with the interpretation of results for other features of the stimuli. Recognition of the 5 cm dipole appears to depend on the aspect angle of that target [Figs. 5(a) and 9(a)], but the rotation of the dipole toward the 90° aspect angle brings both cylinders to similar ranges, creating a masking effect apart from the aspect angle itself. Figure 6(b) shows that the masking effect between either cylinder of the dipole and the monopole has the same strength as the putative dependence on aspect angle approaching 90°, suggesting that the effect of aspect angle is really masking between the cylinders in the dipole. When the effects of masking are taken into account, the bats in fact appear able to recognize the dipole at all aspect angles. When the task is the discrimination of two dipoles (experiment 2), the bats are able to recognize the 5 cm dipole from dipoles with shorter spacings of 1.0–3.0 cm.

The conceptual rationale for these experiments involves a fundamental distinction: The representation of targets in echolocation could be organized in terms of the proximal stimuli—the echoes, or the distal stimuli—that object themselves. That is, echolocation could be based on perception of certain acoustic features of echoes received at the ears (e.g., amplitude, frequency, delay, spectrum) whose inventory in any given circumstances is sufficient to describe the content of the bat's images. However, echolocation might instead be based on the perception of the spatial features of the objects remote from the bat that affect the echoes in the course of the process of reflection (e.g., distance, direction, size, shape). In this case, the bat's images will have an additional content beyond what can be explained by an inventory of echo features because objects rather than sounds are perceived. The bat would have to transform the acoustic information carried by echoes into information about the objects and incorporate this transformation into a representation that, in effect, projects the objects onto their locations in space. Although this transformation would necessarily be more computationally complicated than a direct perception of the sounds as surrogates for the objects, it is quite possible that in the end, it would be more parsimonious for the bat to go to the trouble of converting echoes into perceptual entities more like objects than sounds because subsequent processing in an object-oriented regime could prove to be more effective. That is, if complicated, parallel organization of neuronal computations is a salient characteristic of brain organization, it is not self-evident that perceiving objects in terms of echo features is “simpler” as an explanation than perceiving objects in terms of spatial images. Although more complicated neuronal computational transformations are required to go beyond segregated representations of echo acoustic features to create spatial representations of objects, complex computations are present in the bat's auditory midbrain and forebrain anyway (Simmons *et al.*, 1996), and it may be simpler just to use them. By rendering echo information into spatial images, bats might be able to exploit the presence of all sorts of mechanisms for spatial cognition in general rather than create a stand-alone system based on its auditory system.

Besides, from a comparative perspective, auditory perception is just as much object oriented as it is acoustically oriented: Sounds are not perceived as disembodied acoustic events with characteristic features such as pitch, loudness, and timbre, they are perceived as emanating from sources at well-defined locations—sources whose structure is perceived from acoustic features along with location.

It would be advantageous for bats in flight to perceive the distal stimulus (the object) instead of the proximal stimulus (the echoes) because they must find or avoid aspect-dependent objects (e.g., insects, trees) and are constantly changing their position relative to the objects (thus receiving different echoes from the same object at different orientations). When bats maneuver through vegetation to attack insects surrounded by branches and leaves, when they dodge past rows of obstacles, or when they recognize and intercept specific targets out of a cluster of airborne objects, they evince an awareness of the locations of both the target of interest and surrounding objects that is difficult to avoid calling “spatial perception” (Simmons *et al.*, 1995; Moss and Surlykke, 2001). Another echolocating mammal, the dolphin, must also solve the problem of identifying moving aspect-dependent objects (e.g., fish) in a three-dimensional environment. The acoustic features of fish echoes vary depending on the orientation of the fish with respect to the dolphin (Au *et al.*, 2007). Thus, it would seem to be ecologically sensible for dolphins to perceive objects on the level of the distal stimulus. There is evidence that bottlenose dolphins (*Tursiops truncatus*) form distal instead of proximal representations (Harley *et al.*, 1996; Harley *et al.*, 2003; Helweg *et al.*, 1996a; Helweg *et al.*, 1996b; Herman *et al.*, 1998; Pack and Herman, 1995). This study suggests that bats, like dolphins, transform acoustic information carried by echoes into representations containing object features.

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