

Target-approaching behavior of barn owls (*Tyto alba*): influence of sound frequency

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Abstract We studied the influence of frequency on sound localization in free-flying barn owls by quantifying aspects of their target-approaching behavior to a distant sound source during ongoing auditory stimulation. In the baseline condition with a stimulus covering most of the owls hearing range (1–10 kHz), all owls landed within a radius of 20 cm from the loudspeaker in more than 80% of the cases and localization along the azimuth was more accurate than localization in elevation. When the stimulus contained only high frequencies (>5 kHz) no changes in striking behavior were observed. But when only frequencies from 1 to 5 kHz were presented, localization accuracy and precision decreased. In a second step we tested whether a further border exists at 2.5 kHz as suggested by optimality models. When we compared striking behavior for a stimulus having energy from 2.5 to 5 kHz with a stimulus having energy

between 1 and 2.5 kHz, no consistent differences in striking behavior were observed. It was further found that pre-takeoff latency was longer for the latter stimulus than for baseline and that center frequency was a better predictor for landing precision than stimulus bandwidth. These data fit well with what is known from head-turning studies and from neurophysiology.

Keywords Auditory · Spatial hearing · Sound localization · Interaural time difference · Interaural level difference · Barn owl

Abbreviations

BW	Bandwidth
CF	Center frequency
EMV	Ellipsoid mean vector
IC	Inferior colliculus
ILD	Interaural level difference
ITD	Interaural time difference
KS	Kolmogorov–Smirnov test
KS2D2S	Kolmogorov–Smirnov 2 dimensions 2 samples test
SD	Standard deviation
SPL	Sound pressure level
2D	2-Dimensional
3D	3-Dimensional

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Introduction

Barn owls have multiple optical and auditory adaptations to nocturnal hunting (Payne 1971; van der Willigen et al. 1998; Harmening et al. 2007). These adaptations enable the

birds to orient visually at very low light levels (Dice 1945) or to localize and strike an invisible target in total darkness (Payne 1962, 1971; Konishi 1973a, b). The acoustic pathway in barn owls has been extensively studied and many details of their feature-rich directional-hearing capabilities have been discovered. These details include specialized feather structures like the ruff as well as its asymmetrical ears (Coles and Guppy 1988; Haresign and Moiseff 1988; Campenhausen and Wagner 2006). Prominent neuroanatomical features are the elongated auditory papillae with their overrepresentation of frequencies above 5 kHz (Köppl et al. 1993; Fischer 1994) and enlarged nuclei in the auditory pathway (Kubke et al. 2004; Iwaniuk et al. 2006). Barn owls solely use interaural time differences (ITDs) in the horizontal plane (the azimuth) (Poganiatz et al. 2001), while interaural level differences (ILDs) are a major cue for elevational localization (in the vertical plane) (Poganiatz and Wagner 2001). The absolute hearing thresholds of barn owls were found to be close to -20 dB sound pressure level (SPL) at 6–9 kHz (Konishi 1973a; Wagner 1993; Dyson et al. 1998). Neurons can respond to signals with a signal-to-noise ratio between -20 and -10 dB (Wagner et al. 1994; Takahashi and Keller 1992).

The head-turns of barn owls are fast ballistic saccades (Knudsen et al. 1979, 1993; du Lac and Knudsen 1990). The latencies for these saccades may be as short as 50 ms (Knudsen et al. 1979; Wagner 1993) with the duration of a saccade typically exceeding 100 ms. This observation suggests that barn owls use an “open-loop-strategy” to center the gaze on auditory targets. Hereby, the owls turn their head without referring to the feedback of the sound source. Head saccades have been widely used to measure both detection and discrimination levels of barn owls in terms of stimulus amplitude and frequency as well as interaural processing of time, phase and intensity (e.g., Knudsen and Konishi 1979; Saberi et al. 1998, 1999; Poganiatz et al. 2001; Takahashi et al. 2003; Whitchurch and Takahashi 2006).

Free-flight behavior may be regarded as the 3-dimensional (3D) extension of the 2-dimensional (2D) head-turn behavior. If an owl is able to detect a signal source in 2D, this does not automatically qualify for a successful approaching of the target in 3D. Thus, not only the frequencies emitted by the target, but also its distance from the listener play an important role for accurate striking.

Both localization accuracy (the difference between the mean sound-localization position and the reference target position) and localization precision (the distribution of the localization positions around the mean value) depend on the position of the target and the spectral content of the stimulus. We shall use the term localization error, if we refer to both accuracy and precision together. For example, Knudsen et al. (1979) observed an increasing localization

error with increasing angular distance to the target. Similar observations were later made in experiments with virtual acoustic stimuli (Poganiatz et al. 2001). The effect was more pronounced for open-loop localization than for closed-loop localization, the latter providing the owls with continuous feedback about the location of the target (Knudsen et al. 1979). The highest sound-localization precision amounted to about 3° (Bala et al. 2003, 2007). This corresponds to a temporal resolution in ITD of about $8 \mu\text{s}$ (Keller et al. 1998; Campenhausen and Wagner 2006). Concerning the spectral content, the best localization performance was found in the frequency range from 5 to 9 kHz (Konishi 1973a; Knudsen and Konishi 1979). For an unambiguous localization, a certain bandwidth (BW) was necessary (>3 kHz in barn owls) (Konishi 1973a; Saberi et al. 1998, 1999). This is not surprising since barn owls derive the location of a source by comparing the signals arriving at the two ears by a mechanism resembling cross-correlation (Pena 2003; Fischer et al. 2008). Moreover, barn owls were much worse at detecting (Konishi 1973a, b) or even refused to approach pure tone sources (Payne 1971). Payne (1971, p. 550) also noted that owls refused to attempt to strike when all frequencies above 5 kHz were removed. The results of these behavioral studies from the 1970s argue for a dominant effect of frequencies higher than 5 kHz and broad BW being important for a precise sound localization in barn owls. But as suggested by recent models and data of the representation of ITDs, the low-frequency border could also lie around 2.5 kHz (Harper and McAlpine 2004; Wagner et al. 2007). Harper and McAlpine (2004) proposed a homogeneous distribution of ITD detector neurons only for frequencies above 3 kHz in the barn owl, whereas for lower frequencies their model suggested two distinct subpopulations of neurons being important to code the position of a sound source. This model was not supported by the experimental dataset of Wagner et al. (2007) who did not observe such a break in the distribution but a homogeneous arrangement of ITD detector neurons even in the frequency range below 2–3 kHz. Due to these discussions and new models of sound localization, it was interesting to reinvestigate the barn owl's behavior with stimuli containing only low frequencies (center frequency, CF) <5 kHz and to compare this situation with conditions, where stimuli contained high frequencies (CF >5 kHz). This issue was not systematically investigated neither by Payne (1971) nor by Konishi (1973a, b). The low-frequency border may be defined to be around 5 kHz by referring to Payne's (1971) and Konishi's (1973a, b) observations or even at lower frequencies supporting the model and data of low frequency representation in the barn owl (Harper and McAlpine 2004; Wagner et al. 2007). Since it is typical for barn owls not to take off upon hearing the first signal that a potential prey emits but to

wait for subsequent signals, it was also interesting to test whether the pre-takeoff latency depends on the spectral content of the stimulus.

Materials and methods

Animals

All data were collected from three adult, hand-raised American barn owls (*Tyto alba pratincola*; owls 1 and 3 male and owl 2 female) from our breeding colony. Owls 1 and 2 were novice to free-flight experiments, whereas owl 3 had experience from two previous experimental series in the free-flight room. No owl had experience in capturing living prey. All experiments were carried out in accordance with German law and the NIH guidelines for care and use of laboratory animals and were approved of by the Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany.

Setup and stimulation

The experiments were conducted in a sound-attenuating flight room of 4.2 m × 3.2 m × 3.2 m (length × width × height). At one side of the flight room, the perch apparatus was mounted at a height of 1.8 m (Fig. 1). Since the owls have a body length of about 35 cm, the owls' ears were located about 2.1 m above ground in this situation. Two movable ramps were placed on the floor opposite to the perch. Each ramp contained two fixed target speakers, the first positioned 25 cm from the midline, the next 50 cm more lateral. The ramps were typically positioned at three different distances between 2.35 and 3.35 m from the perch, resulting in 12 speaker positions, 6 flight distances and 12 viewing angles (see Fig. 1; Table 1 for details). Ramp distances were selected randomly on a daily basis, while speaker positions were randomly varied from trial to trial, using a self-written randomizer script (IgorPro, Wavemetrics, Portland, OR, USA). Stimuli were transferred from the personal computer (PC) to the RX6 Multifunction Processor [Tucker-Davis Technologies (TDT), Alachua, FL, USA]. Digital-analog-converted signals (sampling rate: 97 kHz) were adjusted using a PA5 attenuator (TDT) and passed onto a Yamaha AX 730 amplifier, which then drove one of four Visaton F8SC target speakers (Visaton, Haan, Germany, flat frequency response at 80–15,000 Hz, variation of ±5 dB). Signals were monitored using an oscilloscope (Hameg HM 203-7, Mainhausen, Germany). All stimuli were presented in closed-loop mode and stimulus amplitude was set to 35 dB SPL (A-weighted scale) at perch position, calibrated for all 12 speaker positions. This sound level was chosen, because it was

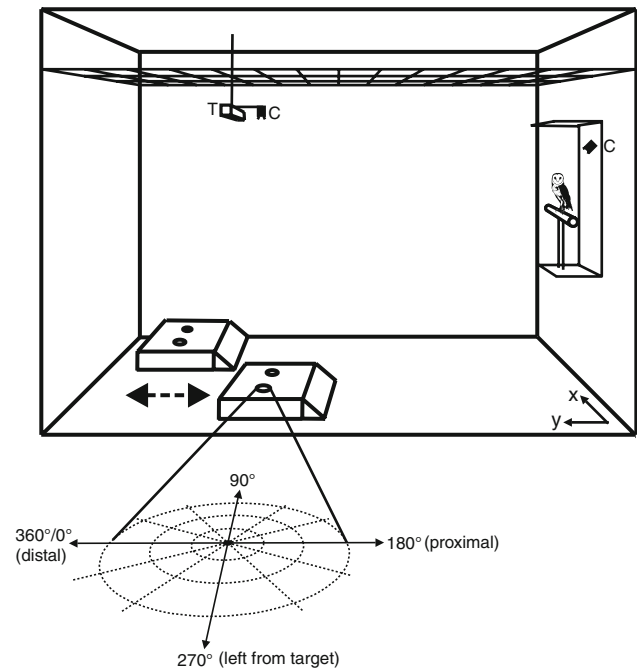


Fig. 1 Setup. The free-flight room has dimensions of 4.2 m × 3.2 m × 3.2 m. The height of the room was limited to 2.7 m by a net to prevent the birds from damaging the power supply as well as the cables of both the head tracking system (T) and the top camera (C). The door (not drawn) was to the left of the perch in the “transparent wall”. The perch was mounted at a height of 1.8 m. Each ramp contained two loudspeakers and could be moved individually from a close (2.35 m) to a distant position (3.35 m) measured from the center of the speaker. Speaker distance on the ramp was 50 cm. The polar plot inset illustrates the coordinate system for the x–y data obtained from the head tracker. The positions of the ramps as well as the sequence of the target speakers were changed in randomized order

clearly above the noise floor of 24 dB SPL, thus yielding a sufficiently high signal-to-noise ratio. For calibration, a sound level meter (Brüel & Kjaer, model 2236, Brüel & Kjaer, Naerum, Denmark) and the Igor Pro software (WaveMetrics, Lake Oswego, OR, USA) were used.

The owls' flight behavior was recorded using two independent tracking systems: two infrared cameras (ELV black/white MiniCamera, 50 Hz PAL resolution, 12 V, 180 mA, wavelength 850 nm; ELV, Leer, Germany) and an infrared head tracking system DynaSight™ Sensor (Origin Instruments Corporation, Grand Prairie, TX, USA). The cameras were mounted behind the perch and above the landing zone to provide optical feedback about the position and behavior of the owl in the flight room (“C” in Fig. 1). The two video streams were recorded using a frame grabber (LeadTek Winfast Guard Pro) and analyzed using virtual dub (<http://www.virtualdub.org>). The video data enabled us to measure the latency as well as the landing position. The top mount camera was also used to monitor the striking success of the owls during the training phase.

Table 1 Azimuthal angles of target speakers as a function of ramp position and distance

Speaker/ distance	Far = 3.35 m	Middle = 2.85 m	Near = 2.35 m
LS1	−12.2°, 3.87 m	−14.3°, 3.45 m	−17.2°, 3.05 m
LS2	−3.8°, 3.81 m	−4.5°, 3.38 m	−5.5°, 2.97 m
LS3	3.8°, 3.81 m	4.5°, 3.38 m	5.5°, 2.97 m
LS4	12.2°, 3.87 m	14.3°, 3.45 m	17.2°, 3.05 m

Loudspeaker (LS) 1 and LS2 are mounted on ramp 1, whereas LS3 and LS4 were mounted on ramp 2. Each ramp can be positioned at three different distances to the perch (far, middle and near). Negative angles were in the counterclockwise direction, positive angles in the clockwise direction with 0° straightforward to the owl's line of sight. The second number in each box denotes the 3D distance from the perch to the respective loudspeaker (LS) in meter. Note that the positions far, near and middle in the first line are given as the 2D horizontal distance between perch and the row of speakers on the speaker device (Fig. 1), while the distances to the respective speakers are given as linear distances, to take into account the height of the perch

Around each speaker a circle with 20 cm radius was marked on the floor, visible through the infrared illumination of the cameras. During the training phase, owls were rewarded only if they hit within this circle. The final striking coordinates were recorded precisely by the second tracking system. The DynaSight sensor allows for real-time 3D measurements using a passive reflector target. This target was attached to the head of the owl and reflected the infrared light emitted by the DynaSight box back to the sensor. The tracking system provided a spatial resolution in the sub-centimeter range at target distances below 3 m. The sensor's updating rate was 65 Hz with a maximum field of detection of 75° azimuth × 75° elevation from the center of the tracking system. The tracking data were fed into IgorPro software in real-time using a self-written program.

Stimuli

The sounds were generated using Igor Pro and infinite impulse response (IIR) filter functions in MatLab (Mathworks, Natick, MA, USA). Individually IIR filtered signals were finally passed through an fourth order Butterworth filter resulting in attenuation of at least 60 dB at 200 Hz on either side of the passband. Five acoustic stimuli with different CF and BW were used: stimulus 1, CF 5.5 kHz, BW 9 kHz; stimulus 2, CF 7.5 kHz, BW 5 kHz; stimulus 3, CF 3 kHz, BW 4 kHz; stimulus 4, CF 3.75 kHz, BW 2.5 kHz; stimulus 5, CF 1.75 kHz, BW 1.5 kHz. Stimulus 1 covered almost the entire hearing range of the owl. Stimulus 2 covered the high-frequency range (CF > 5 kHz) as defined by Payne (1971), while stimulus 3 spanned the low-frequency range (CF < 5 kHz). Stimuli 4

and 5 divided the low-frequency range into two parts, one of which (stimulus 5) is related to recent findings about optimal ITD representation (Harper and McAlpine 2004). Stimuli 2, 4 and 5 were designed to approximately match in octaves of BW. Since all experiments were performed in closed-loop the stimulus duration was not fixed to a defined duration but lasted as long as the owl needed to approach the target. Therefore, the time of stimulus presentation depended on the behavior of the owls and varied from trial to trial. The stimulus was switched off after the owl had landed.

Training

The training protocol was identical for all three owls. During the initial training phase, using operant conditioning, the free-flight room was illuminated and the target position was indicated by a piece of food (a complete 1-day-old dead chick) placed on top of one of the four protected sound-emitting loudspeakers during auditory stimulation (stimulus 1, broadband noise, CF 5.5 kHz, BW 9 kHz). The owls learned to fly toward the speaker in order to obtain the food within 2–4 days. After this first step, the ambient lights as well as the size of the food reward were gradually reduced until the owls finally succeeded in striking the sound-emitting loudspeaker in total darkness without any reward on top of the speaker. While the second step was learned, the owls received a “go-back” signal while standing on the floor using a dim light emitting diode (LED) mounted behind the perch. Owls reached a sufficient level (>75%) of successful flights toward the target speaker in total darkness and back to the perch after no more than 3 months of training.

Once landed, barn owls can cover a radius of 20 cm with their wings and capture whatever lies beneath without additional jumps (Payne 1962; Brandt and Seebass 1994; Singheiser 2006). We therefore considered a striking distance ≤ 20 cm as a successful trial. Each owl performed an average of 8–10 trials on each experimental day. During the experimental series, the owls were kept deprived of food to maintain a stable level of motivation corresponding to ~90% of their free-feeding weight. The weight of the owls was measured before and after the daily experimental session.

Experimental protocol

At the beginning of a session, the experimenter entered the dark flight room through a door located at the left side of the perch and allowed the bird to jump off the hand onto the perch. Afterward, the experimenter left the flight room and the door to the control room was closed. The bird showed searching behavior after a few seconds even if no

sound was present. At the onset of the auditory stimulus the owl turned its head in the direction of the stimulus. It did not show side-to-side movements (peering) with the body or the head as typically observed under lighting conditions (Ohayon et al. 2006). After a certain period of fixation, the owl would bend its body toward the target and take off (see Online Resources 1 and 2). Once the owl landed, it started looking back into the direction of the perch, waiting for the “go-back” signal to be turned on. After the dim LED was switched on, the owl immediately flew back to the perch and awaited its reward (see Online Resource 3). The owl’s performance could be observed on the monitors in the control room. After the owl had landed on the perch, the LED was switched off and the experimenter entered the flight room with a piece of meat from a 1-day-old dead chick. A food reward was provided manually every few trials or after every trial, depending on the owl’s motivation and accuracy. Subsequently, the experimenter left the flight room and after a waiting period of variable duration (10–30 s), the next stimulus was presented. This procedure was similar for all trials and all owls.

Data analyses

For the analysis of the data, we first defined a 2D Cartesian coordinate system on the floor of the room (see Fig. 1). The origin was in the lower left center of the room. The x -axis was parallel to the wall next to which the perch was placed. The y -axis was the line perpendicular to the x -axis. For the analysis of the individual trials, the origin was shifted to the center of the sound-emitting loudspeaker that represented the ideal landing point without rotation. After the shift, positive y values corresponded to points distal to the ideal landing point as seen from the perch (0° in the inset to Fig. 1), while positive x values were to the right of the target speaker (90° in the inset of Fig. 1).

Each landing point i was characterized by its Cartesian x_i and y_i coordinates, or equivalently, by the corresponding polar coordinates, the 2D distance $\rho_i = \sqrt{(x_i^2 + y_i^2)}$ and the angle $\theta_i = \arctan 2(\frac{y_i}{x_i})$. The 2D distances were used to assemble plots of cumulative probabilities, for example to find out how many percent of the landing points lie within the 20 cm radius covered by the wings. Bivariate methods of circular statistics (Batschelet 1981) were used for the data analysis. After first calculating the arithmetic means over all n data points $\bar{x} = \frac{1}{n} \sum_i^n x_i$ and $\bar{y} = \frac{1}{n} \sum_i^n y_i$, we arrive at the mean vector $m = \begin{bmatrix} \bar{x} \\ \bar{y} \end{bmatrix}$. The tip of the mean vector corresponds to the center of mass of the real landing points (ellipsoid mean vector, EMV). It represents landing accuracy. The angle of the mean vector specifies the landing direction relative to the ideal landing point. Standard deviations s_x and s_y , the covariance

$\text{Cov}(x, y) = \frac{1}{n-1} \sum_{i=1}^n (x_i - \bar{x})(y_i - \bar{y})$, and the correlation coefficient r were obtained as well. With these values, the standard ellipse is defined as having the center at \bar{x}, \bar{y} , as well as area and inclination described by the rotation-invariant semi-axes a and b and the angle ϕ (for details, the reader is referred to chapters 7 and 13 in Batschelet 1981). For the present study, it is important that roughly 40% of the landing positions fall inside the ellipse. Thus, the area covered by the ellipse is a measure of landing precision.

In a second step, a 2D extension of the Kolmogorov–Smirnov test (Fasano and Franceschini 1987) was performed. This two-sample test (Kolmogorov–Smirnov 2 dimensions 2 samples, KS2D2S) served to compare the inter-individual landing distributions of the owls or the intra-individual distributions with respect to stimulus type, latency and speaker distance. Note that the KS2D2S analysis tests for localization error, in other words for landing accuracy and landing precision in conjunction. Using the distance and a Mann–Whitney U test, we checked for differences in accuracy while a Levene test was used to detect differences in precision.

Results

A total of 762 trials were obtained with the three owls in 88 daily sessions. In the following analysis, only those trials were used that fulfilled the following criteria: (1) owls had to take off the perch no later than 90 s after stimulus onset. (2) The owl did not show any head shaking, indicating reduced attention, while looking at the floor. (3) The owl was not disturbed before takeoff or during flight by loud noises from outside the chamber. Twenty-eight trials were not counted, 22 of which failed to fulfill criteria 2 and 3. Note that in the experiments with owl 3, more ramp positions than the three mentioned in Table 1 were used. Therefore, if the data were analyzed independent of ramp position, all data collected with owl 3 were used. If the data were analyzed with respect to ramp position, only data obtained with ramp positions as specified in Table 1 were included.

A baseline for landing accuracy and landing precision

Stimulus 1 covered almost the total hearing range of the barn owl. The landing behavior of the owls measured with this stimulus may, therefore, serve as a baseline for striking behavior as occurring in our experimental conditions. The landing positions may be judged by their Cartesian x and y coordinates or equivalently by the polar 2D distance and angle relative to the ideal landing point (Figs. 1, 2 and 3). The landing positions varied considerably in all three owls

(Figs. 2a–c, 3a–c). Qualitatively spoken, each owl had a few outliers, while the rest of the landing positions were close to the ideal landing point. In the following quantitative analysis, we first analyzed the 2D data reflecting the overall landing error that may be further separated in accuracy and precision. We then analyzed the x and y landing positions separately, because the x -direction corresponds to azimuthal localization, while the y -direction reflects elevational localization.

The localization error was smallest in owl 3, followed by owl 1 and owl 2 (owl 1 vs. owl 2, $P < 0.05$; owl 1 vs. owl 3 and owl 2 vs. owl 3, $P < 0.01$ each, KS2D2S tests; also Table 2). The localization error may be separated in accuracy and precision. Striking accuracy may be determined by calculating the center of mass of all landing points, in other words the mean landing position relative to the sound source, the ideal landing position. Mean striking accuracy in response to stimulus 1 was 9.5 cm in owl 1, 11 cm in owl 2 and 2.8 cm in owl 3 (Table 2). The scatter around the mean landing point corresponds to striking precision. A measure for this scatter is the area of the standard ellipse as introduced in “Materials and methods”. The area was 398 cm² in owl 1, 357 cm² in owl 2, and 392 cm² in owl 3 (Table 2). These values were smaller than the target zone of 1,256 cm² around the target speaker.

To judge how often the owl would have caught the prey, in other words, how often the animal landed within the radius of 20 cm around the loudspeaker, we compiled the cumulative probability distribution of the landing positions (Fig. 4a–c). Note that this distribution, in contrast to the standard ellipse, includes both the clustered values as well as the outliers. From the cumulative probability distribution, we read the percentage of landing positions that were

within 20 cm from the ideal landing point. These were 86% in owls 1 and 3 and 87% in owl 2 (Table 2). Thus, in all owls the striking would have been successful in more than 80% of the trials. In addition, we determined the radius from the ideal landing point within which 75% of the landings occurred. This radius amounted to 14 cm in all three owls (Table 2). A Kruskal–Wallis test for accuracy did not show differences between the three owls ($P = 0.67$).

Since the landing positions were scattered in a 2D plane, the angle relative to the ideal landing point, the mean angle, is important in addition to the 2D distance. The mean angle was 177° in owl 1, 173° in owl 2 and 180° in owl 3 (Table 2). Angles from 90° to 270° cover the two quadrants located between the target and the starting point (see Fig. 1). Therefore, these results indicated that the owls tended to land short of the ideal landing point. This is also reflected in the negative mean values of the y distances (Table 2). The Levene test did not reveal significant differences in the scatter between the three owls ($P = 0.58$).

The mean distance of the landing point in the x -direction was less than 1.5 cm from the target or below 0.3° as measured from the starting point in every owl (Figs. 2, 3a–c; Table 2). The corresponding values in the y -direction ranged from –1.8 (owl 3) to –11 cm (owl 2) (Figs. 2, 3a–c; Table 2). The latter value corresponds to a mean striking error of –1.4° in elevation at a horizontal target distance of 235 cm and an elevation of the owl’s ears of 210 cm above ground. The difference in accuracy between the x and y directions was significant for all owls ($P < 0.002$; U tests). Precision was measured as the standard deviation of the landing points. Mean precision for all owls in the x -direction was 10.9 cm. This is equivalent to 2.3°. Precision in the y -direction was 12.6 cm. Since the owl started from

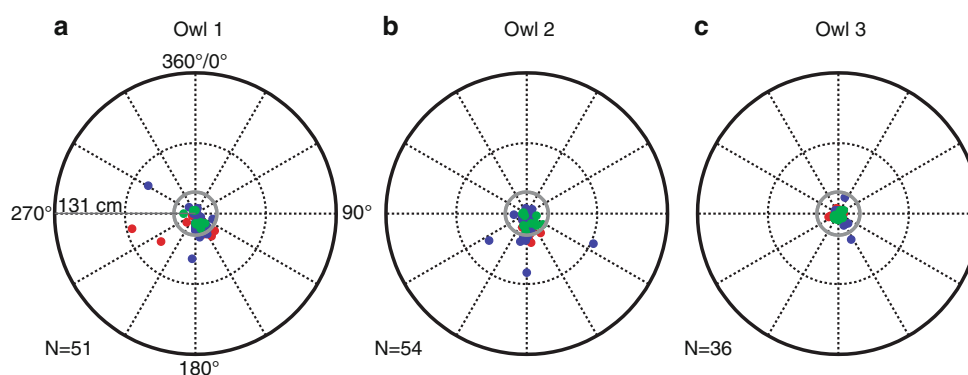


Fig. 2 Landing behavior in the baseline condition. The polar plots show the striking positions for all flights to the baseline condition for each owl and ramp position separately. For a better comparison, all scatter plots are adjusted to the overall maximum striking distance of owl 1 for stimulus 5 with a distance of 131 cm from the target. The innermost gray circles depict the 20 cm target region around the speaker. Color-coded dots represent the final landing positions of

each owl for the three distances between perch and ramp [red = far (3.35 m); blue = middle (2.85 m) and green = near (2.35 m)]. Angles between 90° and 270° indicate a proximal landing position whereas angles between 270° and 90° denote striking positions distal to the target speaker. The number of flights for each owl is given below the scatter plots. Note that most of the strikes were within the target area (color figure online)

Fig. 3 Effects of stimulus frequency on striking behavior. For each owl, mean striking position resembling striking accuracy as well as the standard deviation in azimuth and elevation resembling striking precision are plotted for each stimulus and distance between perch and target (N number of total flights, divided into flights to *red* = far; *blue* = middle and *green* = near). The responses of each owl to the five stimuli are shown in columns (owl 1: *left column*; owl 2: *middle column* and owl 3: *right column*). The intersections of the *dotted lines* represent the position of the target. Deviances in mean striking position along the *horizontal line* come along with a shift in azimuth whereas deviances along the *vertical line* represent a shift in elevation. **a–c** Stimulus 1, CF 5.5 kHz and BW 9 kHz; **d–f** stimulus 2, CF 7.5 kHz and BW 5 kHz; **g–i** stimulus 3, CF 3 kHz and BW 4 kHz; **j–l** stimulus 4, CF 3.75 kHz and BW 2.5 kHz; **m–o** stimulus 5, CF 1.75 kHz and BW 1.5 kHz. Note the high accuracy as well as precision for stimuli with CF > 5 kHz (**a–f**) and the decreasing accuracy and precision for CFs in the low-frequency range (CF < 5 kHz; **g–o**) (color figure online)

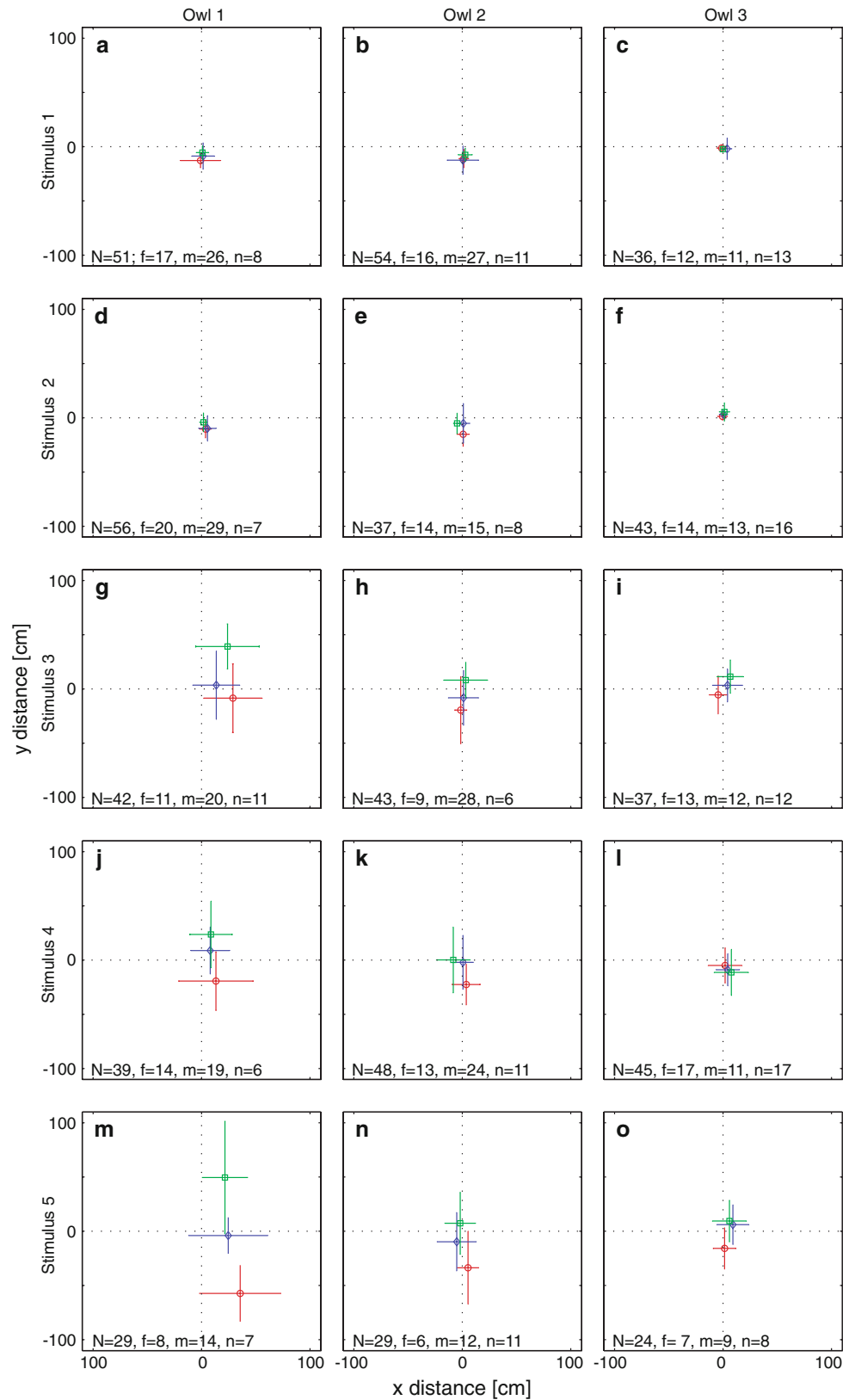


Table 2 Quantitative data on the effects of stimulus frequency on striking accuracy and precision

Owl	Stimulus	EMV (cm)	EMV (°)	Hits (%) at 20 cm	Distance (cm) at 75%	Size of ellipse (cm ²)	Distance in <i>x</i> (cm) mean ± STD	Distance in <i>y</i> (cm) mean ± STD	Median latency (s)
1	1	9.5	177	86	14	398	0.6 ± 13.2	-9.5 ± 9.9	5.0
	2	10.2	155	86	15	223	4.3 ± 6.9	-9.2 ± 10.3	5.0
	3	22.5	65	39	50	2,674	20.3 ± 25.6	9.67 ± 33.9	7.5
	4	10.3	73	49	45	2,262	9.9 ± 24.5	3.1 ± 31.8	8.5
	5	27.5	102	38	79	4,891	26.9 ± 33.3	-5.8 ± 49	8.0
2	1	11.0	173	87	14	357	1.3 ± 10.8	-11.0 ± 10.6	4.0
	2	9.4	183	86	13	250	-0.4 ± 5.7	-9.4 ± 14.8	4.0
	3	8.4	174	72	22	968	0.9 ± 13.4	-8.3 ± 26.3	4.0
	4	7.1	185	65	24	915	-0.6 ± 12.6	-7.1 ± 26.1	5.0
	5	8.4	192	55	34	1,469	-1.8 ± 15.3	-8.2 ± 31.9	5.0
3	1	2.8	180	86	14	392	0.1 ± 7.0	-1.8 ± 8.5	4.0
	2	4.2	4	94	5	161	0.3 ± 7.1	4.2 ± 8.0	4.0
	3	7.1	28	71	22	584	3.0 ± 13.1	6.5 ± 16.9	5.0
	4	5.8	124	65	24	1,102	4.9 ± 17.9	-3.3 ± 19.8	5.0
	5	4.2	116	42	28	1,081	3.9 ± 15.9	-1.8 ± 23.0	5.0

Given are the length (cm) and the angle (°) of the EMVs, the percentages of hits at 20 cm distance from the ideal landing point, the distance at which 75% of hits occurred, the distance in the *x* and *y* directions as well as the size of the standard ellipse. Additionally, median latencies (s) are listed as well

an elevated position, this difference corresponds to only 1.6°.

High-frequency versus low-frequency stimuli

In the next step, we compared the landing positions in response to stimuli 2 and 3 with each other and with the baseline condition. While the scatter in response to stimulus 2 was similar as the scatter in response to stimulus 1, the scatter of the landing points was clearly larger for stimulus 3 (Fig. 3a–i). The KS2D2S test confirmed this impression: In all owls, the localization error was smaller for stimulus 2 than for stimulus 3 ($P < 0.001$ for owls 1 and 3, $P < 0.05$ for owl 2). The same held, if the responses to stimulus 1 were compared with the responses to stimulus 3 ($P < 0.001$ for owls 1 and 3, respectively; $P < 0.01$ for owl 2), while a difference between stimuli 1 and 2 was only observed for owl 3 ($P < 0.001$).

In the cumulative probability distributions (Fig. 4a–c), the differences were reflected by a clear decrease in the number of landings within the 20 cm radius from stimuli 2 to 3 in all owls, while the percentage did not change much between stimuli 1 and 2 (Table 2). Consequently, the distributions corresponding to stimulus 3 were shifted to the right compared with the distributions corresponding to stimuli 1 and 2 for all owls (Fig. 4a–c). The *U* test showed significant differences between stimuli 2 and 3 in owls 1 and 3 (both $P < 0.001$), but not in owl 2. Similar effects were found for the scatter with the Levene test concerning landing precision (Fig. 3d–i). This was reflected in the

larger area of the standard ellipse in response to stimulus 3 (Table 2). Consistent with the latter finding, the landing angles varied slightly from stimuli 1 to 2, but widely between owls and stimuli 2 and 3 (Table 2).

When the landing positions for the *x* and *y* directions were analyzed separately, landing accuracy was typically not different between stimuli 1 and 2 (*U* tests). The same held for landing precision (Levene tests). On the other hand, the responses to stimulus 3 were typically less accurate and precise than the baseline responses in the *y*-direction (Table 2). If the *x*-direction was considered in this comparison, accuracy was reduced in owl 1, while precision was reduced in owls 1 and 3.

Is the behavioral low-frequency limit at 2.5 or at 5 kHz?

Below a frequency of 2.5 kHz, ITD curves exhibit only one peak within the physiological range of the barn owl, while above 2.5 kHz more than one peak and, thus, ambiguities will occur (see Wagner et al. 2007). Therefore, optimality models have identified 2.5 kHz as an important corner frequency (Harper and McAlpine 2004). We used stimuli 4 and 5 to find out more about the owls' ability to strike targets above or below this corner frequency. The localization error in response to these two stimuli was clearly larger (Fig. 3j–o) than for the baseline condition (Fig. 3a–c) as demonstrated by the KS2D2S test ($P < 0.05$ in all comparisons and all owls). The scatter in the landing positions in response to stimuli 4 and 5 was similar or even

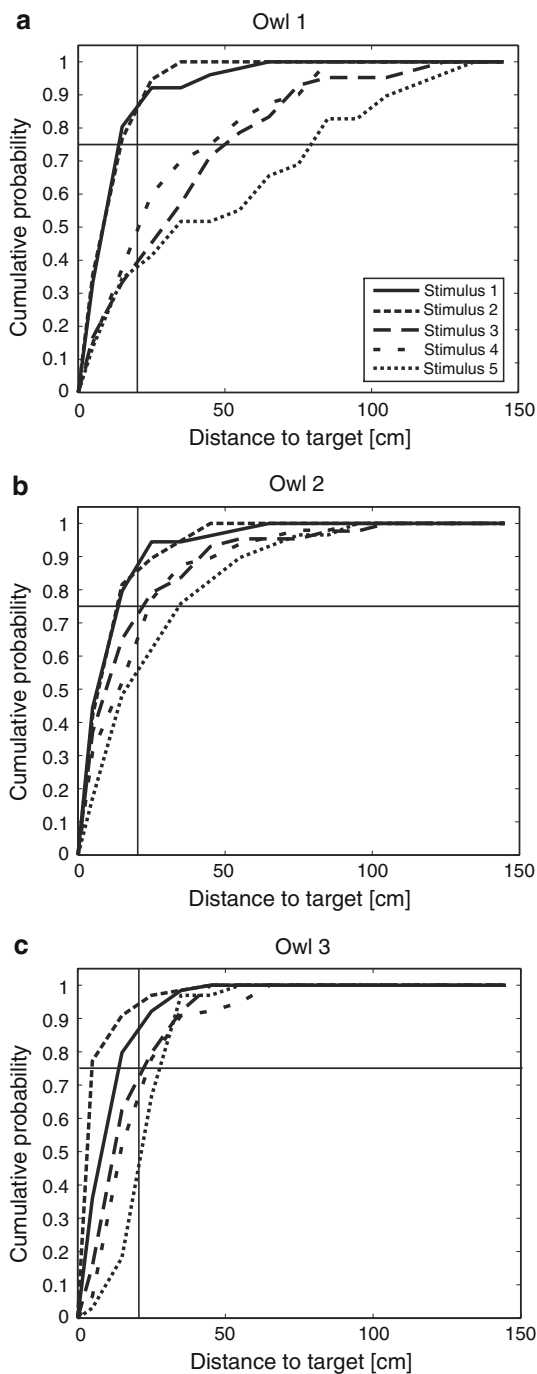


Fig. 4 Cumulative probability distributions of striking success and striking distance. The cumulative probability distributions are given for each owl (a–c) and stimulus (see inset in a). For comparative reasons, two solid lines are drawn: the horizontal line indicates 75% success level while the vertical line indicates the maximum distance of 20 cm from the target center

larger than the scatter in response to stimulus 3 (Fig. 3g–o). This held especially for stimulus 5 and is reflected in the larger size of the ellipse compared with stimulus 3 (Table 2). As the area of the ellipse was increased, the

number of hits within the 20 cm radius was decreased for all owls (Fig. 4a–c; Table 2) when the responses to stimulus 5 were compared with the landings elicited by stimulus 3, albeit this decrease was marginal for owl 1 (Table 2). Although differences between stimuli 4 and 5 seem obvious by looking at Figs. 3 and 4, most of them turned out to be not significant.

With respect to the *x* and *y* directions, the responses to stimuli 4 and 5 were typically less precise when compared with baseline and the effect was more pronounced in the *y*- than in the *x*-direction (Fig. 3; Table 2).

Influence of bandwidth and center frequency

Stimuli 2, 4 and 5 had similar relative BWs in terms of octaves, but different CFs. A comparison of the landing behavior with these three stimuli may thus help to find out whether BW or CF has more influence on target-approaching behavior. In all owls, the number of hits within the 20 cm radius decreased from the stimulus with the highest CF (stimulus 2) to the stimulus with the lowest CF (stimulus 5), with the data for the medium CF (stimulus 4) lying in between (Table 2). This indicated an influence of CF at a given relative BW.

In a second step we plotted the area of the standard ellipse as a function of CF for all five stimuli tested (Fig. 5). The coefficient of determination was higher when the areas were sorted with respect to CF than when they were sorted with respect to BW. For example, in owl 1, 83% of the variability could be explained by a linear regression, if CF was used as the independent variable, while only 51% were explained using BW as the independent variable. Similar relations held for the owls 2 and 3. The upper cutoff frequency was a similarly good

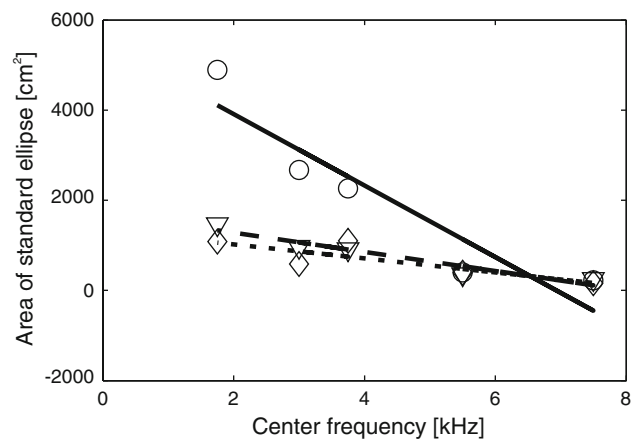


Fig. 5 Correlation of center frequency and striking precision. The area of the calculated standard ellipse for each stimulus is plotted as a function of CF (owl 1: open circle, owl 2: inverted triangle and owl 3: diamond). Note the decreasing size of the standard ellipse with increasing CF of the stimulus

predictor as CF, while the predictive value of the lower cutoff frequency was close to zero.

Effects of stimulus frequency on pre-takeoff latency

Response latency may be a useful indicator for the difficulty of a task. We used the video material to determine the owl's pre-takeoff latency, the delay from the onset of the stimulus to the takeoff from the perch (Fig. 6). After the stimulus was switched on, the owls waited for some time, often first looking into the direction of the sound source, before they took off. Once airborne, the owls always approached the target directly. Pre-takeoff latencies showed a big variation between owls as well as between stimuli. The shortest latencies were in the range of a few hundreds of milliseconds, while the longest latencies were around 20–25 s. Note that there were no latencies between 25 s and our criterion for terminating the trial after 90 s. There were six trials that were terminated without the owl taking off.

The pre-takeoff latencies in response to stimulus 1 will again be used as a reference. Median latencies were around 4–5 s in all three birds (Fig. 6) with no statistical differences between the birds (Kruskal–Wallis test, $P = 0.278$). When latencies measured in response to the high-frequency stimulus 2 were compared with the baseline, no differences

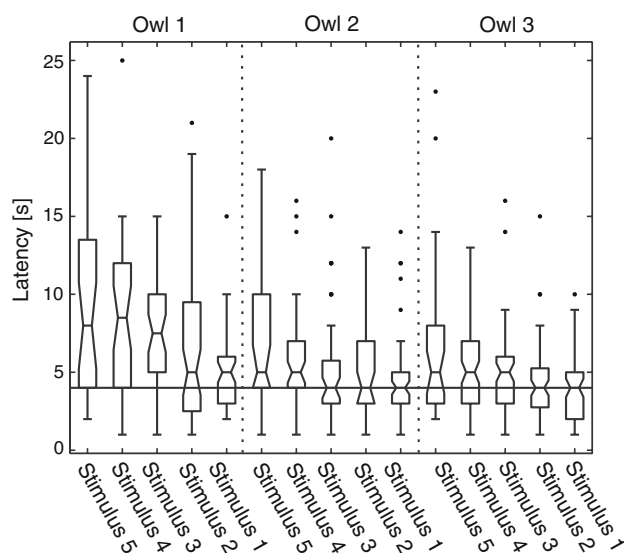


Fig. 6 Effects of stimulus frequency on pre-takeoff latency. The different distributions of the owl's latencies are quantified in the box-and-whisker plot in terms of medians. The tops and bottoms of each box represent the upper (75%) and lower (25%) quartile of the samples, respectively. The line in the middle of each box indicates the sample median. The whiskers extend to at most 1.5 times the interquartile range. All observations beyond the whiskers (black dots) are considered as outliers. The solid horizontal black line indicates 4 s of pre-takeoff latency for comparative reasons. As the CF of the stimulus was increased, the median latencies of the owls gradually decreased

were observed in any owl (U tests, all $P > 0.05$). On the other hand, in each owl, the pre-takeoff latency in response to stimulus 5 was higher than the baseline (U tests, $P < 0.05$ for each owl). The comparisons of the latencies measured for the other stimuli and the baseline were typically not significant, with the exception of owl 1 (stimulus 3 and baseline, U test, $P < 0.001$) and owls 1 and 3 (stimulus 4 and baseline, U tests, $P < 0.05$).

Other effects on striking behavior

The ramps holding the loudspeakers in our free-flight room were positioned at three different distances from the perch: 2.35 m (near), 2.85 m (middle) and 3.35 m (far). The overall cumulative probability distributions were virtually identical for all three distance conditions for owls 2 and 3, while some differences for the three distances seemed obvious in the responses of owl 1 (Fig. 7a–c; Table 3). Nonetheless, no statistically significant differences were detected in the overall accuracy of the landing positions (Kruskal–Wallis tests, all $P > 0.05$).

We next compared the striking distances separately for each owl and stimulus at the three ramp positions. Striking accuracy and striking precision did not depend on ramp distance ($P > 0.05$, Kruskal–Wallis tests and Levene tests, respectively). The same held for the x -direction, while some effect of ramp distance was observed in the y direction, if the stimulus contained only low frequencies.

Finally, we tested whether the owls had a bias in the x -direction. Indeed, owl 1 tended to land too close to the midline for all stimuli. In owl 2, such an effect was only observed for the baseline stimulus but not for the other stimuli. In the landing positions of owl 3 no such bias was present.

Discussion

We investigated the effects of stimulus frequency and BW on striking accuracy, striking precision and pre-takeoff latency in three free-flying barn owls. Stimuli were parameterized by distance. We observed a clear influence of center frequency on striking behavior and response latency. We shall first discuss these main findings with respect to the literature on free-flight behavior and then relate the outcomes with respect to frequency to the known cues used by the barn owl for sound localization. Finally, we compare our findings regarding the neural representation of sound-localization cues.

The baseline condition with respect to other free-flight studies

We established a baseline condition for striking behavior during ongoing sound stimulation based on a broadband

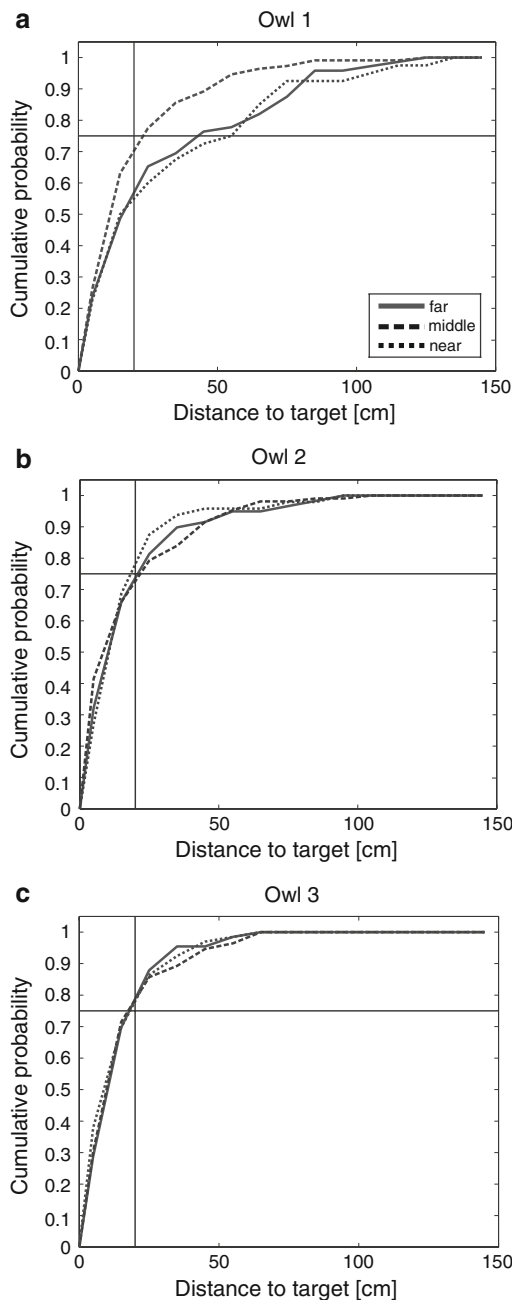


Fig. 7 Effects of perch-target distance on striking accuracy. For each owl (a–c), cumulative probability distributions of striking success are pooled across all frequencies for each distance between perch and target. The horizontal line indicates 75% success level, while the vertical line indicates a distance of 20 cm from the target. The inset in a shows the line symbols for the three distances tested. Whereas owl 2 (b) and owl 3 (c) showed almost no difference in the overall cumulative probability distribution to the three different spacings between perch and target, owl 1 (a) had a slightly better performance for the near most position of the target than for the other targets

stimulus that covered most of the owl’s hearing range, which extends from about 100–11,000 Hz (Dyson et al. 1998). In this baseline task, all owls would have been able to catch a stationary target from a distance of

Table 3 Quantitative data on the effects of stimulus frequency on perch-target distance

Owl	Ramp position	Hits (%) at 20 cm	Distance (cm) at 75%
1	Far	57	43
	Middle	70	23
	Near	55	55
2	Far	74	21
	Middle	73	22
	Near	78	18
3	Far	79	18
	Middle	79	18
	Near	78	18

Given are the cumulative probabilities of hits within the target area (20 cm) and the maximum distance of the landing positions at 75% hits for the cumulative probability distributions in Fig. 7

approximately 3 m in more than 80% of the cases (Fig. 4a–c). This observation is consistent with reports on striking success in a simulated grassland-type habitat (Derting and Cranford 1989). Moreover, our data on striking success rate are in accordance with an earlier study (Shiffermann and Eilam 2004) that reported a striking success of 90% for stationary prey but only of 21% for moving prey. A reduced rate of striking success was also observed in our setup if the sound was switched from one loudspeaker to a second one after the owl had left the perch (Hausmann et al. 2008).

Effects of frequency composition

Our data are generally consistent with earlier reports by Payne (1962; 1971) and Konishi (1973a, b): barn owls were more successful in striking high-frequency targets than low-frequency targets. However, our owls did not refuse to fly toward sound sources emitting signals having only energy below 5 kHz as was reported by Payne (1971). Konishi (1973a) used noise sources with one CF (7.5 kHz) and varying BWs (1–4 kHz). We additionally varied CF and observed that, indeed, the CF of a sufficiently broad stimulus (about one octave) was a better predictor for the owls’ behavior than BW. Within the range of frequencies tested (1–10 kHz), the upper cutoff frequency explained the observed variability similarly well as CF, while the lower cutoff frequency had no predictive value for striking behavior.

The lowest frequency tested by Konishi (1973b) was a 3 kHz pure tone. We also tested stimuli having only energy at frequencies below 2.5 kHz (stimulus 5). Thus, our data also provide novel evidence that barn owls are even capable of successfully striking a target that exclusively emitted frequencies below 3 kHz. Our results remain inconclusive whether the important border for the low-

frequency limit is at 2.5 kHz as suggested by optimality models (Harper and McAlpine 2004) or at higher frequencies. We could not find large and consistent differences in landing position or pre-takeoff latency between stimuli having upper cutoff frequencies of 2.5 and 5 kHz. Since a linear model of precision as a function of CF explained most of the variance in the landing positions, the decrease of striking position with frequency content seemed smooth and not all-or-nothing.

Langemann et al. (2005) found that in a Go/NoGo procedure, barn owls were able to discriminate broadband signals only slightly better than narrowband signals as long as these signals contained uncorrelated spectral components. As soon as temporal correlation was added, the broadband advantage became stronger. We were surprised that an increase in BW at low-frequency stimulation (stimulus 3 compared with stimuli 4 and 5) did not improve the owls' localization accuracy and precision in significant ways for all owls as might be deduced from earlier studies (Saberri et al. 1999).

Relation to known cues of sound-localization behavior in the barn owl

Barn owls use ITDs for localization of targets in azimuth, corresponding to the x -direction in our set up (Poganiatz et al. 2001). ITD is largely independent of CF within the range tested in this study (Campenhausen and Wagner 2006). Owls made localization mistakes when the BW of a 5 kHz sound was below 3 kHz (Saberri et al. 1999). These mistakes are due to phase ambiguities present at high frequencies. Likewise, phase ambiguity disappeared in the responses of cells of the inferior colliculus when the signal BW exceeded about 3 kHz (Mazer 1998). As expected from these data, no significant differences in azimuthal localization were found when the owls had to approach wideband signals with high-frequency energy. The responses to the stimuli containing only low frequencies were impaired. Since the ITD range does not change much for low frequencies (Campenhausen and Wagner 2006), this increase in localization error does not depend on the available ITDs. Two reasons might be attributable for the errors in precise localization: first, for frequencies below 4 kHz, the interaural canal is less effective in attenuating sounds (Moiseff and Konishi 1981) and second, ITD tuning curves are no longer arranged in columns in the inferior colliculus for these low frequencies (Wagner et al. 1987, 2007).

We observed an influence of stimulus frequency on the localization precision in the y -direction, which corresponds to a change in elevation in our setup. In barn owls, ILDs are a very important cue for localization in elevation (Moiseff 1989a, b; Poganiatz and Wagner 2001) and ILDs clearly depend on frequency (Keller et al. 1998; Campenhausen

and Wagner 2006). Therefore, the observed change in localization behavior was not surprising.

In the baseline condition, the owls tended to undershoot the target. This is reminiscent of classical head-turning experiments, where barn owls showed an analog effect. If the stimuli came from more than 10° – 30° up or down of the gazing direction, the localization error rose because the owls did not turn their heads far enough (Knudsen et al. 1979; Moiseff 1989b; Poganiatz and Wagner 2001). In free-flight behavior landing short may be useful, because the owl might be able to launch a second attack more easily, if it does not have to turn around as it would need, if it landed long. With the low-frequency stimuli the owls tended to land short for the most distant target, while they landed wide for the closest target. The reason for this is not known. It might be that the owls memorized the mean target position and used a strategy to land at the mean position if the task was difficult.

Relation to neural representation of sound sources

Our findings are consistent with the neural representation of high frequencies in the midbrain pathway mediating precise sound localization (Knudsen et al. 1993; Wagner 1993; Saberri et al. 1999) and lacking the neuronal representation of frequencies below 2.5 kHz in the external nucleus of the inferior colliculus (Knudsen and Konishi 1978; Wagner et al. 2007). The observations made in this study argue for a smooth transition of important frequencies between 2.5 and 5 kHz for barn owls to approach a distant target. This is supported by another study from our laboratory (Wagner et al. 2007). These authors did not observe a break in the representation within this frequency range in the time-sensitive subnuclei of the IC. Neuronal processing of frequencies below 3 kHz takes place in the forebrain pathway originating in the central nucleus of the IC (ICC) (Proctor and Konishi 1997; Cohen et al. 1998; Arthur 2004) and innervating neurons in the nucleus ovoidalis, the field L and the auditory arcopallium (Cohen et al. 1998). In these nuclei, neurons have been shown to be sensitive to best frequencies below 3 kHz (Cohen and Knudsen 1996; Perez and Pena 2006; Vonderschen and Wagner 2009). However, there is no map of space in the forebrain as there is in the midbrain (Cohen and Knudsen 1995, 1999; Knudsen and Konishi 1979). Therefore, the forebrain pathway is thought to be involved in coarse rather than precise sound localization as well as in top-down control of space specific units in the OT (Winkowski and Knudsen 2006; Vonderschen and Wagner 2009). This is consistent with our observation of an increase in localization error for stimuli containing only low frequencies, because these are only processed in the forebrain and not in the midbrain pathway.

Effects of stimulus frequency on pre-takeoff latency

We observed that our barn owls took more time to process low-frequency signals prior to takeoff than baseline. This prolonged pre-takeoff latency during low-frequency stimulation might be due to the difficulties of the extraction of spatial information emitted by the sound source. Head saccades have typical latencies around 100–200 ms (Knudsen and Konishi 1979; Wagner 1993), which is much shorter than the pre-takeoff latencies measured in our free-flight experiments. Generally, if owls first hear a sound, they turn toward it with their head and body and do not immediately take off. This is presumably an adaptive behavior to increase hunting success. The long response latencies in our experiments might reflect this natural behavior and include cognitive elements like working memory (Cohen and Knudsen 1996; Knudsen and Knudsen 1996) as well. Additionally, internal factors such as motivation and experience could also contribute to this observation and play an important role for owls catching living prey (Edut and Eilam 2004). In line with this consideration, the processing through the forebrain pathway would also require longer latencies, although the latencies we observed were much longer than the additional processing time required by the forebrain. Therefore, we suggest that the longer response latencies for the low-frequency stimuli mainly reflect task difficulty. It is generally known that response latency is a good indicator for task difficulty. Nodal et al. (2008) showed in a study on sound localization in ferrets an increase in response latency with decreasing stimulus duration. Therefore, the significant longer latencies in the present study to approach the low-frequency target (stimulus 5) compared to baseline might reflect the increased difficulty to extract the spatial position of the sound source from the low-frequency signal.

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