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Sound localization in a small passerine bird: discrimination of azimuth as a function of head orientation and sound frequency

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Summary

Sound localization is critical to communication when signalers are distributed widely in space and when reverberations that accumulate over distance might otherwise degrade temporal patterns in vocalizations. We readdress the accuracy with which a small passerine bird, the eastern towhee, *Pipilo erythrophthalmus* L., is able to resolve azimuth in the field. We then report results from two-alternative forced-choice (2AFC) experiments in which three of four subjects were able to discriminate an estimated speaker separation angle of approximately 7°. Subjects oriented laterally when discriminating azimuth in the 2AFC task and each subject preferred a different head orientation. Side biases occurred as a function of head orientation and, as a consequence, we conducted a second 2AFC experiment in which subjects were required to discriminate between two closely spaced lights. Subjects oriented similarly in this visual task, however, side biases did not occur as a function of head orientation. Despite side biases in the auditory task, performance generally declined when subjects were played tones with frequencies near ~3 kHz.

Key words: sound localization, azimuth, songbird, orientation.

Introduction

Accurate sound-localization abilities are often associated with a predatory life style. Barn owls, *Tyto alba*, for example, use auditory cues to locate prey in the dark (Konishi, 1973) and can resolve azimuth (direction in the horizontal plane) with a minimum resolvable angle of less than 5° (e.g. Bala and Takahashi, 2000). Similarly, female parasitoid flies, *Ormia ochracea*, use auditory cues to locate their hosts and can resolve azimuth with an error of only 2° (Mason et al., 2001). Nevertheless, and aside from animals who use active echolocation for navigation, there may be little reason to assume that predators alone should possess outstanding sound-localization abilities. Indeed, if accurate sound localization can improve an animal's ability to hear over distance or in noise (e.g. Dent et al., 1997; Grothe and Neuweiler, 2000), then one might also expect to find notable sound-localization abilities in other animals. Small birds, for example, not only need to localize sound sources accurately to track the locations of signalers over vast areas, but they might also discriminate reverberations separately from direct sound to resolve fine spectral and temporal patterns in complex vocalizations (Dent and Dooling, 2003; Dent et al., 1997).

Studies have suggested that small birds may be unremarkable in their abilities to resolve azimuth (Klump, 2000; Klump et al., 1986; Park and Dooling, 1991). Nevertheless, pigeons, *Columba livia*, were found to resolve azimuth with surprising accuracy (4–7°; Lewald, 1987) and a previous investigation demonstrated that eastern towhees, *Pipilo erythrophthalmus*, resolve azimuth nearly as well as the pigeon (Nelson and Stoddard, 1998). In this study we describe how towhees were able to assess azimuth across three sound-localization experiments that were conducted in the field. We then report results from a two-alternative forced-choice (2AFC) experiment in which towhees in the laboratory were required to discriminate between two speaker locations.

Animals typically use several cues when localizing sound sources. Humans, for example, use interaural time differences (ITD) when localizing relatively low sound frequencies (<~1.5 kHz) but use interaural level differences (ILD) or spectral cues when localizing relatively high sound frequencies (>~1.5 kHz; Moushegian and Jeffress, 1959; Rayleigh, 1907; Stevens and Newman, 1936). Small birds are thought to use these same sound-localization cues (Klump, 2000; Larsen, 2004) although the transition between using ITD and ILD is expected to occur at a higher sound frequency since phase-locking might be limited to below 3–4 kHz (Gleich and Narins, 1988) and because the towhee's relatively small head (1.8–2.0 cm) may generate useful ILDs only over relatively high sound frequencies. Towhees also use different cues when judging distance to stimuli produced with sound frequencies above and below ~3.5 kHz (Nelson, 2002). As a consequence, we investigated how well towhees are able to resolve the azimuth of tones between 2–5 kHz. We hypothesized that towhees might have difficulty resolving the azimuth of tones near 3.5 kHz since these frequencies may produce relatively weak ITDs and ILDs.

Subjects oriented their heads laterally with respect to speaker locations in our 2AFC sound-localization experiment. Orienting laterally increases interaural cue magnitude but limits the extent to which cues change with direction (μs deg.$^{-1}$; Klump, 2000; Kuhn, 1977). Thus, individuals are not expected to orientate laterally in an effort to increase interaural cue magnitude and thereby improve localization accuracy.

Small birds possess highly lateralized visual systems (e.g. Andrew and Dharmaretnam, 1993; Bischof, 1988; Martin, 1986) and animals, in general, use visual cues to calibrate their auditory space maps (King, 2002; Knudsen, 2002). We therefore conducted a third experiment in which subjects were required to determine which of two light sources presented a brief stimulus. We hypothesized that towhees should again orient laterally in this comparable 2AFC visual task. If so, an alignment between preferred orientations in each task might be viewed as evidence that birds with lateralized visual systems use visual cues to calibrate their auditory space maps in lateral, rather than forward directions.

Materials and methods

Experiment I: azimuth judgments in the field

A previous study demonstrated that towhees, *Pipilo erythrophthalmus* L., in Florida, USA, are able to resolve azimuth accurately in their natural habitat (Nelson and Stoddard, 1998). Two similar studies have since been conducted with different stimuli and different subjects from this same population. Only the distances over which these subjects flew in response to stimuli have been published (Nelson, 2000, 2002). We now report the accuracy with which subjects assessed azimuth as they flew towards speaker locations in each of these experiments. Incorporating data from all three experiments increases our sample size (*N*=298) and allows us to quantify more accurately how towhees resolve azimuth over biologically relevant distances in natural habitat.

Towhees are highly territorial and will aggressively approach speaker locations in response to 'tow-hee' call stimuli (Nelson and Stoddard, 1998). In each experiment, subjects were first attracted to an initial starting perch near a territory boundary. Whole calls or experimentally manipulated calls (see below) that were calibrated to match either a normal or adjusted (–6, +6, or +12 dB) source sound-pressure level (SPL) were then played from a second speaker located near the middle of each subject's territory. From 1 to 30 calls were played to subjects on their starting perches, however, no calls were played after subjects took flight. Stimuli consisted of recorded calls (Nelson and Stoddard, 1998), whole synthetic calls (Nelson, 2000, 2002) and synthetic calls that were divided in half so as to span a range of sound frequencies either above or below ~3.5 kHz (Nelson, 2002).

In addition to 'tow-hee' call stimuli, we played a single synthetic 'seet' call to nine of these same subjects. This synthetic stimulus was produced with an overall duration of 500 ms, was frequency modulated in a sinusoidal manner between 7 and 8 kHz (1.5 cycles), gated with 10 ms linear onset and offset ramps, and played with a source amplitude of 72 (*N*=5) or 78 dB (*N*=4; ±3 dB, with speaker elevation, re. 20 μPa). Eastern towhee 'seet' calls are highly variable in acoustic structure (B.S.N., unpublished data) and seem to be used in a variety of behavioral contexts. Subjects approached this synthetic seet call as aggressively as they approached tow-hee calls and recorded seet calls. However, we do not know if this synthetic stimulus is representative of 'seet' calls in general.

After a 5 min observation period, we measured the distances and directions to branches on which subjects perched while searching for the intruder that was simulated by our playbacks (Fig. 1A; see Nelson and Stoddard, 1998). We then calculated flight error (FE) for each perch as the mean angle subtending the 'distance' between each perch location and the axis between the starting perch and the playback speaker (Fig. 1A). Subjects often landed on more than one perch and when this occurred we calculated mean error for all perches and used this mean value as a single measure of overall flight error (FE) for the entire trial.

Speakers were positioned randomly and were rarely placed near branches where towhees would normally perch. As a consequence, towhees commonly perched on several branches near the speaker while searching for the simulated intruder. Observations of flight paths indicated that diversions to prominent (or possibly familiar) perches near the speaker often led to inflated measurements of overall error. We therefore estimated error that can be attributed to perch distribution by measuring the angles that subtended perches whenever subjects chose to fly to more than one perch location during a trial (Fig. 1A). Perch error (PE) is assumed to represent perch availability and we use PE for a better estimation of the accuracy with which subjects might assess azimuth if provided with a uniform distribution of perches.

Subjects on perches near the speaker often oriented their bodies towards speaker locations and often flew over speaker locations while searching for the intruder that had been simulated by the speaker (observations from video recordings; Nelson, 2000, 2002). To arrive at a more conservative estimate of error that can be attributed to perch distribution, we divided our estimate of PE in half and subtracted this value from our estimate of FE. We use this corrected distribution of FE as our best estimate for how well towhees can resolve azimuth in the field. Further descriptions of stimuli and experimental protocols can be found in prior publications (Nelson, 2000, 2002; Nelson and Stoddard, 1998)

Experiment II: discrimination of azimuth in the lab

Towhees assess azimuth well over distance in their natural habitat (Experiment I). Nevertheless, studies conducted in the field do not provide many insights into the sound-localization mechanisms that towhees, and other small birds, might employ when discriminating azimuth. We therefore conducted a two-alternative forced-choice (2AFC) experiment in the laboratory. Subjects were required to fly to a starting (listening) perch (1.3×12 cm) and were then required to determine which of two horizontally apposed 2.54 cm dome speakers (Kappa 10.2t; Infinity, USA) played a sound stimulus (Fig. 1B). Subjects were then required to fly a distance of 1.5 m to a perch (1.3×18.5 cm) associated with each speaker (Fig. 1B). The angle separating each speaker was varied from 2° to 30°. We defined performance for each speaker separation angle as a percentage, calculated as the number of trials in which subjects flew to the perch associated with the speaker that played the stimulus (the 'correct' perch) divided by the total number of responses in which subjects flew to either perch. Trials in which subjects did not fly within 10 s, or flew to another location in the room, were aborted and subjects were allowed to receive another stimulus after a 30 s delay. Individuals were required to remain on the starting perch until the stimulus was played, however, we allowed them to predict the time of stimulus onset by always triggering playback 1 s after they landed on the starting perch. Trials were aborted if subjects were not on the starting perch immediately after a stimulus presentation.

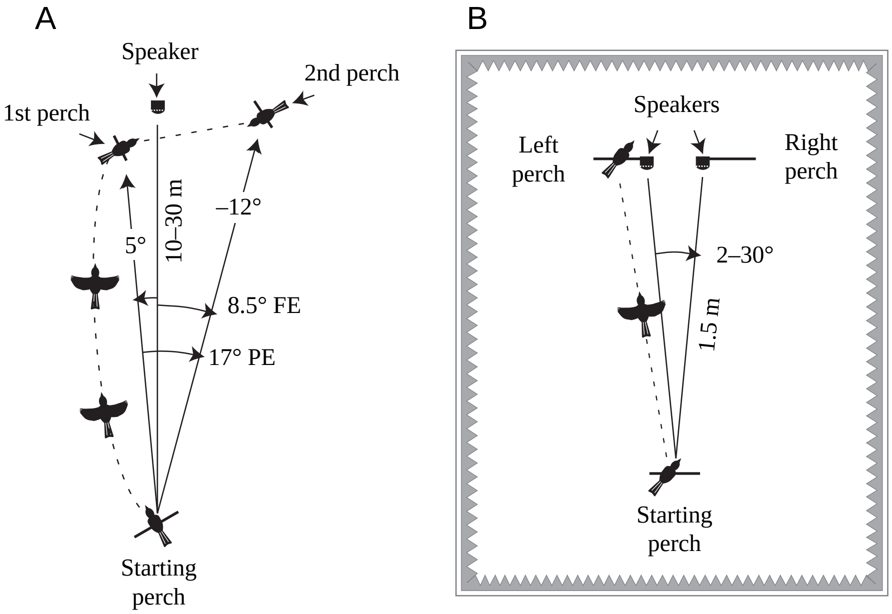

Fig. 1. Illustrations of our field (A) and laboratory (B) sound-localization experiments. In the field (A; Experiment I), flight error (FE) was calculated for each trial as the mean angle subtending the 'distance' between each perch location, and the axis between the starting perch and the playback speaker. Perch error (PE) was calculated as the angle subtending the 'distance' between each perch location. PE describes how perches are distributed in Florida scrub habitat and we use FE (PE/2) as our best estimate for how towhees resolve azimuth the field. In the laboratory (B; Experiment II), we employed a two-alternative forced-choice (2AFC) task in which subjects were required to discriminate between two horizontally apposed speaker positions and fly to perches associated with each speaker. To gauge performance as a function of speaker separation angle, we calculated the percentage of trials in which subjects were able to fly to the perch associated with the speaker that played the sound stimulus.

Three male towhees (325, 392 and 000) and one female towhee (404) were used as subjects. All four individuals were captured near Bloomington, IN, USA. Subjects 392 and 000 were captured as adults and were trained immediately. Subject 325 was also captured as an adult but was held in an indoor aviary for six months before testing began. Subject 404 was captured as a fledgling and was raised in a large (5×25 m) outdoor aviary that was surrounded by several towhee territories for nine months before training began.

All subjects were trained in a 2×2.4×2.75 m sound-attenuating chamber (Fig. 1B; Industrial Acoustic Company, Inc., Bronx, NY, USA). All six sides of the chamber were lined with acoustic foam (Sonex classic 7.62 cm wedges; Sonex, Minneapolis, MN, USA) to attenuate reflections above 2 kHz that might otherwise be produced by the perforated steel walls of the acoustic chamber. The starting perch was positioned 11 cm above the acoustic foam panels that were used to cover the floor of the chamber and response perches were positioned 13.5 cm above these same acoustic foam panels. All acoustic foam panels on the floor were covered with thin cotton sheets. Additional perches and supporting posts in the room were constructed and positioned to minimize reflections at the starting perch.

Since subjects did not naturally land on starting or response perches in this relatively large chamber, they were first trained within a 1.5×0.75×0.75 m wire-mesh enclosure placed within the chamber. During this period (2–4 weeks) individuals were required to discriminate between speakers placed on each side of the starting perch (180°; 30–40 cm). Once subjects learned to discriminate between speakers in this relatively small enclosure, the enclosure was removed from the chamber and subjects were allowed to live in the entire chamber throughout the experiment and perform freely throughout the day.

Perches were monitored using photoelectric switches (E3T-ST; Omron, Schaumburg, IL, USA) and a parallel port interface [PI2; Tucker–Davis Technologies (TDT), Alachua, FL, USA]. Food rewards were presented to subjects from small cylindrical (4 cm depth × 6 cm wide) cups made out of perforated aluminum that were mounted behind the left and right response perches. Food cups were covered with perforated aluminum lids and subjects were able to access food within each cup only when the lid on top each food cup was rotated backward and away from the response perch. A stepper motor mounted near the floor was used to rotate the lid.

Band-limited noise (2–5 kHz) or tones (*N*=17, 2–5 kHz, 1/12th octave) were used as stimuli and were generated prior to each trial using an array processor (AP2; TDT). All stimuli were generated using a calibrated spectrum obtained for each speaker (see below) and an inverse Fast Fourier Transform (FFT) function. FFT bin magnitudes were randomly varied in 0.1 dB increments over ±1 dB to eliminate any residual spectral cues in noise stimuli that might have been used to determine which speaker played the sound stimulus. All stimuli were produced with an overall duration of 164 ms and were gated with a 5 ms raised cosine function. Calibration spectra for speakers were obtained weekly using a microphone (4189 with preamplifier 2671; Brüel & Kjaer, Nærum, Denmark; MA2 preamplifier; TDT) placed 2.5 cm above the starting perch where subjects normally positioned their heads. Spectra obtained for each speaker were referenced to a 1 kHz, 94 dB signal produced by a microphone calibrator (4321; Brüel & Kjaer). Finally, stimulus amplitudes were roved randomly between 62 and 66 dB using an attenuator (PA4; TDT; RMS dB re. 20 μPa measured where subjects normally positioned their heads). Stimuli were presented using a stereo digital to analog converter (DD1; TDT) and audio amplifier (AB International series 200; Smyrna, Georgia, USA).

We measured head orientation with an accuracy of ±1° relative to the direction of each speaker position using grayscale images (640×480) captured at the time of stimulus offset (±5 ms). Images were obtained using an overhead asynchronous video camera (GP-MF802 with Rainbow S6X11 lens; Panasonic, Secaucus, NJ, USA) positioned 1.3 m above the starting perch. Images were then captured using a video card (Flashbus MV Pro; Integral Technologies, Indianapolis, IN, USA) and saved to disk using custom software integrated into the stimulus generating application. Since subjects could perch anywhere along the 12 cm starting perch, we accounted for lateral head position (with respect to the axis between the center of the starting perch and each speaker, S.D.=1.75 cm) when calculating head orientation. We captured two sequential frames (separated by 33 ms) before stimulus offset so that we could identify trials in which subjects were moving during stimulus presentation.

We discouraged side preferences (biases) by providing food rewards only when subjects chose the correct perch in three (or occasionally four) consecutive trials. In addition, no more than three (or occasionally four) consecutive stimuli were presented from each speaker. We discouraged incorrect responses by extinguishing overhead lights for 30–60 s whenever subjects chose the incorrect perch.

Individual trials accumulated slowly as a function of head orientation (3° bins) and sound frequency (17 tones). We were mainly interested in how well towhees discriminate azimuth as a function of these two variables, so we began testing each subject at a single speaker separation angle as soon as we were able to identify an angle at which the bird was able to choose the correct perch in ~70% of trials. Subjects were tested at additional angles throughout their tenure to verify that performance continued to vary with speaker separation angle (2°, 3°, 5°, 7°, 9°, 10°, 12°, 13° or 15°). Nevertheless, most trials were conducted with 9° or 10° speaker separation angles.

Four identical speakers (Kappa 10.2t; Infinity) were calibrated and exchanged in a random order on a weekly basis to assure that subjects did not learn to identify cues associated with each individual speaker. Different speakers were used briefly in trials conducted with subject 325 (MB Quart 25.61, 2.54 cm domes; Obrigheim, Germany) and switching speaker type did not influence performance. No known visual cues were available, however, subjects 325 and 392 were occasionally required to fly up and over a thin visually opaque, but acoustically transparent, layer of open-cell foam. To make sure that subjects 325 and 392 were not using cues associated with the chamber, the entire set-up shown in Fig. 1 was rotated 30° (within the acoustic chamber) at least once for several days so that the birds were required to discriminate between speakers that were positioned near the corners of the chamber. Finally, to make sure that subjects 325 and 392 were not using cues associated with the starting perch, this perch was occasionally rotated ±45° with respect to the axis between the two response speakers.

Experiment III: head orientation in a comparable visual task

Towhees oriented laterally with respect to speaker locations in our 2AFC sound-localization task (Experiment II). We hypothesized that towhees might also orient laterally in a comparable visual task. Since subjects were often biased towards either the left or the right speaker in this auditory task, we further hypothesized that similar biases should not exist in a visual task if they are due to sound-localization mechanisms and abnormal acoustic conditions in the laboratory.

We trained three previously tested subjects (325, 392 and 000) to discriminate between two small (3 mm) red or green light emitting diodes (LED) separated in azimuth by 1.6°. We were not interested in whether subjects were able to discriminate LED colors. Nevertheless, the colors of left and right LEDs were occasionally reversed. Similarly, we were not interested in temporal discrimination and varied stimulus duration (1–50 ms) only as a means for controlling performance.

Four cylindrical red (700 nm) or green (565 nm) 3 mm LEDs (LN263CPP or LN363GCPP; Panasonic) were embedded within a black 15×30 cm panel so that light was emitted only from the flat surface of each LED set flush to the surface of the panel. This panel was then attached to the side of a 61×46×84 cm cage located in a sound-attenuating chamber (Fig. 2). A 1.3×46 cm starting perch was positioned 35 cm from the LED panel and was monitored continuously using a photoelectric sensor (E3T-ST; Omron). A response perch extending across the cage was then positioned 28 cm from the starting perch and 7 cm from the LED panel. A light reflector was used to divide this response perch into left and right (response) halves and each half of the perch was monitored using a separate photoelectric sensor (E3T-SR, Omron). LEDs were activated and perches were monitored using a real-time processor (RP2; TDT).

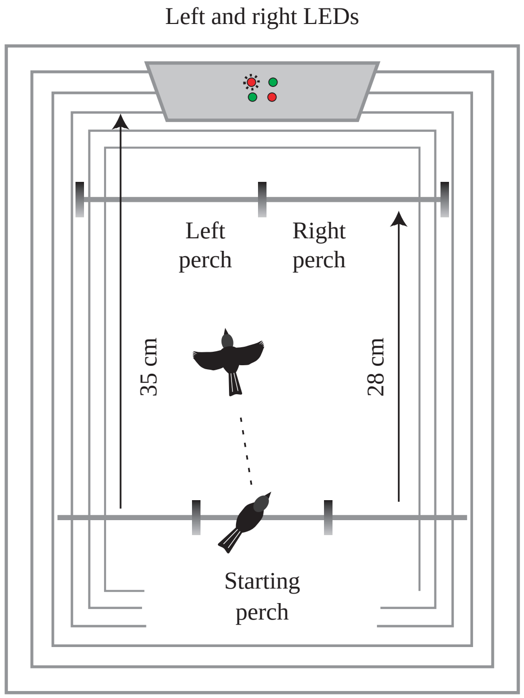

Fig. 2. Illustration of the two-alternative forced-choice (2AFC) experiment used to measure head orientations when subjects were required to discriminate between two closely spaced LEDs (1.6°; see text).

Subjects lived in the cage throughout the experiment and were free to perform throughout the day. We defined performance as a percentage, calculated as the number of trials in which subjects flew to the 'correct' side of the response perch divided by the total number of responses in which subjects flew to either side of the response perch. We were not interested in performance *per se* except as a rough approximation for how well subjects were able to discriminate between stimuli as a function of head orientation. Trials in which subjects did not fly within 10 s or flew to another perch in the cage were aborted and the birds were allowed to receive another stimulus after a 30 s delay. Subjects were required to remain on the starting perch until stimuli were presented, although we allowed them to predict the time of stimulus presentation by always presenting the stimulus 1.5 s after they landed on the starting perch. Trials were aborted if subjects were not on the starting perch immediately after stimulus presentation.

Food rewards were presented in a cup that was manufactured for use with the cage. The food cup was covered by a plastic lid and subjects were able to access food only when the lid on top of the cup was rotated upwards and away from the food cup. A stepper motor mounted on the side of the cage was used to rotate the lid.

Side preferences were discouraged by providing food rewards only when subjects chose the correct perch in 3–5 consecutive trials. In addition, no more than three or four consecutive stimuli were presented from each LED. We discouraged incorrect responses by extinguishing overhead lights for 30–60 s.

We measured head orientation with an accuracy of ±1° relative to the direction of each LED using an interlaced grayscale image (640×480) captured before, or during, each LED flash (±15 ms). Images were obtained using an overhead asynchronous video camera (GP-MF802, Panasonic; with H0612F1 lens, Computar, Commack, NY, USA) positioned 30 cm above the starting perch. Images were then captured using a video card (Winnov Videum, Sunnyvale, CA, USA) and saved to disk using custom software integrated into the stimulus-generating application. Short (15 cm) perches were attached to the sides of the cage just above the photoelectric sensors that monitored the starting perch (46 cm) so that trials would be initiated only when subjects perched near the center (±8 cm) of the starting perch. We accounted for lateral head position (with respect to the axis between the center of the starting perch and each LED, S.D.=4.5 cm) when calculating head orientation. We captured interlaced images so that we could identify trials in which subjects were moving during stimulus presentation.

Results

Experiment I: azimuth judgments in the field

Nelson and Stoddard (1998) used mean error as a conservative estimate for how well towhees assess azimuth in the field. Nevertheless, median error may function as a more appropriate summary value for this task since relatively large errors (>~15°) could often be attributed to specific factors. For example, trials were excluded if males flew directly to the location of a female (within ~5 m) as long as the female could be visually observed. Trials were not excluded, however, if the female could not be directly (visually) observed. In addition, while the 2AFC and field sound-localization tasks are qualitatively different, median error in the field is most easily compared with performance in a 2AFC task since both measurements can be expressed as percentages. That is, maximum error in our cumulative distribution of field error is best equated with 50% correct in a 2AFC task, median error (*vs* mean error) is best equated with 75% correct, and minimum error (1°) is best equated with 100% correct (see below and Fig. 3).

Across all experiments, subjects resolved azimuth with a median flight error (FE) of 6.9° (mean±S.D.=8.4±7.1°, N=298; Fig. 3). FE did not vary significantly with stimulus type (analysis of variance, ANOVA, d.f.=297, F=0.09, P=0.9), stimulus amplitude (–12, –6, 0 or +6 dB; ANOVA d.f.=297, F=0.332, P=0.8), speaker distance (r=–0.006, F=0.013, P=1.0), or the number of stimuli played to subjects before they took flight (r=–0.02, F=0.135, P=1.0). FE did not increase significantly when subjects were played only a single call stimulus before they took flight (P=0.39, Student's t-test). Median FE decreased slightly in the last two experiments (median=6.5°, Nelson, 2000, 2002; *vs* median=7.5°, Nelson and Stoddard, 1998), presumably because trials in these latter studies were video-taped and perches could be located more accurately. Nevertheless, this difference is not significant (*P*=0.9, *t*-test).

Subjects approached presentations of synthetic ‘seet’ calls as accurately as ‘tow-hee’ calls (median FE=2.6°, mean±s.d.=6.1±11°, *N*=9; speaker distance=21.3±7.5 m). These results are interesting because ‘seet’ calls are produced with relatively high sound frequencies (~7–8 kHz), leading to the suggestion that they might be difficult to localize (e.g. Larsen, 2004; Marler, 1955).

Subjects often perched on several branches near the speaker while searching for the simulated intruder. Diversions to these branches inflated estimates of overall error (see Materials and methods) and, as a consequence, we calculated error that could be attributed to perch distribution. Median perch error (PE) was 5.1° (mean±s.d.=6.9±6.2°). Video recordings suggested that this error estimate should be divided in half since subjects often oriented towards, and flew across, speaker locations while searching for a perceived territorial intruder (see Materials and methods). After adjusting for perch error (PE/2) our best estimate for how well towhees are able to resolve azimuth in the field is 4–5° (6.9–[5.1/2]=4.35°).

Experiment II: discrimination of azimuth in the lab

Overall performance

Towhees resolve azimuth well in the field (Experiment I) and we did not necessarily expect subjects to discriminate azimuth as accurately in our 2AFC task. Nevertheless, three (325, 392 and 000) out of four subjects were able to discriminate an estimated angle of approximately 7° in 75% of trials when played band-limited noise near the end of their tenure (2–5 kHz; *N*>100 for all angles tested; Fig. 3). Subject 404 never reached this 75% correct criteria regardless of stimulus but was able to discriminate correctly an angle of 20° in 66% of trials when played band-limited noise (2–5 kHz; *N*>200 for all angles tested; Fig. 3). Performance levels often varied widely over time (e.g. ±5% between days), however, variation could usually be attributed to variation in head orientation or sound frequency (see below).

Head orientation

Distributions of head orientations increased in width as speaker separation angle increased and, thus, subjects appeared to orient laterally with respect to either the left or the right speaker as opposed to with respect to a location midway between the two speakers. Therefore, we describe head orientation as the direction in which subjects directed their beaks with respect to the direction of the speaker that played the sound stimulus in each trial.

Subjects 392 and 000 oriented their heads so that their beaks were directed to the left or right sides of speaker locations as soon as they began discriminating closely spaced speakers (<30°). Sample sizes accumulated slowly as a function of head orientation and we are unable to quantify reliably how performance varied with head orientation during these early trials. Nevertheless, after performing freely in the chamber for one or two weeks, subjects 392 and 000 both began orienting primarily to the right (subject 392, mode=51°; subject 000, mode=48°; Fig. 4).

Subject 325 performed relatively poorly in our experiment for ~2 months. We did not have image capturing capabilities at this time and, thus, do not know how this subject oriented his head during these early trials. This subject began discriminating relatively small speaker separation angles (<15°, >75% correct) shortly before we began capturing images and was found to be orienting to the left (mode=–30°) and right (~20°) at this time (Fig. 4).

Subject 404 tended to orient both to the left (~–60° to –15°) and to the right (mode=39°). Nevertheless, head orientation distributions for this subject are relatively wide (Fig. 4). Interestingly, both the widths and the peaks of this distribution (404) resemble distributions produced for subjects 392 and 000 during early trials.

Subjects often rotated their heads to the left and right several times before stimulus presentation (within 1 s), but almost always oriented in a preferred direction

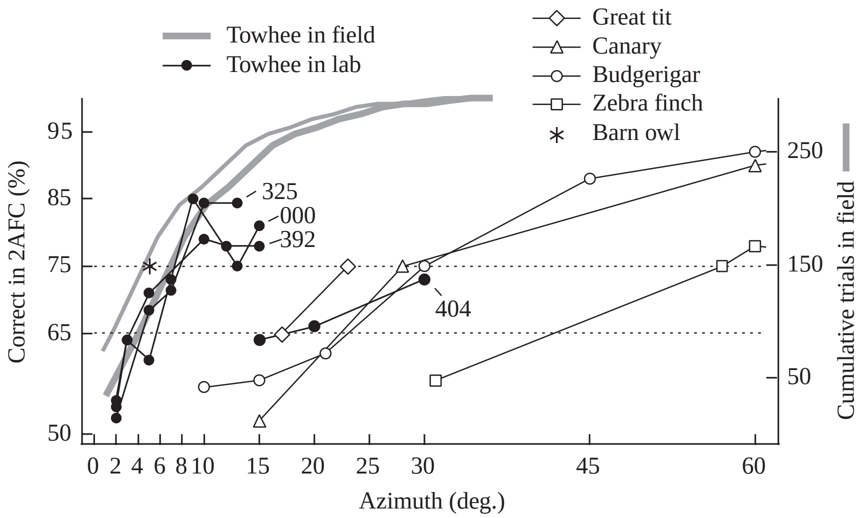

Fig. 3. Towhees resolve azimuth well in the field and perform nearly as well in the laboratory. Thick gray line denotes cumulative distribution of flight error observed in field experiments (Fig. 1A; *N*=298). Thin gray line denotes cumulative distribution of flight error after subtracting error that can be attributed to perch distribution in Florida scrub habitat (see text). Closed symbols denote performance observed in our auditory two-alternative forced-choice (2AFC) task as a function of speaker separation angle (noise 2–5 kHz; *N*>98; Fig. 1B). Data for each subject tested in this task are plotted separately. Open symbols denote performance observed as a function of speaker separation angle in previous 2AFC tasks conducted with other small birds (Klump et al., 1986; Park and Dooling, 1991). Asterisk denotes performance estimated for the barn owl, *Tyto alba*, using several methods deemed comparable with a 2AFC task (Bala and Takahashi, 2000).

immediately prior to stimulus presentation. Video recordings and analyses of captured images also demonstrated that subjects rarely moved their heads during stimulus presentation. For example, subject 325 was found to be moving his head during the stimulus in only 1.8% of trials, subject 392 in 4.4%, subject 000 in 2.6%, and subject 404 in 3.1% of trials. Subjects performed similarly whether or not they were moving their heads during stimulus presentation (percent correct moving/not moving across all stimuli: subject 325, 72.5/70.9; subject 392, 61.6/64.9; subject 000, 66.5/67.4; subject 404, 63.2/64.4).

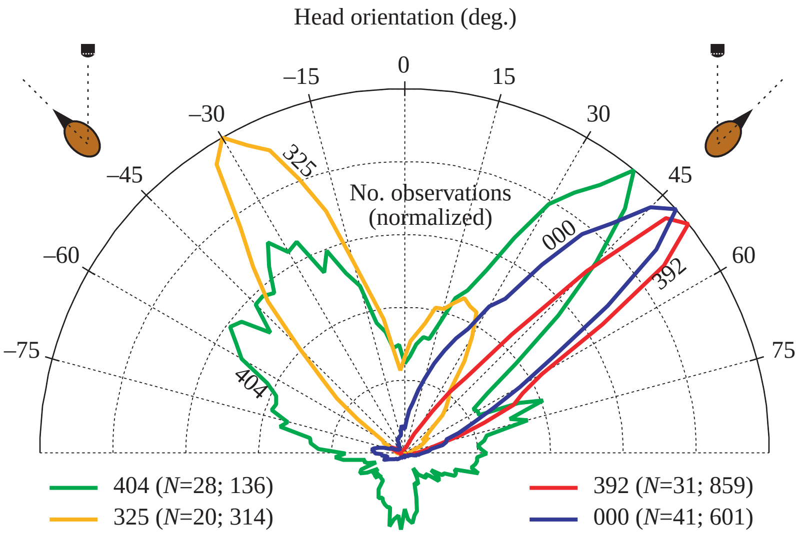

Fig. 4. Normalized histograms of head orientations (deg.) used by subjects when listening to stimuli presented in our auditory two-alternative forced-choice (2AFC) task (Fig. 1B; 3° histogram bins). Frequency of occurrence is represented by the radial axis and samples sizes for each subject are listed below the graph. Distributions are calculated for auditory stimuli presented from speaker separation angles <15° (<30° for subject 404).

Subjects often flew directly from response perches to the starting perch and, thus, often landed on the starting perch facing away from each speaker. Individuals usually hopped upwards and rotated their bodies around on the starting perch under these conditions before stimulus presentation. However, subjects sometimes did not turn their bodies around but simply rotated their heads in the opposite direction an additional 30–55° (Fig. 5). For example, while subject 392 often rotated his head to the right relative to a forward body orientation (~51°), this same subject also sometimes rotated his head in the opposite direction (to the left) relative to a backward body orientation to achieve a similar head orientation with respect to each speaker (Fig. 5C,D). Subjects tended to orient their heads further to the left or the right when their bodies were facing away from the speakers, however, distributions of head orientations obtained under these two conditions overlap considerably and similar side biases (see below) exist under both conditions.

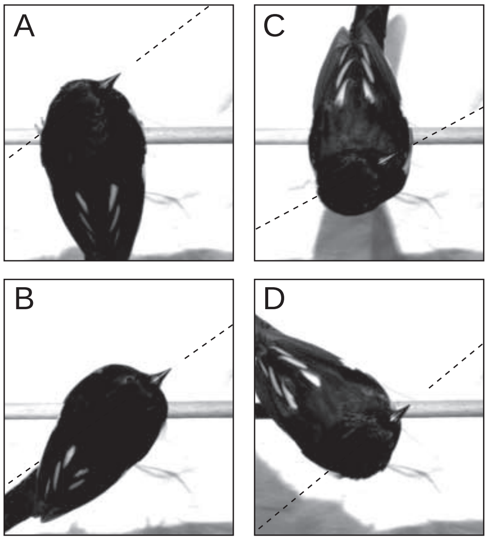

Fig. 5. Images of subject 392 captured in our auditory two-alternative forced-choice (2AFC) experiment demonstrating how this subject tended to orient his beak to the right (~45°) regardless of whether his body was oriented forward (A and B) or backward (C and D) on the starting perch. In all four images the left and right speakers were located beyond the top edges of the images. Head orientations obtained for subjects 325, 000 and 404 also occurred independently of body orientation.

Subjects occasionally oriented their heads away from the speaker that played the sound stimulus (<–90° and >90°) and did not reliably discriminate between closely spaced speakers (<15°) under these conditions (i.e. individuals chose the correct perch in less than 55% of trials, *N*>200). We do not know whether subjects might be able to discriminate larger speaker separation angles (>15°) when oriented beyond ±90°.

Performance with head orientation and speaker

Performance varied with head orientation and each subject performed best when oriented in a preferred direction. Subjects performed less well when oriented away from their preferred head orientation due, in part, to side biases that occurred as a function of head orientation (Fig. 6). For example, when tested with a 10° speaker separation angle, subject 325 tended to fly, on average, to the right perch when his head was oriented beyond –30° but to the left perch when his head was oriented within ~–30°. Similarly, subjects 392 and 000 tended to fly, on average, to the right perch when their heads were oriented within ~45° but to the left perch when their heads were oriented between ~45° and ~65° (9° or 10° speaker separation angles; Fig. 6). On average, subject 325 was also biased towards the right speaker when his head was oriented between 0° and ~45° although this trend varied over time (from week to week) and was, on average, relatively weak. Subject 404 tended to fly to both the left and the right perches with equal frequency when oriented between ~20° and 55° (Fig. 6). Subject 404 otherwise tended to fly primarily to the perch associated with the right speaker regardless of speaker separation angle (>20°).

On average, subjects 325, 392 and 000 were biased neither towards the left or the right perch. That is, overall biases on any given day could usually be attributed to head orientation or sound frequency and overall biases tended to disappear over days as a greater number of responses over a wider range of head orientations were obtained. Responses accumulated slowly as a function of head orientation (3° histogram bins), speaker (left and right), and stimulus (17 tones plus noise). As a consequence, performance as a function of head orientation could be investigated using only a few, relatively small, speaker separation angles within a reasonable length of time (8–14 months per subject). Subjects were biased as a function

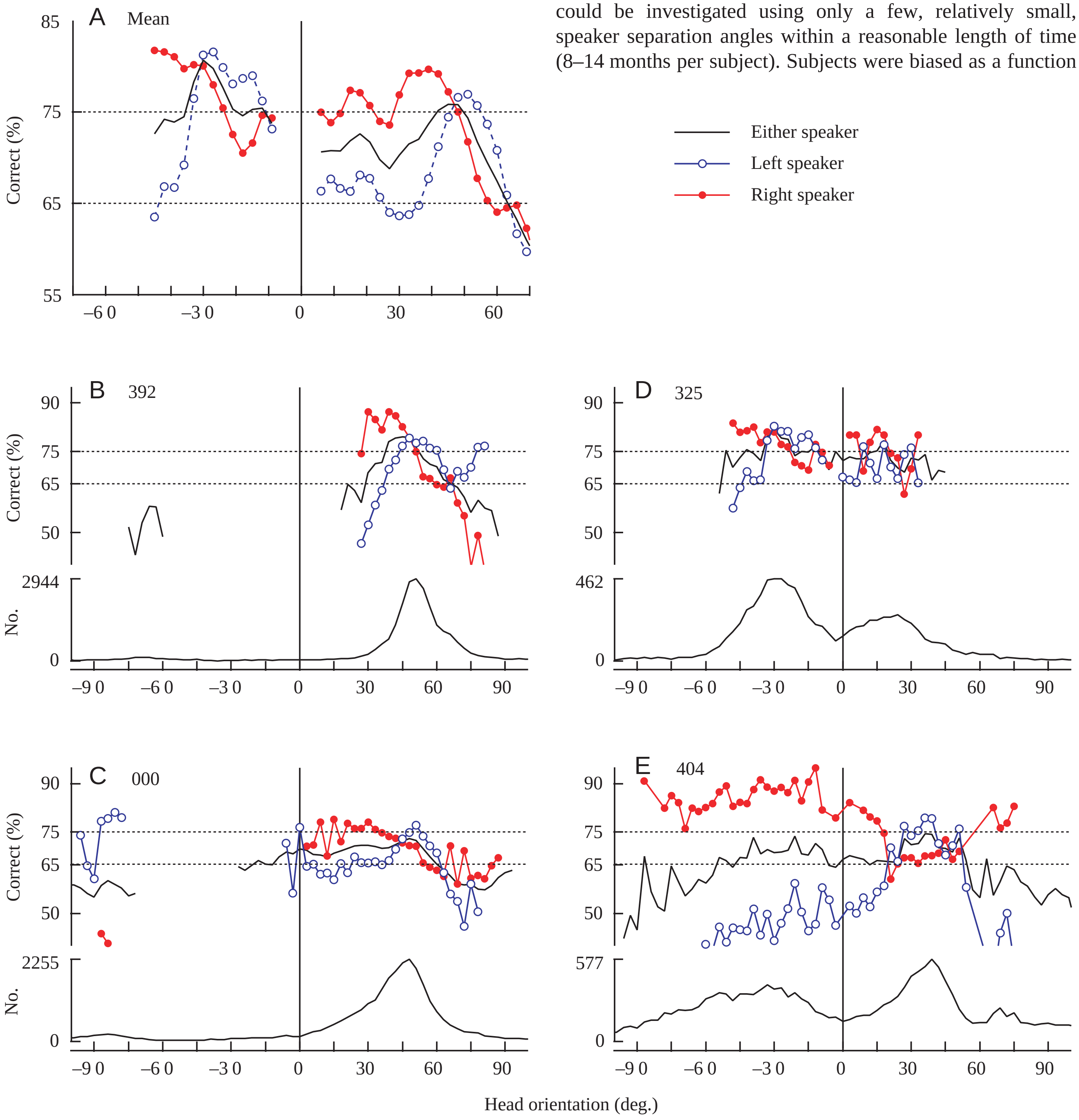

Fig. 6. Performance varies with head orientation and with which speaker presented the sound stimulus. (A) Mean percentage of trials in which subjects 392, 000, 325 were able to fly to the correct response perch. (B–E) Performance levels observed for each subject as a function of head orientation and which speaker presented the sound stimulus. Solid lines with no symbols represent performance levels observed when stimuli were played from either speaker. Lower traces in B–E depict sample sizes without respect to which speaker presented the sound stimulus. Dashed lines indicate 65% and 75% correct performance levels.

of head orientation regardless of stimulus type (tone or noise), although the extent of the bias often varied substantially with sound frequency. Unfortunately, limited observations obtained away from each bird's preferred head orientation (as a function of frequency) prevent us from reliably quantifying how biases vary both as a function of head orientation and sound frequency.

Performance and sound frequency

We hypothesized that towhees might discriminate azimuth poorly when played sound frequencies near 3.5 kHz since neither strong interaural time nor intensity differences may exist near this midrange sound frequency. On average, subjects 325, 392 and 000 performed slightly worse when played sound frequencies between ~2.5 and ~3.5 kHz (Fig. 7) than when played lower or higher sound frequencies. Nevertheless, a clear test of this hypothesis was complicated by the fact that performance as a function of sound frequency was also highly dependent on head orientation and on which speaker presented the sound stimulus (see above). Interaural cues vary with head orientation and, as a consequence, the frequencies over which ITD and ILD operate should vary with head orientation. Indeed, if these cues operate over separate sound frequency ranges, then changes in interaural differences may explain why performance varies both as a function of sound frequency and which speaker played the sound stimulus. For example, performance generally decreased with sound frequency when stimuli were played to subject 325 from the right speaker, but generally increased with sound frequency when stimuli were played from the left speaker (Fig. 7; *N*>100 for all frequencies). In contrast, subject 392 nearly always performed better when stimuli were played from the right speaker although this subject performed poorly when either speaker played a stimulus between 2.8 kHz and 3.5 kHz (Fig. 7; *N*>100). Trends were less clear for subject 000 although performance still varied with both sound frequency and which speaker played the sound stimulus (Fig. 7; *N*>100). Side biases again dominated trends observed for subject 404 (Fig. 7; *N*>100) although this subject also performed poorly overall and was only tested using relatively large speaker separation angles (>20°).

We did not explicitly compare how subjects discriminated tones and broadband noise stimuli. Nevertheless, we found (on average) that when noise stimuli were randomly mixed in with tones, subjects were more likely to discriminate the noise stimuli correctly. For example, subject 325 discriminated a 10° angle correctly in 79% of trials when played noise (*N*=717) but discriminated the same angle correctly in only 69% of trials when played a tone (*N*>80; head orientations limited between –42° and –22° and between 15°

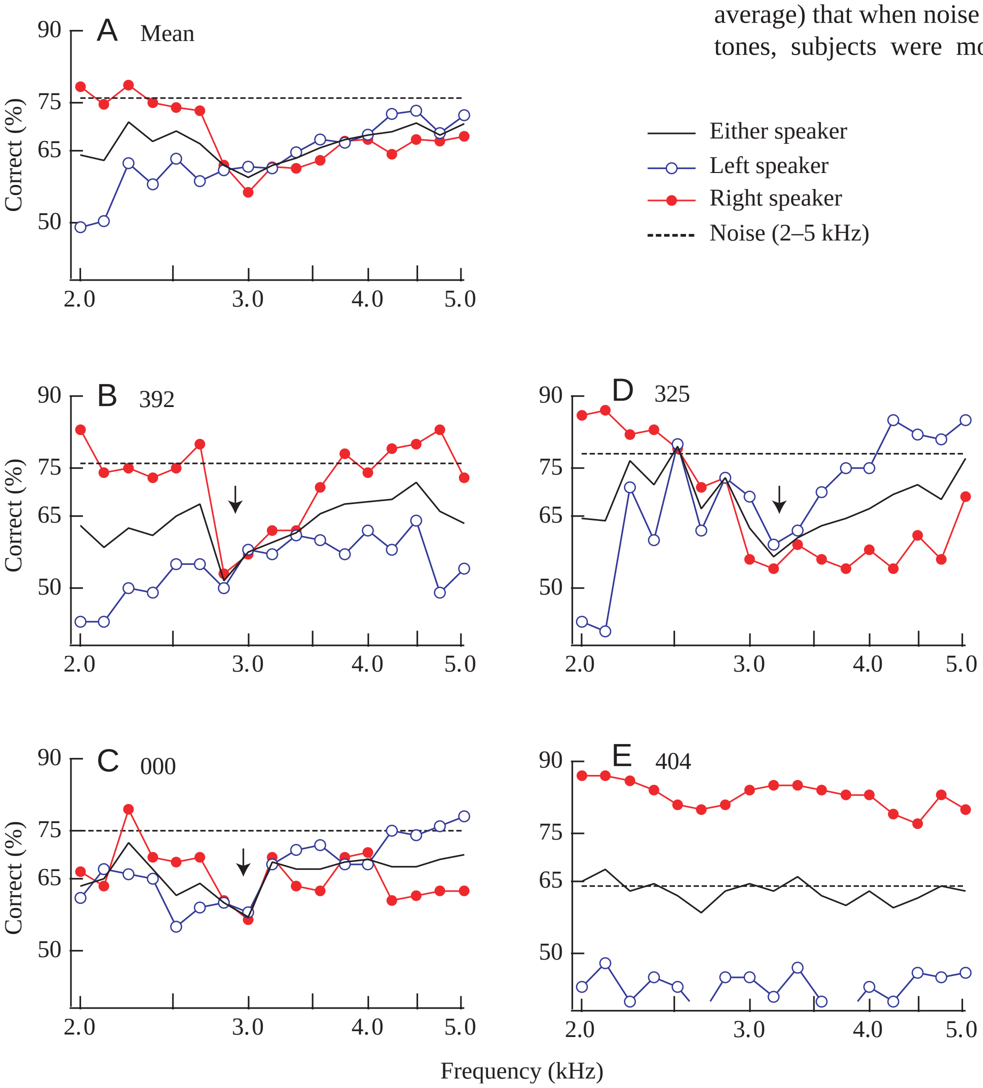

Fig. 7. Performance varies with sound frequency (2–5 kHz) and which speaker played the sound stimulus. (A) Average percentage of trials in which subjects 392, 000 and 325 were able to fly to the correct response perch when tested using a 9° or 10° speaker separation angle. (B–E) Performance levels observed for each subject as a function of sound frequency (392 at 10°; 000 at 9°; 325 at 10°; and 404 at 20°; *N*>100). Dashed lines indicate performance levels observed across trials in which subjects were played noise stimuli (2–5 kHz, *N*>200) mixed in with tones. Arrows in B–D point to sound frequencies for which subjects did not reach a 65% correct performance level, regardless of which speaker played the sound stimulus.

and 32°). Subject 392 discriminated a 10° angle correctly in 76% of trials when played noise (N=3331) but discriminated the same angle correctly in only 70% of trials when played a tone (N>240; head orientations limited to between 40° and 60°). Subject 000 discriminated a 9° angle correctly in 75% of trials when played noise (N=5360) but discriminated the same angle correctly in only 67% of trials when played a tone (N>780; head orientations limited to between 37° and 57°). Subject 404 discriminated a 15° angle correctly in 64% of trials when played noise (N=3276) but discriminated the same angle correctly in only 60% of trials when played a tone (N>90; all head orientations). Despite these overall trends, subjects were occasionally able to discriminate relatively high or low frequency tones as well as noise stimuli, depending on head orientation and which speaker played the sound stimulus (Fig. 7).

Controls

Reversing the left and right inputs from the photoelectric perch sensors and all electrical channels did not influence performance. In contrast, subjects were unable to choose the correct perch when outputs to the left and right speakers were briefly (100–200 trials) reversed only at the digital to analog converter, or at the power amplifier. These results demonstrate that subjects were not relying on cues associated with either electronic device. Subjects were also unable to discriminate reliably between speakers when their heads were oriented away from the speakers (<–90° or >90°; see above); again suggesting that subjects were unlikely to be attending to acoustic cues associated with either speaker.

Neither performance nor head orientation with respect to each speaker varied after: (1) rotating the starting perch 45°; (2) rotating all three perches together in the room 30°; or (3) placing a thin visually opaque layer of open-cell foam between the starting perch and each speaker (subjects 325 or 392). Side biases also did not differ under these experimental conditions although we could accurately compare biases only near each subject's preferred head orientation due to limited sample sizes.

Subjects often oriented their bodies backwards on the starting perch and side biases did not change substantially regardless of whether subjects rotated their heads to the left or to the right before attaining a similar head orientation with respect to speaker locations (i.e. whether subject's oriented their bodies forward or backward). Subjects needed to rotate their heads a greater number of degrees under these conditions and we can therefore also eliminate both the direction and the extent to which heads were rotated as variables that might have influenced performance as a function of which speaker played each sound stimulus.

Experiment III: head orientation in a comparable visual task

In this experiment, we were mainly interested in how previously tested subjects would orient their heads with respect to each LED. In particular we were interested in whether subjects would orient their heads similarly in both a visual and auditory localization task (Experiment II). Subject 404 was not available for testing, however subjects 325, 392 and 000 oriented similarly in both the visual and auditory tasks (Fig. 8).

Subject 325 oriented his beak to the left and right of speaker locations in the auditory task, but usually oriented to the right

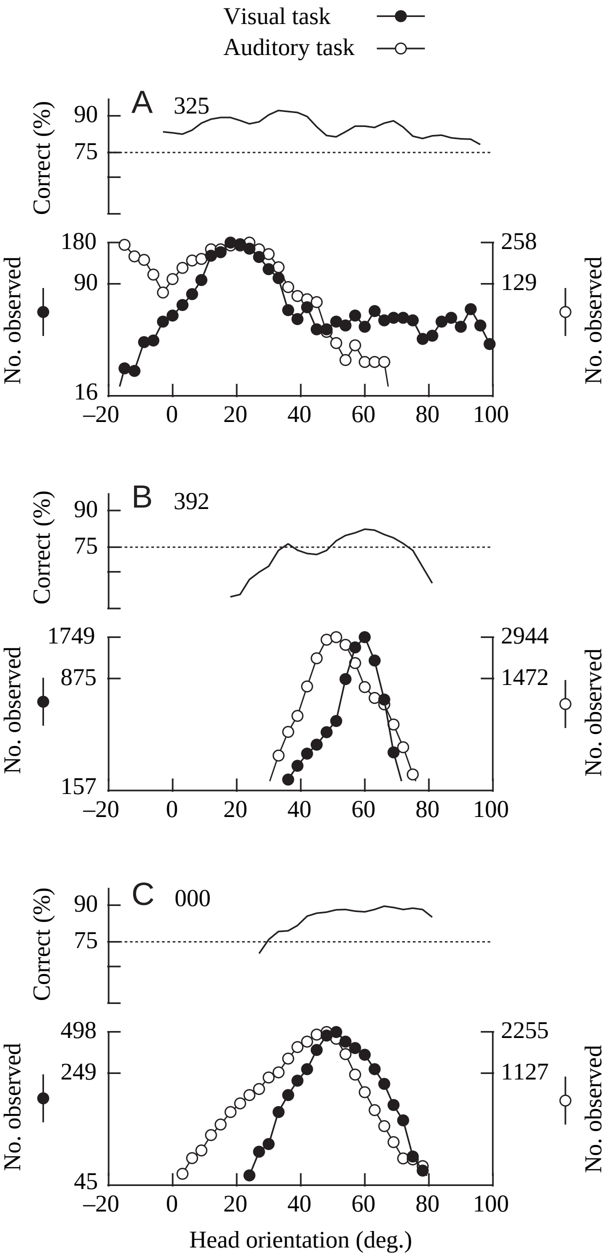

Fig. 8. Individual subjects tended to favor different head orientations in our auditory and visual two-alternative forced-choice (2AFC) tasks, however each subject oriented similarly in both tasks (see text). Normalized distributions of head orientations used by subjects 325 (A), 392 (B) and 000 (C) in our auditory (open circles) and visual (closed circles) 2AFC discrimination tasks. Plotted above each distribution is the proportion of trials in which subjects flew to the correct response perch in the visual task. Distributions for the auditory task (open circles) are the same as those shown in Fig. 6.

of LED locations in the visual task (mode=~22°). Subject 392 oriented to the right of speaker and LED locations in both tasks but often used slightly different head orientations in both tasks (modes=50° and 60°). That is, subject 392 appeared to favor a 50° orientation in the auditory task but favor a 60° orientation in the visual task. Nevertheless, both head orientations (50° and 60°) were commonly used by this subject in both tasks. Much like subject 392, subject 000 tended to orient to the right in both tasks.

All subjects, both in the auditory and in the visual tasks, appeared to favor several head orientations within the relatively broad distributions that we present (Fig. 8). For example, several well-defined peaks often characterized distributions obtained over several days. Independent peaks often corresponded with the angle that subtended each stimulus (LED or speaker). Nevertheless, it is our impression that subjects often chose to orient in several specific directions.

Subjects performed well in this visual task even when the duration of the TTL pulse sent to each LED was as short as 1 ms. In addition, subjects generally performed best when their heads were oriented in a preferred direction. Subjects were occasionally biased towards the left or right LED, however the direction of this bias varied across days and biases did not vary with head orientation (<±1%). That is, on any given day, subjects were just as likely to be biased towards the left or right perch regardless of head or body orientation.

Discussion

Overall performance

Towhees resolve azimuth well in the field, flying towards speaker locations with a raw median error of 6.9° and with an estimated error of 4–5° after correcting for perch distribution (availability). In contrast with field data, subjects were only able to discriminate an angle of ~7° in our laboratory task. Subjects were required to perform very different tasks in these two experiments. Nevertheless, our results suggest that towhees may be able to assess azimuth more accurately in the field. These results are surprising if one assumes that interference from reflections and other noise sources are likely to degrade sound stimuli. Conversely, these results may not be surprising if one considers that sound-localization mechanisms may possibly benefit from the reverberations that accompany direct sound in the bird’s natural habitat (Nelson and Stoddard, 1998).

Towhees have relatively small heads that are unlikely to generate significant interaural cues. Conversely, the left and right tympanic membranes of small birds are acoustically coupled by an interaural pathway and it has been hypothesized that an acoustic interaction across this pathway may function to produce larger than expected interaural cues (e.g. Calford and Piddington, 1988; Hyson et al., 1994). We do not yet fully understand how the interaural pathway functions in small birds (Klump, 2000; Larsen, 2004; Larsen et al., 1997), however female parasitoid flies can assess azimuth with a resolution of only 2° (Mason et al., 2001) and these flies appear to use mechanical coupling between the left and right tympani to achieve this high level of performance (e.g. Mason et al., 2001; Miles et al., 1995; Robert et al., 1996). Furthermore, it remains unclear whether overall cue magnitude limits localization accuracy or whether a more critical factor is the extent to which cues change with direction (μs deg.^{-1}).

Towhees in our 2AFC experiments performed better than other species that have been tested using similar methods (Fig. 3, Klump et al., 1986; Park and Dooling, 1991). We do not know why this is the case but have no reasons to believe that towhees are unique among songbirds in their ability to resolve azimuth accurately. We allowed subjects to perform: (1) over an extended period of time; (2) in a relatively large chamber; and (3) over a relatively long distance (1.5 m). These conditions may have influenced performance. More likely explanations, however, may have to do with the fact that, unlike previous experiments, we allowed our subjects to predict the time of stimulus presentation. Without this information, subjects in previous experiments may have been unable to orient their head in a direction that improves performance under laboratory conditions. Allowing our subjects to orient in a preferred direction might be viewed as unrealistic. Conversely, by allowing our subjects to predict stimulus presentation we are able to describe how towhees choose to behave when forced to discriminate between two potential sound source locations.

Towhees in the field are able to resolve both distance and direction accurately after hearing only a single, relatively short (~150 ms), stimulus and there is no evidence to indicate that sound-localization ability varies with head orientation in the field. Since sound is unlikely to arrive from only a single direction in the field (Nelson and Stoddard, 1998), head orientation may be less important for wild birds.

Head orientation

Field experiments allow us to estimate the accuracy with which small birds can resolve azimuth over distance in their natural habitat (Experiment I), but tell us little about the sound-localization cues they use. To address this question, we conducted 2AFC experiments in the laboratory to see if we could gain insights into the mechanisms that small birds use.

Subjects did not orient their heads forward towards speaker locations in our 2AFC task but instead oriented laterally prior to stimulus presentation. These results are surprising since it is usually presumed that animals should orient forward when trying to resolve azimuth most accurately (e.g. Heffner and Heffner, 1992). Barn owls, for example, assess azimuth most accurately when facing (±30°) a sound source (Knudsen et al., 1979).

Head orientation cannot be accurately quantified from video recordings of subjects on their starting perches in the field. Nevertheless, head movements can be discerned from these recordings and observable movements that were made by subjects on their starting perches suggest that towhees do not precisely position their heads. Indeed, precise movements could not be made when subjects were played only a single stimulus. It should be noted, however, that head movements made in an attempt to improve sound-localization accuracy cannot be easily distinguished from those made while attempting to visually locate an object of interest.

Birds do not use saccadic eye movements to acquire objects in space but instead rely on rapid head movements to position images on retinal areas of high acuity (e.g. Land, 1999; Pratt, 1982). Dawkins (2002) hypothesized that birds may use several different head orientations to view objects in different ways. Thus, audiovisual calibrations in small birds may need to be made in distinct directions within each lateral hemifield as opposed to with frontal visual fields in the case of barn owls. We do not know whether the slightly different head orientations we observed in our visual experiments corresponded with different visual fields, but our results suggest that experience may play a significant role in determining how songbirds orient when localizing sound sources.

Sound frequency

We hypothesized that towhees might have difficulty judging azimuth when played sound frequencies near 3.5 kHz if relatively weak interaural time differences (ITD) and interaural level differences (ILD) are produced near this frequency. Subjects 325, 392 and 000 tended to have greater difficulty localizing sound frequencies between 2.5 and 3.5 kHz, and these results suggest that towhees may indeed use different cues when localizing sound frequencies to each side of ~3 kHz. A more dramatic decrease in performance over midrange sound frequencies may be avoided if relatively small changes in head orientation overcome deficiencies that might exist for any single combination of sound frequency and head orientation. Furthermore, spectral cues may normally allow small birds to localize midrange sound frequencies accurately since vocalizations are often frequency modulated and typically span sound frequencies both above and below ~3 kHz.

Auditory biases

We do not know why subjects were biased towards either the left or right speaker as a function of head orientation and sound frequency. A relatively simple behavioral reward strategy might explain why subject 404 tended to fly predominately to the perch associated with the right speaker. Nevertheless, similar reward strategies are unlikely to explain the biases that we observed in our other subjects (325, 392 and 000). For example, it remains unclear why a behavioral reward strategy might vary systematically with head orientation, but not also as a function of the extent and direction the head is turned (with respect to body orientation). Indeed, subjects were not simply biased towards the speaker they were ‘facing’ when they heard a stimulus, and two subjects (325 and 392) were biased similarly even when required to fly up and over an acoustically transparent barrier. We are also unable to explain why a behavioral reward strategy would vary systematically with sound frequency. Finally, we can think of no clear reason why subjects would not employ a similar behavioral reward strategy when performing in a comparable 2AFC visual task.

Behavioral implications

Each subject behaved differently in our laboratory 2AFC experiments, making it difficult to draw general conclusions about how towhees behave when attempting to discriminate azimuth. Conversely, individual birds also orient differently when viewing similar objects (Dawkins, 2002) and it is therefore interesting to consider the possibility that individuals use different orienting ‘strategies’ when they listen to sounds. We are unaware of studies in which head orientation has been quantified in tasks involving stimulus discrimination. Nevertheless, zebra finches, *Taeniopygia guttata*, discriminate sounds differently depending on whether they have received a left or right thalamic lesion (Cynx et al., 1992). In addition, raptors orient in different directions depending on context and level of experience with behaviorally relevant stimuli (Palleroni and Hauser, 2003).

Location is often disassociated from other forms of information that birds might convey in their vocalizations (e.g. quality, identity, etc.). Nevertheless, a signaler’s location can often have a strong influence on how a listener will respond to a conspecific vocalization (e.g. Stoddard, 1996). In addition, although small birds in the laboratory can resolve fine temporal patterns in vocalizations (Dooling et al., 2002), these patterns may degrade over distance unless listeners are able to discriminate direct sound (i.e. sound that propagates along relatively direct pathway) from reflections arriving by indirect pathways over a similar time course (e.g. Dent and Dooling, 2003; Dent et al., 1997; Klump, 1996). Furthermore, the ability of small birds to resolve relatively small spectral changes in vocalizations (Amagai et al., 1999; Lohr and Dooling, 1998) may deteriorate if they are unable to resolve independently reflections that might otherwise sum together with direct sound. Towhees, for example, can estimate sound attenuation over distance (Nelson, 2002) despite that fact that reflections from the ground influence experimental measurements of amplitude (Nelson, 2003). Listeners may avoid much of this ambiguity if their ability to localize allows them to distinguish reflections from direct sound. We do not know how well songbirds are able to discriminate elevation. Yet, high sound-localization acuity may influence not only how individuals interpret and respond to vocalizations, but also their ability to resolve acoustic patterns in vocalizations.

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