

In-flight corrections in free-flying barn owls (*Tyto alba*) during sound localization tasks

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SUMMARY

Barn owls localize a stationary auditory target with high accuracy. They might also be able to hit a target that is intermittently moving while the owl is approaching. If so, there should be a critical delay before strike initiation, up to which the owl can adapt its flight path to a new stimulus position. In this study, this critical stimulus delay was determined in a three-dimensional free-flight paradigm. Barn owls localized a pulsed broadband noise while sitting on a perch in total darkness. This initial signal stopped with the owl's take-off and an in-flight stimulus (target sound), lasting 200 ms, was introduced at variable time delays (300–1200 ms) during the approximate flight time of 1300 ms. The owls responded to the in-flight signal with a corrective head and body turn. The percentage of trials in which correction turns occurred (40–80%) depended upon the individual bird, but was independent of the stimulus delay within a range of 800 ms after take-off. Correction turns strongly decreased at delays ≥ 800 ms. The landing precision of the owls, defined as their distance to the in-flight speaker, did not decrease with increasing stimulus delay, but decreased if the owl failed to perform a correction turn towards that speaker. Landing precision was higher for a short (50 cm) than for a large (100 cm) distance between the initial and the new target. Thus, the ability of barn owls to adapt their flight path to a new sound target depends on the in-flight stimulus delay, as well as on the distance between initial and novel targets.

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Key words: barn owl, auditory, hearing, sound localization, flight, three-dimensional, target approaching, behavior.

INTRODUCTION

Barn owls (*Tyto alba*) have developed many auditory adaptations to nocturnal hunting. For example, they have asymmetrically arranged ears (Knudsen et al., 1984; Wagner, 2002) that enhance spatial localization and a facial ruff that is extremely directionally sensitive (Brainard et al., 1992; Campenhausen and Wagner, 2006; Coles and Guppy, 1988; Haresign and Moiseff, 1988; Keller et al., 1998). These features help the owl to catch prey in complete darkness (Konishi, 1973a; Konishi, 1973b; Payne, 1962). In a natural environment, prey animals do not necessarily emit ongoing noises. Hence, striking barn owls must be able to localize short, interrupted stimuli. Even though owls favor swooping on stationary prey, or at least have higher success rates on stationary prey (Ilany and Eilam, 2008), they need to adapt their trajectories during flight with respect to the target if the prey is moving. Thus, it is interesting to investigate whether barn owls are able to strike at a sound target in darkness, if the stimulus stops with the owl's take-off and reappears after a varying time delay (in-flight stimulus delay) at a horizontally displaced spatial position (Konishi, 1973a; Konishi, 1973b). Such a task requires fast processing of auditory stimuli, as well as behavioral adaptation to changing target positions.

The ability to hit a target is crucially influenced by the ability to localize the target. Auditory targets appearing close to the midline are being localized by barn owls with an accuracy of at least 3 deg., if the bandwidth of the signal is wide enough and covers the behaviorally relevant range of about 5.5 to 9.5 kHz (Bala et al., 2003; Bala et al., 2007). With increasing eccentricity of the sound source, the accuracy decreases, especially for the elevational component of the target (Knudsen et al., 1979). In free-flight experiments, where

the owl had to strike a distant target, striking accuracy in the horizontal plane was 5 deg., whereas it was 7 deg. in the vertical plane (Konishi, 1973b).

As the eyes and ears of the owl are virtually immobile, barn owls perform a saccadic head movement in the direction of broadband stimuli (Knudsen et al., 1979) to bring the target into sensory focus. This natural saccadic response was exploited as a means for localization precision mainly in experiments in which owls remained sitting on a perch and did not fly ('stationary setups') (Bala and Takahashi, 2000; Bala et al., 2003; Knudsen et al., 1979; Poganiatz and Wagner, 2001; Poganiatz et al., 2001; Saberi et al., 1999). In these experiments, no impairment in sound localization was observed when the stimulus was as short as 75 ms (Knudsen and Konishi, 1979), supporting the notion that barn owls may use an open-loop strategy for sound localization. Open loop refers to experimental conditions in which the reaction time (here the latency until the head turn starts) exceeds the stimulus duration, which prevents ongoing feedback; under closed-loop conditions, the stimulus duration exceeds the reaction time (see Knudsen et al., 1979). We created an open-loop scenario by stopping the stimulus at take-off and let it reappear after a variable in-flight delay.

Experimental setups using head turns are appropriate to investigate the basic principles and relevant parameters for sound localization, but do not take into account the total behavioral sequence of target striking. Recently, Shiffman and Eilam, Edut and Eilam, and Ilany and Eilam studied how owls strike at moving prey (Shiffman and Eilam, 2004; Edut and Eilam, 2004; Ilany and Eilam, 2008). Approaching a distant target requires a higher effort than does performing a ballistic head saccade in the direction

of a sound source. Free-flight tasks therefore provide more natural conditions for the investigation of localization performance. Payne and Konishi were the first to conduct such studies (Payne, 1962; Konishi, 1973a; Konishi, 1973b). These authors exposed barn owls to tonal or noise stimuli and determined the influence of parameters such as the bandwidth and the duration of the stimulus on striking precision. Konishi found that three noise bursts, each of 50 ms duration with a silent interval of 300 ms, enabled target striking equally as well as with ongoing stimulation (Konishi, 1973b). These findings led to the hypothesis that barn owls are able to adapt their flight path to a new target location as a reaction to short stimuli provided during flight, even if the stimulation is interrupted.

Although Konishi (Konishi, 1973b) gives insights into the barn owl's general ability to strike a distant target, it is not clear whether target striking resembles an all-or-none law or gradually decreases depending on the stimulus parameters. The present study is the first to measure in-flight correction in a free-flying owl. We investigated whether the time delay of an in-flight stimulus is a crucial parameter for accurate target localization when in-flight corrections are required. In addition, we wanted to learn at which threshold delay the owl is no longer able to adapt its flight path to a new target sound during flight.

MATERIALS AND METHODS

Animals

Three adult, captive-bred, American barn owls (*Tyto alba pratincola* L.) participated in the experiments. Care and treatment of the owls was in accordance with the guidelines for animal experiments as approved by the Landespräsidium für Natur, Umwelt und Verbraucherschutz Nordrhein Westfalen, Recklinghausen, Germany, and complied with the NIH Guide for the use and care of laboratory animals. All owls were used to perform free-flight experiments for at least one year. Their initials (H, W and Q) will be used for identification. The owl's weight was measured before and after daily experimental sessions. The owls were held at approximately 90% of their free-feeding weight. They were typically fed only during the daily experimental session, unless they did not receive enough food to maintain their criterion weight. A session consisted of 6 to 20 trials depending on the owl's motivation, and continued until the owl refused to fly for at least 5 min.

Apparatus and stimuli

All free-flight experiments were carried out in a sound-proof room of 4.2 m × 3.2 m × 3.2 m (length × width × height, Fig. 1). Sound attenuation was achieved by covering the walls, ceiling and floor with planar and pyramidal foam. Two devices, each containing two shielded loudspeakers, could be placed at variable horizontal distances (2.35 m, 2.85 m and 3.35 m) to a wooden perch (1.75 m above the floor; Fig. 1). The speakers formed a row approximately perpendicular to the owl's flight direction and were numbered from LS1 to LS4, with LS1 being the outermost left speaker and LS4 the outermost right speaker, seen from the owl's perspective. The solid angles from the perch to the speakers varied inherently with the resulting distance that the owl had to fly from the perch to the speaker (Table 1).

The signals consisted of 1–10 kHz broadband noise bursts with 10 ms rise/fall time, either as a pulsed stimulus of 500 ms length and 500 ms silent interval (initial stimulus), or as a single stimulus of 200 ms length (in-flight stimulus). These auditory targets simulated prey location (Konishi, 1973a; Konishi, 1973b) and were presented via loudspeakers (Visaton F8 SC, 80–15,000 Hz) with a

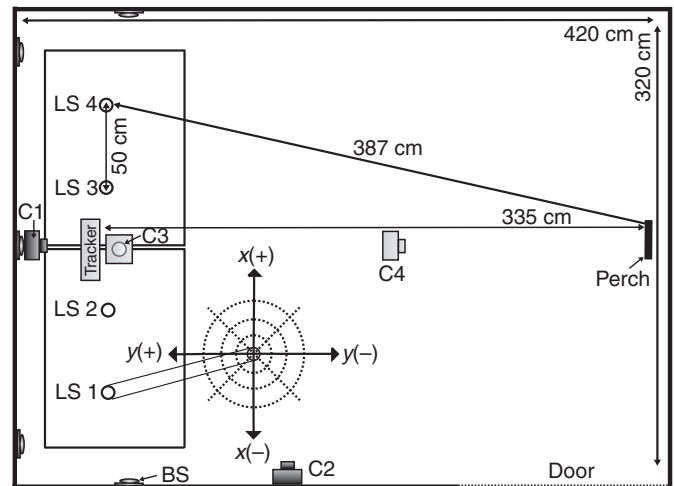


Fig. 1. Schematic of the experimental setup. The room of 4.2 × 3.2 × 3.2 m (length × width × height) was covered with planar and pyramidal foam. Speaker devices contained target loudspeakers LS 1 to LS 4. The two-dimensional horizontal distance to the speaker row was 2.35 to 3.35 m, whereas the linear distance from the perch (owl position) to the speakers was 2.97 to 3.87 m (cf. Table 1). Background speakers (BS) provided masker noise. C1 to C4 are infrared cameras. Cameras C3 and C4 were mounted on the ceiling. Camera C1 was mounted at a height of 25 cm on the wall opposite the perch; camera C2 was placed at a height of 95 cm on the side wall. Tracker, DynaSight head tracking device. Landing positions of the owls as deviation (in cm) from the center of the target LS were plotted in a polar coordinate system as positive and negative x - and y -coordinates, respectively (see inset).

flat frequency spectrum (± 5 dB) in the relevant range from 80 Hz to 15 kHz. An array of five background speakers (Visaton F8 SC, Haan, Germany) in the rear ('target') half of the free-flight room provided an equally distributed noise (1–12 kHz) at 33 dB sound pressure level (SPL) as measured from the position of the owl's perch. The target stimulus was attenuated to 10 dB above the background masker amplitude for any of the 12 possible speaker positions. Sound level was calibrated prior to experimentation for all speaker positions using a sound level meter (Brüel and Kjaer, model 2236, Brüel and Kjaer, Naerum, Denmark) with an accuracy of ± 0.5 dB at the position of the owl's head on the perch in the free-flight room.

A red laser beam (model OLSH 705P, 650 nm wavelength) was mounted above the perch. When the owl was sitting on the perch,

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

Speaker	Distance = 3.35 m	Distance = 2.85 m	Distance = 2.35 m
LS1	-12.2 deg., 3.87	-14.3 deg., 3.45	-17.2 deg., 3.05
LS2	-3.8 deg., 3.81	-4.5 deg., 3.38	-5.5 deg., 2.97
LS3	3.8 deg., 3.81	4.5 deg., 3.38	5.5 deg., 2.97
LS4	12.2 deg., 3.87	14.3 deg., 3.45	17.2 deg., 3.05

Negative angles are in the counterclockwise direction, positive angles in the clockwise direction with 0 deg. straightforward to the owl's line of sight.

The second number is the distance from the perch to the respective loudspeaker (LS) in m. Note that 'distance' in the column headings is given as the two-dimensional horizontal distance between the perch and the row of speakers on the speaker device (see Fig. 1), whereas the distances to the respective speakers are given as linear distances, to take into account the height of the perch.

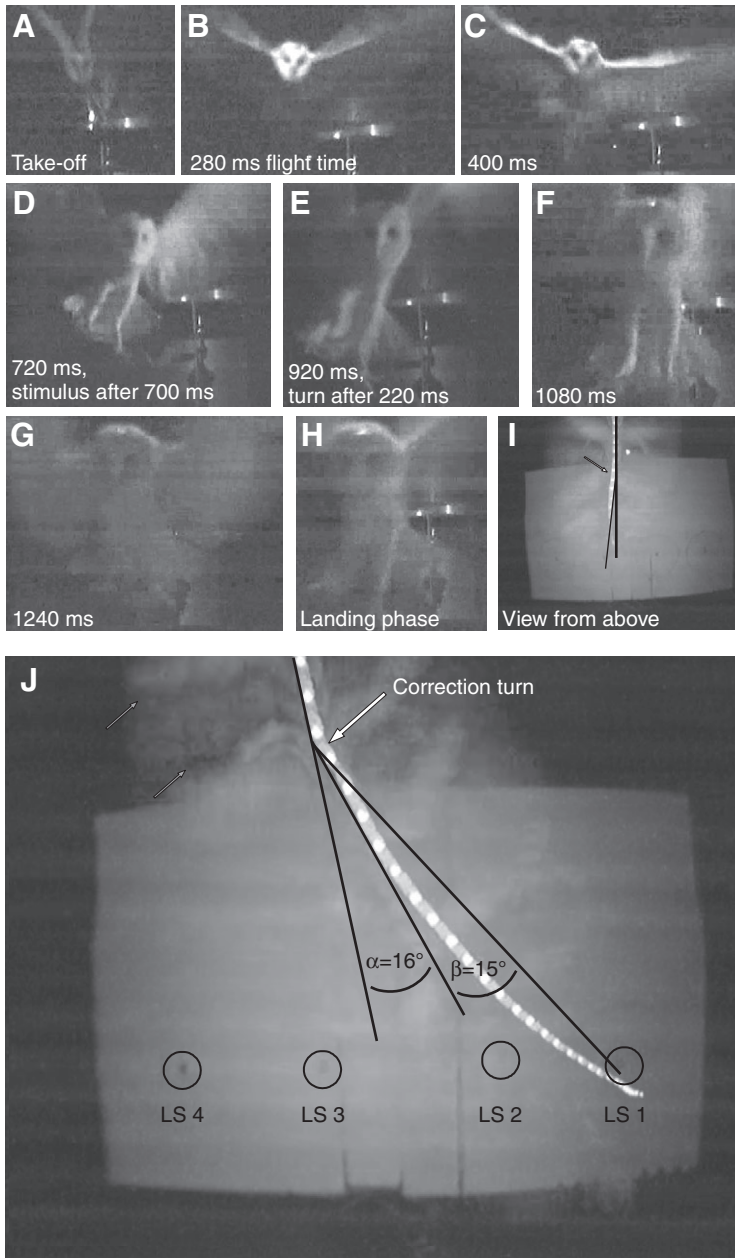


Fig. 2. Typical flight path. (A–H) The head turn movement during a flight is shown in an example with the stimulus sequence LS 3-2, with a 700 ms stimulus delay. (I) The same flight as in A–H shown from above. The individual images of the flight path recorded by camera C1 (Fig. 1, 25 Hz sampling rate) are overlaid. (J) As in I, images of a flight sequence are overlaid. The initial stimulus was emitted by LS 3, the in-flight stimulus by LS 1 with a 900 ms delay. The reflections of the head tracker are visible as a white, dotted line. The body and wings appear as low-contrast shades (small arrows). The positions of the speakers LS 1 to LS 4 are marked with circles. The turning angle, α , in degrees was calculated by extending the lines formed by the head tracker reflections before and after the correction turn, which appears as a sharp discontinuity in the trace of tracker reflections (white arrow). Although the trajectory could be curved, only the first prominent discontinuity corresponded to the saccadic head turn visible in the frontal view (C1) and was used for determination of the turning angle. The remaining (or error) angle β to the target is given as the angular difference between the actual flight trajectory and the extended line to the center of the target speaker. Note that the room is not lit, but the images were recorded with infrared cameras.

the laser beam was directed to the back of its head and was thus prevented from hitting a receiver box below the perch. As soon as the owl left the perch, the laser beam hit the receiver box and triggered a latency counter (the time difference between stimulus onset and the owl's take-off for target striking). Latency was used as an indicator for motivation during experiments, as latency is correlated with an animal's arousal level and motivation (Damos, 1991).

The flight chamber was monitored from four different positions (Fig. 1) using infrared cameras with a 25 Hz frame rate (ELV, Leer, Germany). Visual monitoring allowed the observation of the owl's performance and landing position in real time. The assembly of cameras gave an almost complete picture of the whole flight sequence. However, none of the individual cameras captured the complete flight sequence, including take-off and landing, in every case. The position of the owl's head was recorded using a tracking system (DynaSight, Origin Instruments Corporation, Grand Prairie,

TX, USA) that allowed for three-dimensional tracking at a 65 Hz sampling rate. The limited range of the DynaSight system restricted head tracking to the target half of the free-flight room, i.e. during the landing phase of the owl. A reflector foil, attached to the upper side of a $1.5 \times 1.5 \times 3$ cm (length \times width \times height) large polystyrene cube, served us as reference target. This cube was fixed at the owl's head. An infrared light beam emitted from the DynaSight tracker was reflected back to the sensor by the foil on the cube. The reflection of the cube was also visible on the video as a bright dot (cf. Fig. 2, and Movies 1 and 2 in the supplementary material). The tracker measured the horizontal (x) and vertical (y) positions of the reflector cube, which were analyzed offline (GraphPad Software). As soon as a x -, y - and z -data point did not deviate for more than 1 cm from the following data point, these coordinates were defined as the owl's landing position, which was confirmed by comparing them with the owl's position in the top view of the landing (camera C3). Note that this measurement could not be used to measure flight

duration, because the DynaSight tracker did not cover the owl's position at take-off.

Training

The owls learned the paradigms within 15–20 days by operant conditioning. In the early training phase, a piece of meat was placed in the illuminated room on top of one of the target loudspeakers during isochronous emission of ongoing broadband noise from the target speaker. Once the owls associated the auditory stimulus with the food reward, the illumination was reduced until the owl struck the target speaker in complete darkness (no light detectable with a luminescence meter). The owls remained on the floor after landing. Turning on a pale white light diode (LED) mounted above the perch triggered the return flight. In the following trials, food was provided only after the owl flew back to the perch. During later experiments, the owl received a small piece of chicken meat as reward for successful task accomplishment (i.e. the owl flew in the direction of the target speaker, waited for the LED to turn on, then returned to the perch) before the next trial was initiated.

Procedure

The task required that the owl should localize the initial stimulus emitted from one of four target speakers at variable distances to the perch. The distance from the speaker devices to the perch was varied only between daily experimental sessions, and not within a session. The average flight duration for the most distant speaker device position (3.35 m) was determined in preliminary experiments and confirmed in the actual experiments to be about 1300 ms. After the owl left the perch to strike the target, the in-flight stimulus was introduced with a variable delay of 300, 500, 700, 900, 1000, 1100 or 1200 ms. Stimulus delays were randomized within a daily experimental session.

Either LS 2 or LS 3 emitted the initial stimulus (Fig. 1, Fig. 2J). The active speakers were chosen in random order. The in-flight stimulus appeared from any of the four loudspeakers, also chosen on a random basis. This resulted in eight different stimulus sequences, which ensured that the owl could not predict whether the in-flight stimulus would arise left or right from the direction of the initial stimulus. In the following, the stimulus regime (speaker sequence) is noted by separating the location of the initial stimulus from the location of the in-flight stimulus by a hyphen (e.g. LS 2-3).

Although three different loudspeaker device positions were used during experiments to prevent the owls from memorizing speaker positions, it is mainly the flights to the position with maximum distance (3.35 m) from the perch that are taken into account in the present study. This particular distance was chosen because it provided a longer flight time and thus a maximum of testable delays. Each speaker sequence was tested in at least 10 trials per delay. At 1100 and 1200 ms delays the owls did not perform any correction turn in initial trials. These delays were not tested further in the course of the experimental series.

Data analysis

The timing device measuring the in-flight stimulus delay started with the activation of the laser trigger caused by the owl's take-off. Head turn latency after the onset of the in-flight stimulus was defined as the period between the onset of the in-flight stimulus (the first video frame in which the laser beam was no longer visible on the back of the owl's head) and the first video frame in which the owl had started to turn its head in the direction of the in-flight target speaker. For the analysis of head turn latencies, the flight time

between take-off and completion of the head turn was determined with 40 ms accuracy, owing to the frame rate of the cameras being 25 Hz. The in-flight stimulus delay, however, was provided with an accuracy of about 1 ms. The delay was subtracted from the flight time calculated from the video recordings. Hence, if the flight time was, for example, 800 ms, and the in-flight stimulus was provided with 700 ms delay, the head turn latency was determined to be 100 ms. Therefore, the head turn latency could be determined with higher accuracy (± 20 ms) from the video recordings.

The head turn could be observed best on the video recordings from a frontal or sideward perspective (cameras C1 and C2; Fig. 1; Movie 1 in the supplementary material), as a sudden change of the owl's eyes and beak position (Fig. 2D,E), followed by a change of the body position into the direction of the in-flight target (the correction turn). Only the video recordings from C1 and C2 captured the flight from take-off until the last phase of the flight. Some of these video recordings captured the stretching out of the owl's feet immediately before landing. An exemplary flight path from owl W, seen from the frontal camera's (C1) perspective, is shown in Fig. 2A–H (see also Movie 1 in the supplementary material). The image sequence shows the head turn movement during a flight where LS 2 emitted the initial stimulus and the in-flight stimulus came from LS 3 with 700 ms delay.

In contrast to head turn latencies, the angles of the head and body turns were calculated based on the video recordings that showed the last few hundred milliseconds of the owl's flight path from above the speaker devices (camera C3, Fig. 1; see Movie 2 in the supplementary material). For this purpose, the images of a flight sequence were overlaid and the position of the head tracker was analyzed, i.e. the direction of the flight trajectory before and after the owl performed a correction turn. In the overlaid images recorded from camera C3, the discontinuity (bending) of the line formed by the head tracker reflections (light dots, Fig. 2I) reflects the change of the owl's trajectory. Another example of this bending is given in Fig. 2J. In this particular trial, LS 3 emitted the initial stimulus and LS 1 provided the in-flight stimulus with a delay of 900 ms. After the in-flight stimulus, the owl performed first a head turn, with a latency of 200 ms, towards the novel speaker. This head turn was succeeded by a turn of the body resulting in a curvature of the flight path. The line through the last three reflections of the head tracker prior to the characteristic bending of the trajectory (cf. Fig. 2J, white arrow) was defined as the initial flight direction. The initial flight direction in the sample flight is indicated by the first three white dots at the top of Fig. 2J. The altered flight direction, defined by the line through the first three reflections of the head tracker after the sharp bending, differed from the original flight direction by 16 deg. (angle α , Fig. 2J). Angle α , measured between the lines through initial and altered flight direction, is referred to as the turning angle. Although the flight path was occasionally curved in the last part of the flight (see Fig. 2J), we analyzed only the initial curvature (white arrow) because there was only one prominent head turn (as in Fig. 2D,E) visible in the recordings from camera C1. A remaining angle (β) of 15 deg. would have been necessary in order to hit the center of the target speaker, which was defined as the error angle (Fig. 2J).

The turn of the head was clearly visible from the frontal camera perspective (cf. Fig. 2D,E) and allowed the determination of head turn latencies. By contrast, the trace of head tracker reflections in the top view results from both the head turn and the following change of trajectory, which incorporates a body turn. Consequently, head and body turns were segregated for the calculation of head turn latencies, but not for the calculation of turning angles. For some

target positions, the owl flew out of sight during the actual landing, which did not influence the analysis of the head turning latencies but which did prevent calculation of the total flight time in most trials. It is not likely that further head turns occurred during this very last flight phase, as no further prominent bending of the flight trajectory (as visible in Fig. 2J, white arrow) was observed in the top view (camera C3) of the landing phase.

The percentage of trials in which correction turns occurred, calculated as the proportion of the absolute number of trials with differing initial and in-flight target speaker at the given stimulus delay, were analyzed for significant differences between two in-flight stimulus delays or between two owls at the same stimulus delays using Fisher's Exact Test (two-tailed, 95% confidence interval). Whenever two sample groups, like turning latencies, were equally distributed (as indicated by a Kolmogorov-Smirnov normality test), a two-tailed *t*-test (95% confidence interval) served to test for significant differences between them. A Mann-Whitney test (two-tailed) was used if the data samples were not evenly distributed, and a one-sample *t*-test (95% confidence interval) if only one data sample was available in one of the two sample groups.

For analysis of the landing precision, the distance (in cm) from the landing position to the target loudspeaker was calculated from the *x*- and *y*-coordinates (horizontal and vertical deviation) that the DynaSight tracking system recorded. The *x*- and *y*-coordinates were transformed into a scalar distance by unit vector conversion:

$$|v| = \sqrt{x^2 + y^2}, \quad (1)$$

where *v* is the resulting distance, *x* is the horizontal deviation (in cm) and *y* is the vertical deviation of the owl's landing point from the center of the target speaker. For an analysis of angles, the landing positions were transformed into degrees by trigonometric transformation.

To test whether the landing positions were evenly distributed around the center of the target speaker, a modified [by Fasano and Franceschini (Fasano and Franceschini, 1987)] KS2D1S test (Kolmogorov-Smirnov two-dimensional distributions and one sample) was used, and a two-sample KS2D2S test (Kolmogorov-Smirnov, two dimensions, two samples) for comparison of two different samples.

With the help of Kuiper's test, it was possible to calculate whether the angles were equally distributed, and to find out whether significant differences occurred between the angle distributions of two owls at one parameter, or between the data of one owl at two stimulus parameters.

RESULTS

Data were obtained from three owls over a period of 11 months, including training sessions. From a total of 2247 flights, 815 flights were obtained from owl H, 720 flights from owl W and 712 flights from owl Q.

The owls pointed their heads into the direction of the initial stimulus while sitting on the perch. After a mean pre-flight latency, i.e. the time span between stimulus onset and take-off, of 10–17 s, they left the perch to strike the target. If the initial and the in-flight stimuli were not emitted by the same speaker, the owl turned its head and body towards the novel target speaker in a certain percentage of trials depending on the in-flight stimulus delay.

Pre-flight latencies were assumed to be indicative of the owl's motivation, which might influence its performance. The distribution of the pre-flight latencies was, therefore, tested for significant differences between trials with and without correction turns, or

between the three owls. The latencies were not normally distributed and varied within a daily session; the standard deviation was in the range of the overall mean latency. Owl H responded significantly ($P \leq 0.009$) faster in trials with correction turns (latency 10.52 ± 7.94 s, mean \pm s.d.) than in those without correction turns (13.08 ± 10.31 s). For owl W (with turns, 17.41 ± 11.79 s; without turns, 16.63 ± 11.92 s) and owl Q (with turns, 16.69 ± 11.91 s; without turns, 16.83 ± 11.91 s), this was not the case. In summary, variation within a session with a particular owl was larger than differences between the owls. This was also the case for most other parameters studied. Therefore, the data for the three birds were pooled for most of the following analyses.

We used the turning of the owl's head in the direction of the target speaker as an indicator for a correction turn, as it always preceded a change of the owl's trajectory (see Materials and methods). In order to quantify the adaptive change of the flight path, we analyzed the percentage of trials in which the owl performed a correction turn, as well as the head turn latencies and the angular extent of the change in the trajectory. Trials in which the owls flew out of the camera's sight, left the perch prior to stimulation, or showed signs of irritation due to disturbing noises from outside the experimental chamber were excluded from the analysis. In total, we were able to analyze 1936 valid trials. One trial for owl W (with a correction turn) was captured in the video recordings, but was not tracked by the DynaSight system. This trial was included in the analysis of head turn latencies, but not in the analysis of landing precision.

Correction turns and hit rates

The effect of displaced target locations was compared with the situation in which the target position remained constant. We used the loudspeaker sequences LS 2-2 and LS 3-3 as a control for the owl's striking precision for in-flight stimulation that did not require correction (483 trials). Under these control conditions none of the owls performed a head turn. Here, the owls landed with mean distances of 21.29 cm (owl W, 152 trials), 22.19 cm (owl Q, 168 trials) and 25.20 cm (owl H, 163 trials) to the center of the target speaker. No significant differences were found for varying stimulus delays. Hence, when no correction turn was required, the owls achieved a mean landing precision of around 20 cm, which can be considered as a 'baseline' for striking accuracy in the present paradigm.

In 634 out of 1453 trials (rate of correction turns: 43.63%; owl W, 60.47%; owl Q, 42.95%; owl H, 28.51%) where the in-flight target speaker differed from the initial speaker, the owls performed a correction turn. The relationship between in-flight stimulus delay and the rate of correction turns can be described by a sigmoid-like curve (Fig. 3A). The shape of the curves did not depend on whether initial and in-flight target speakers were separated by a distance of 50 cm or 100 cm (data not shown). The rate of correction turns was about 40–80% for in-flight delays up to 700 ms, and decreased almost linearly with longer in-flight stimulus delays down to 0% at an in-flight stimulus delay of 1000–1100 ms. The decrease in percentage became significant (Fisher's Exact test, $P \leq 0.05$) at an in-flight delay of 800 ms for owl H and of 900 ms for the other two owls (dotted lines, Fig. 3A). Owl H performed significantly ($P \leq 0.01$) fewer correction turns than owl W for any in-flight stimulus delay below 1100 ms (Fig. 3A).

Striking at an auditory target resembles the owl's natural behavior during hunting, with the constraint that doing this in darkness is an extreme condition. Therefore, it seemed reasonable to analyze the proportion of trials in which the owl would have caught any prey (the 'hit rate'). A trial was counted as a 'hit' if an owl landed within

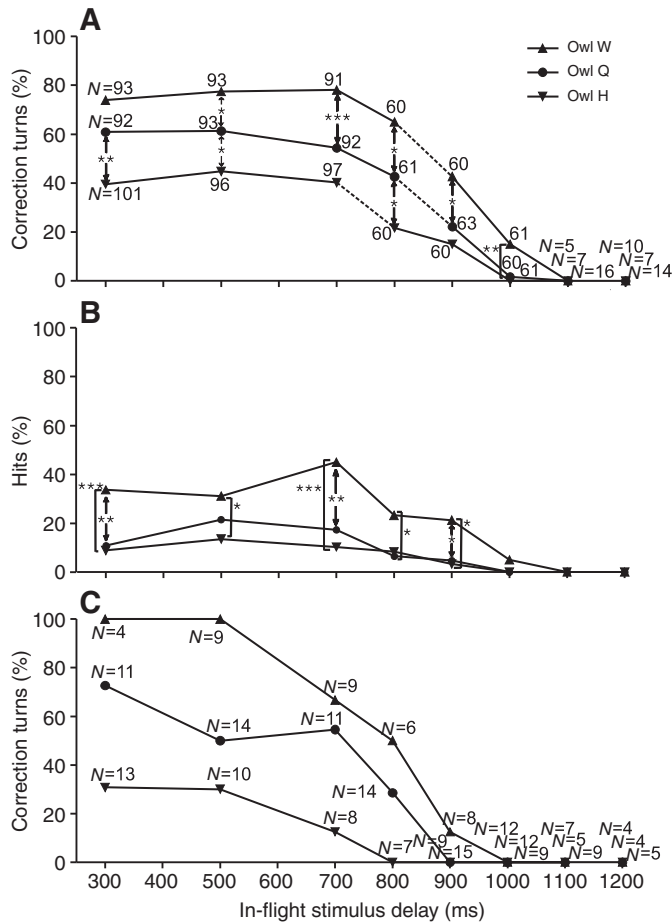


Fig. 3. Correction turns and hits. (A) The percentage of trials in which the owl performed a correction turn towards the in-flight target loudspeaker is plotted against the in-flight stimulus delay. Significant differences between the owls are indicated and marked with asterisks depending on the significance level (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$). The difference between owl W and owl H was highly significant for any in-flight stimulus delay smaller than 1100 ms, but is not shown for clarity. Dotted lines indicate a significant decrease of correction turns (%) with respect to the baseline (0–700 ms). Note the decrease of the performance with increasing in-flight stimulus delay for long delays. (B) For each owl, the percentage of hits within a 20 cm radius of the in-flight target speaker is plotted. The percentage refers to the overall number of trials where the in-flight target speaker differed from the initial target speaker (owl W, 472 trials; owl Q, 475 trials; owl H, 505 trials). Significant differences are marked with asterisks (Fisher's exact test). (C) In trials in which the distance to the speaker devices was less than 3.35 m (either 2.85 m or 2.35 m), the owls failed to perform correction turns at lower in-flight stimulus delays.

a 20 cm radius of the target speaker. The hit rates at a given stimulus delay are shown in Fig. 3B. For in-flight latencies below 800 ms, the owls achieved 20–40% hits.

Trials using shorter distances (2.85 m and 2.35 m) between perch and the speaker device (cf. Fig. 1) were introduced in 10–20% of the experimental sessions (Fig. 3C). The percentage of correction turns correlated with the in-flight stimulus delay in a similar way to in trials using the largest perch-to-speakers distance (3.35 m), in that the owls achieved a relatively high percentage at short in-flight delays that dropped down to 0% at longer delays. However, the resulting curves were shifted to the left (compare Fig. 3C with Fig. 3A), indicating that the owls failed to correct their flight path

at shorter in-flight stimulus delays. For example, the decrease in the percentage of correction turns started already at 500 ms in owls W and H. The differences between the owls were not significant, but this analysis was based on only a small number of trials (owl W, $N=59$; owl H, $N=76$; owl Q, $N=80$).

Although the three owls differed slightly from one another at some stimulus delays, the general tendency in all owls was a decrease of hit rates for longer in-flight stimulus delays. This emphasizes that the adaptation of flight direction is restricted in the last part of the target approach. The later a change of the target position occurred, the harder it was for the owl to react properly.

Head turn latencies

Head-turn latencies were only determined for those trials that included correction turns. If the video sequence of a trial included the correction turn but failed to capture the take-off moment, this trial was excluded from the analysis of head-turn latencies. Such trials were nevertheless valid for the analysis of the percentage of correction turns performed, as well as for the analysis of the landing precision. In total, 249 out of 286 turns were analyzed to determine the head-turn latencies for owl W, 197 out of 204 turns for owl Q and 137 out of 144 turns for owl H. The minimum head turn latency ever observed for all owls was 60 ms; the maximum was 360 ms for owl W, 340 ms for owl Q and 500 ms for owl H. The median latency was 180 ms averaged over all turns of each owl (Fig. 4A). Significant differences between owls or stimulus delays were not detected.

Head turn latencies were significantly ($P \leq 0.001$) smaller in trials with a shorter distance between the initial and the in-flight target speaker, i.e. 50 cm vs 100 cm (Fig. 4B). Likewise, latencies significantly decreased with increasing stimulus delay for each owl (linear regression, $P \leq 0.0307$; goodness of fit, $r^2 = 0.7280$ to 0.9524), as well as for the pooled owls (Fig. 4C, $P \leq 0.0070$, $r^2 = 0.8661$; slope, -0.14930 ± 0.02935). Head-turn latencies were significantly correlated with landing precision (Pearson correlation test, $P \leq 0.001$), measured as deviation in centimeters from the target loudspeaker, meaning that shorter head-turn latencies typically caused more precise landings (Fig. 4D). Head turn latencies directly relate to the remaining flight time. The shorter the head turn latency, the more time is left for the owl to perform a correction turn. This explains the correlation between short latencies and higher landing precision. In addition to head turn latencies there are further parameters that, likewise, can influence the owl's landing precision after a correction turn; for example, the extent of the head turn (the turning angle) and the following change of trajectory.

Turning angles

If the owl performed a correction turn towards the target speaker in order to strike it, the angle of the turn should be larger for long in-flight stimulus delays than for short delays. This situation is demonstrated in Fig. 5 for a short and a long in-flight stimulus delay. It was assumed that the time needed to process the stimulus and the time needed for the generation of the motor reaction (the head and body turn) remained constant irrespective of the stimulus delay. For the same reason, with increasing distance between the initial and the in-flight target, the turning angle was supposed to be larger. This hypothesis was tested by comparing the turning angle of each owl after different stimulus delays, as well as following trials with a distance of 50 cm and a distance of 100 cm between the initial and the in-flight target speaker, respectively.

We considered the initial directional change in the owl's trajectory (cf. Fig. 2J, white arrow) for the analysis of turning angles, because

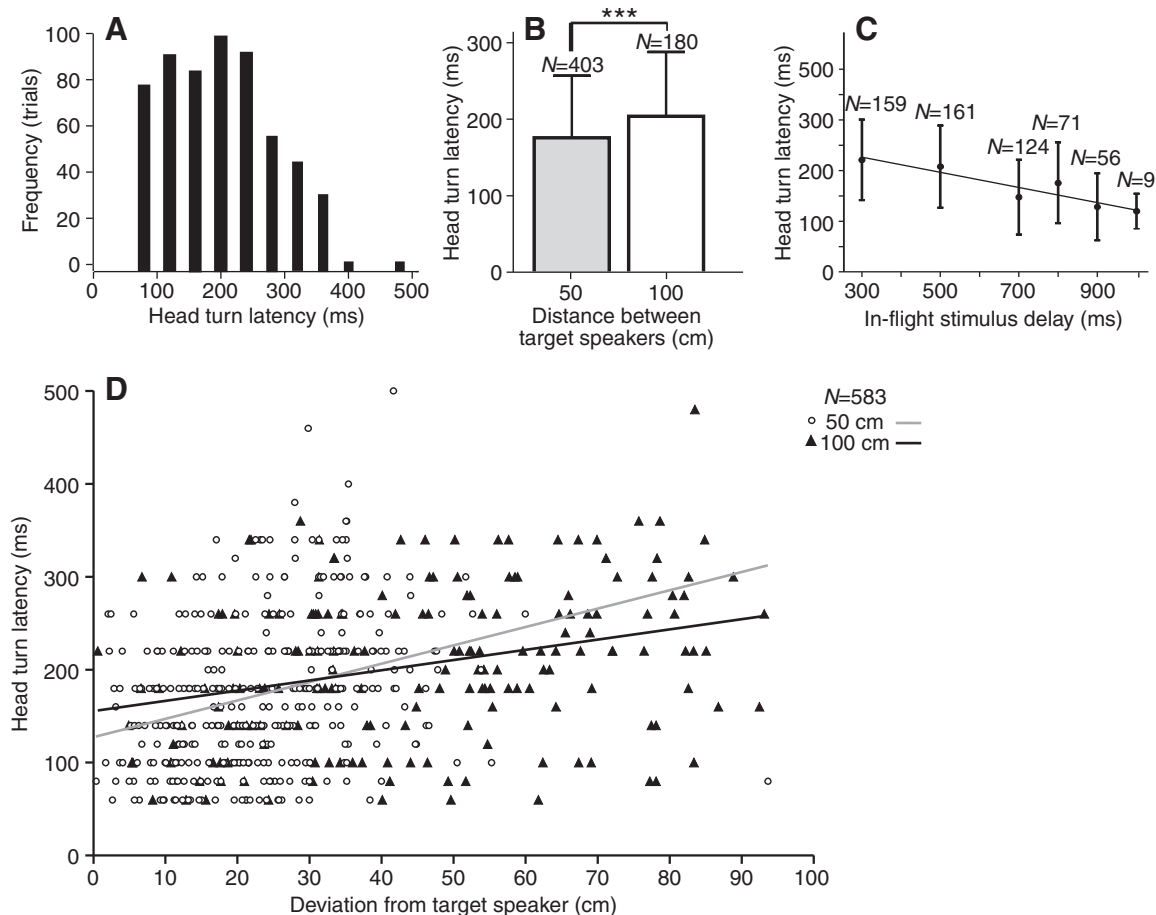


Fig. 4. Head turn latencies. (A) Histogram of the pooled head turn latencies [number of trials (N) with the particular head turn latency]. Bin size was 40 ms. Head turn latencies were cumulated between about 150 and 250 ms, with a median of 180 ms. (B) Head turn latencies in ms (mean \pm s.d.) were pooled for trials with a distance of 50 cm and 100 cm between the initial and the in-flight target speaker, respectively. (C) Head turn latencies (ms; mean \pm s.d.) of the owls significantly decreased with increasing stimulus delay (ms) (black regression line, slope -0.1493 ± 0.02935 ; goodness of fit, $r^2 = 0.8661$; $P \leq 0.0307$). (D) Head turn latencies of all trials are plotted against the landing precision in cm for trials with a distance of 50 cm (circles, grey regression line, $y = 127.3 + 1.976x$) and 100 cm (triangles, black regression line, $y = 155.6 + 1.096x$) between the initial and the in-flight speaker. The linear regression was highly significant ($P \leq 0.001$).

it corresponded to the saccadic head turn we could observe in the frontal view (camera C1). The turning angle, α , could be determined best using the video recordings of the camera mounted at the ceiling (C3 in Fig. 1), which showed the flight trajectory directly from above; however, this camera covered only the last 500–600 ms of the flight. Therefore, the turning angle was measured only for stimulus delays between 700 (if the moment of the head turn was captured in the video recording) and 1000 ms. Some recordings were excluded from the analysis because the head tracker was not continuously visible, predominantly because the owl bent its head, so that the reflection of the tracker disappeared. A total of 90 trials were analyzed for owl W, 45 trials for owl Q and 28 trials for owl H.

The turning angles increased significantly with increasing stimulus delay (Fig. 6A; Spearman correlation test, $P \leq 0.0018$). The linear regression (black line, Fig. 6A) was significantly non-zero ($P \leq 0.0001$) and had a slope of 0.03691 ± 0.009410 (goodness of fit, $r^2 = 0.09250$). The turning angles for speaker sequences with a distance of 100 cm between the initial and the in-flight target were significantly larger than for sequences with a distance of 50 cm between speakers (Fig. 6B) in all owls. Hence, the owl adapted the change of its trajectory to both the stimulus delay and the speaker

distance, as would be expected (cf. Fig. 5). It was of further interest whether these adaptive changes had an impact on the accuracy of target strike, i.e. the landing precision.

Landing precision

The landing positions of the owl relative to the in-flight target speaker were pooled for the varying stimulus sequences, plotted and statistically analyzed (see Fig. 7A for a representative example). To compare the striking precision of trials with and without correction turns, the angles and distances of the landing positions were sorted into bins of 30 deg. (angles, Fig. 7B,C) or 10 cm (distances, Fig. 7D,E). The landing positions were not evenly distributed around the center of the target speaker (KS2D1S test, $P \leq 0.001$), neither in tests of the speaker sequences, nor for delays or individual owls. The angles (theta, θ) exhibited a two-peaked distribution for trials without a correction turn, which resulted from pooling speaker sequences where the in-flight target speaker lay left (LS 2-1, 3-2 and 3-1) or right (LS 2-3, 3-4 and 2-4) of the initially aimed speaker. One peak lay between 75 and 135 deg. and a second peak of similar height between 195 and 255 deg. (Fig. 7B). This implies that all three owls landed short of the target in most of the

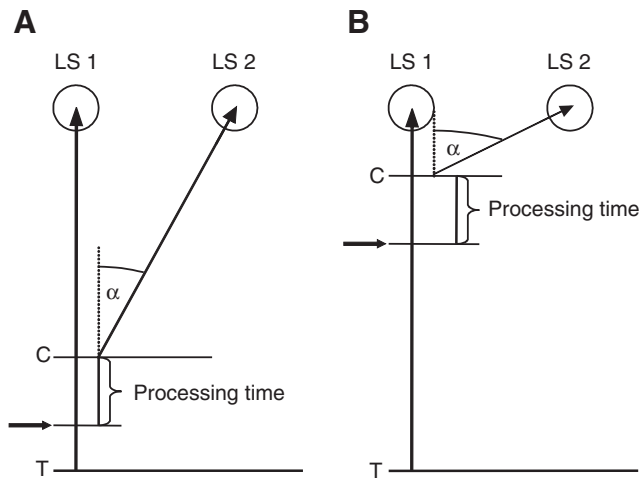


Fig. 5. Processing of in-flight stimuli and correction turns. If the initial stimulus was emitted by LS 1 and the in-flight stimulus by LS 2, the angle α of the correction turn required to hit the target is smaller for a short in-flight stimulus delay (A) than for a longer delay (B). T is the take-off of the owl for target strike. The black horizontal arrow marks the moment where the in-flight stimulus is given, C refers to the beginning of the correction turn. The neuronal and motor processing time is assumed to be constant for any stimulus delay.

trials. In trials with a correction turn the angles were widely spread (Fig. 7C). Within the no-turn trials, the landing distances (ρ) were concentrated between 35 and 115 cm from the target. (Fig. 7D). By contrast, in trials with correction turns, the distribution of the landing distances was asymmetric, with most lying between 5 and 35 cm off the target (Fig. 7E). The median distance in trials without a correction turn was 61.96 to 62.93 cm for the three owls. In trials with correction turns, the median distance was 21.52 to 30.03 cm, comparable to the landing precision in control trials. The distribution of both distance towards the target speaker (KS2D2S test) and angles (Kuiper's test) of the landing positions differed between trials with and without a correction turn (Table 2A), as well as between the three owls (Table 2B).

Landing precision was thought to be of great importance, as it influences the amount of prey the owl can catch in a natural environment. The landing precision hardly varied as a function of the in-flight stimulus delay, so these trials were pooled for further analysis for each owl. All three owls were significantly ($P \leq 0.001$) more precise when they had performed a correction turn, than in trials without a correction turn (Fig. 8). The landing precision of the owls was also dependent on the speaker sequence. In the speaker sequences LS 2-1, LS 2-3, LS 3-2 and LS 3-4, the distance between initial and in-flight target speaker was 50 cm, whereas in LS 2-4 and 3-1 both speakers were separated by 100 cm. Supposedly, the owls might land more precisely if the speakers were adjacent to each other, compared with double the distance. The mean precision was higher ($P \leq 0.001$) for speaker sequences with adjacent speakers than for those with a distance of 100 cm between the speakers (Fig. 8). It was, however, not correlated with the turning angle (Pearson correlation test, two-tailed, 95% confidence interval).

In summary, the findings suggest a higher success rate in striking potential prey if the owl reacts to changing target positions with a corrective turn, and if the target is displaced by only a small extent. However, the data presented so far have shown that a correction turn does not necessarily result in hitting the target. The owls might have performed a correction turn without hitting the target speaker

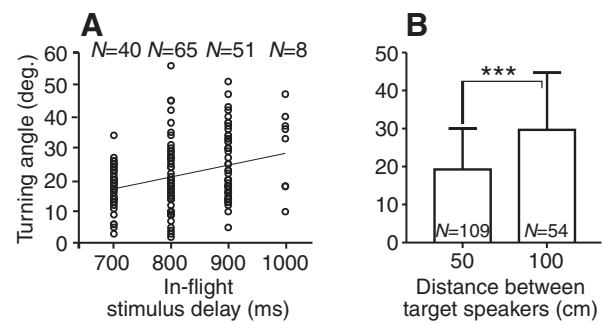


Fig. 6. Turning angles. (A) The mean turning angles in degrees are plotted against the stimulus delay. The linear regression (solid line, slope 0.03691 ± 0.00941) shows that the turning angle increases with the stimulus delay. Both parameters are significantly correlated. The number (N) of analyzed trials is given below each data point. Angles were not significantly different between stimulus delays or owls. (B) Turning angles were significantly ($P \leq 0.05$) smaller for speaker sequences with a distance of 50 cm than of 100 cm between the initial and the in-flight target. The number of trials (N) is given above each column.

precisely for two reasons. Firstly, the owl might have turned to the correct direction but landed too early. In this case, the expected error angle would be 0 deg. Secondly, the turning angle might have been too small. Then the expected error angle would be larger than 0 deg. In order to test these two possibilities, the error angles (β , cf. Fig. 2J) were measured. A correlation between the error angle and landing precision would indicate case two to be the valid option.

Error angles ranged from 0–39 deg., with a mean of 12.78 deg., for the 50 cm distance, and from 0–42 deg., with a mean of 20.14 deg., for the 100 cm distance. They were larger for the 100 cm distance than for the 50 cm distance between the target speakers at any delay (Fig. 9A), without any significant difference between the owls. The only exception was owl Q, which had a significantly ($P \leq 0.0247$) larger error angle at a 700 ms delay and a 100 cm distance than did the other owls. The difference between the 50 and 100 cm distance between target speakers was highly significant ($P \leq 0.0003$) when the angles were pooled over all owls and delays (Fig. 9B). The error angles of each owl were analyzed for correlation with the landing precision for the varying stimulus delays (700–1000 ms), and for the two distances between the target speakers, respectively. Each of these groups contained between one and 21 samples. In five cases with a sample number of less than three, no correlation test could be performed. The landing precision was typically not correlated with error angles within a stimulus delay and target speaker distance. By contrast, the correlation was highly significant if the delays and speaker distances were pooled (Pearson correlation test, $P \leq 0.0015$), meaning that the landing precision was lower, the larger the error angle was. The rate of early landing (i.e. the proportion of trials with undershooting or landing at angles between 90 and 270 deg., Fig. 7) in control flights with identical initial and in-flight targets (72.09%) matched that of early landing in trials where in-flight correction was required because the initial and the in-flight target speaker were not identical (75.09%). Conclusively, the owls exhibited vertical striking errors in control trials, as well as in trials that required in-flight correction. Both findings support option two (see above), that the owl's decreased landing precision in in-flight correction trials was due to additional angular errors (compared with control trials), whereas distance errors occurred in both control and in-flight correction trials and caused an undershooting of the target speaker in any case.

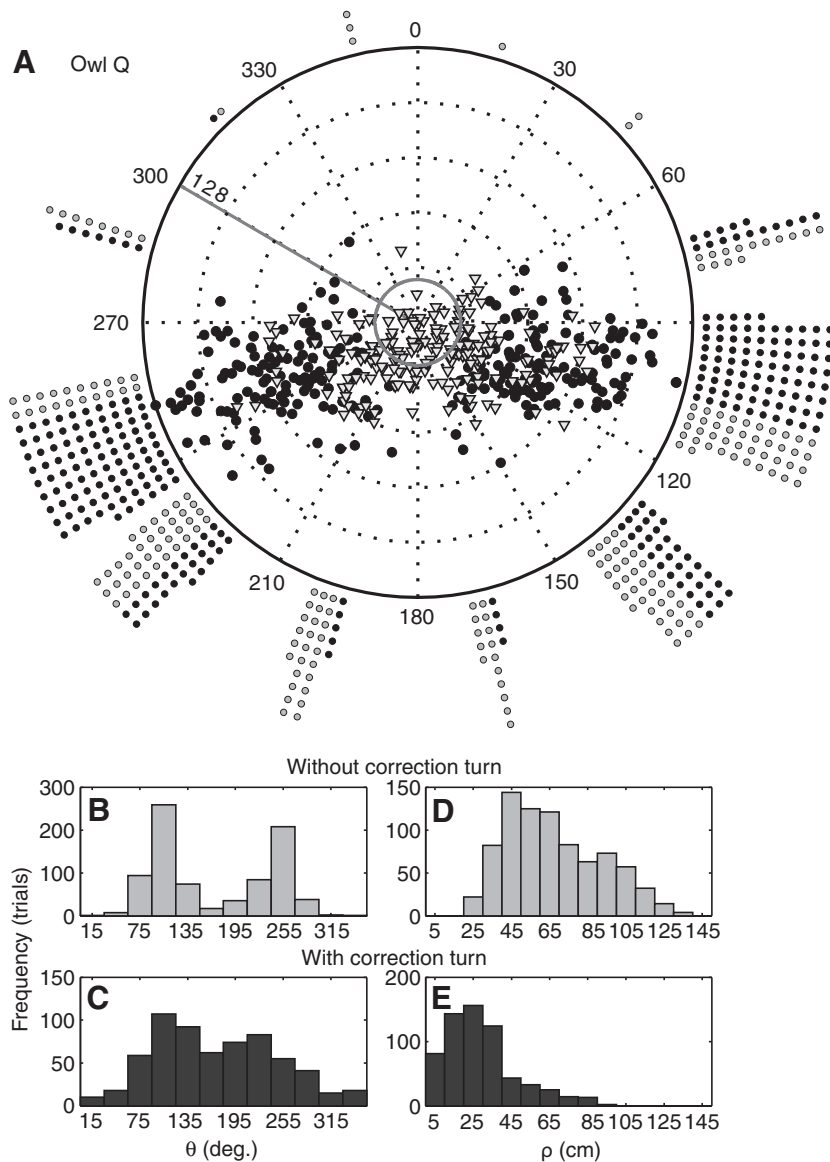


Fig. 7. Representative polar scatter plot of landing positions (owl Q). (A) The center of the plots corresponds to the target speaker position. The landing positions of trials with a correction turn (triangles) or without a correction turn (black dots) are plotted clockwise from 0 to 359 deg. in a circular diagram. The central gray circle indicates the 'hit' area of a 20 cm radius around the centre of the target speaker. The maximum landing distance was 128 cm (see gray line and number). Gray and black dots outside the circle indicate the landings in a particular quadrant. (B-E) The landing positions of the three owls were analyzed for trials without (B,D) or with a correction turn (C,E) for the distribution of their angles [θ (degrees); B,C] and distances [ρ (cm); D,E]. The positions were divided into bins of 30 deg. (θ) or 10 cm (ρ) and plotted into histograms. In trials without correction turn the distribution of angles is double-peaked between 75 and 135 deg. and between 195 and 255 deg. (B). The distances exhibit one peak at distances between 35 and 115 cm (D). In trials with a correction turn, the distribution of angles is less bifurcated than in trials without a correction turn (C). Distances are distributed around values between 5 and 35 cm (E).

In conclusion, a correction turn at short head turn latencies – leaving more time for corrective movements – led to higher striking precision. Hence, if the owl performed a correction turn, landing precision was comparable to that in control trials, but the percentage of trials in which the owl performed a corrective turn decreased with increasing stimulus delay. Therefore, the mean striking precision averaged over all trials at a given delay decreased likewise with increasing stimulus delay. The time needed for in-flight corrections limited striking accuracy when the change in target position fell within the range of the final landing phase. The owl achieved high striking accuracy only if the extent of corrective turning angles matched the altered target position. This was the case as the turning angle increased with increasing stimulus delay, as well as with increasing distance between initial and in-flight targets (cf. Fig. 6).

DISCUSSION

The data presented here demonstrate that barn owls correct their flight path by performing a head and body turn into the direction of an in-flight sound stimulus. In our experimental design, with an

overall flight time of approximately 1300 to 1500 ms, the percentage of trials in which the owl performed such a correction turn decreased significantly if the in-flight stimulus delay exceeded 800 to 900 ms. As laboratory tests can only investigate a limited range of stimulus properties, we will interpret our findings in the context of existing sound localization studies with barn owls, as well as with other species.

Correction turns

In our experiments, we investigated the flight behavior and landing precision of barn owls reacting to in-flight broadband sound stimuli at variable delays. For short in-flight delays the owls adapted their flight path to the new target in a certain percentage of trials. This adaptation rate was independent of the in-flight delay and served as a baseline. Above a certain threshold (defined as the in-flight stimulus delay at which the percentage of correction turns decreased for the first time significantly compared with the previous delay, cf. Fig. 3A) this rate decreased gradually with increasing in-flight stimulus delays. With an overall flight time of approximately 1300 to 1500 ms, the threshold was 800 ms. The shortest in-flight stimulus

delay that elicited no in-flight corrections by the owls was found to be between 1000 and 1100 ms. Thus, if the in-flight stimulus appeared before around 50% of the flight time was over (700 ms out of 1300–1500 ms), the number of correction turns was high and was not influenced by the timing of the in-flight stimulus. By contrast, if the in-flight stimulus was broadcast after about 80% of the total flight time (1100 ms out of 1300–1500 ms), a correction turn was not elicited at all. Our study was similar to a previous study conducted by Konishi (Konishi, 1973b). The target stimuli he used disappeared at the owl's take-off and reappeared, after varying delays, for the remaining flight time at a different location. Under these conditions, the owl was able to strike the target as precisely as with ongoing stimulation until the delay exceeded about 80% of the total flight time.

These observations are comparable to our results. Taking the above mentioned total flight time into account, the owls essentially needed a remaining flight time of some 200–500 ms after stimulus onset to make a correction turn. This measured remaining flight time fits well to the measured head-turn delays (60–500 ms). As the flight time depends on the flight distance, a decrease in flight distance was assumed to result in a decrease of the threshold time necessary for correction turns. Such a dependency was indeed observed (Fig. 3C). At a flight velocity of 3.6 to 4.0 m s⁻¹ (Konishi, 1973b), a decrease in the distance to the target of 1 m should result in a time shift of about 250 ms, which is close to the observed 200 ms. In the present experiments, flight velocity lay in a comparable range (about 2.6 to 3.0 m s⁻¹ if the linear distance to the target speaker was divided by the approximate flight time of the owl). The data suggest that the owl's attack flight might be divided in two parts, a first part during which the owl can react to changes in target position, and a second part during which the owl prepares for target striking and does not react to further changes in target position. Potentially, there is a phase during late flight prior to initiation of the landing where the owl reacts faster to displaced stimulus locations, as suggested by the decreasing head turn latencies during late flight (Fig. 4C).

If the stimulus delay was the only relevant parameter for in-flight correction turns, the baseline of performed correction turns should have been at 100%. However, the overall maximum baseline observed in our study was 80%, which was for owl W; it was even lower for owls Q (60%) and H (40%). We speculate that general arousal or attentiveness, which also seemed to differ between the individual owls, was responsible for this. As shown in Fig. 3, the absolute performance level (percentage of correction turns and hits) of owl W exceeded those of owls Q and H, and owl Q generally outperformed owl H. Besides differences in the absolute performance level, the threshold delay for correction turns lay in a comparable range for all owls (800–900 ms). These results suggest that individual owls are subject to comparable sensory and motor restrictions that limit the maximum stimulus delay for in-flight corrections. However, the percentage of trials during which the owl is attentive enough to react to an in-flight stimulus might, at least partially, be influenced by the owl's individual arousal.

Table 2. Significance levels for the distribution of distances and angles of the owl's landing positions

A	KS2D2S test (distribution)		Kuiper's test (angles)	
	Without turn (nt) vs with turn (wt)		Without turn vs with turn	
Owl W	1.7258 × 10 ⁻¹⁸ *** (186 nt, 286 wt)		8.6199 × 10 ⁻⁶ *** (186 nt, 286 wt)	
Owl Q	1.9707 × 10 ⁻¹² *** (271 nt, 204 wt)		7.6927 × 10 ⁻¹⁰ *** (271 nt, 204 wt)	
Owl H	6.8662 × 10 ⁻¹⁴ *** (361 nt, 144 wt)		3.3746 × 10 ⁻¹² *** (361 nt, 144 wt)	
B	KS2D2S test (distribution)		Kuiper's test (angles)	
	Without turn	With turn	Without turn	With turn
Owl W/Owl Q	0.0023738**	6.6153 × 10 ⁻⁸ ***	3.9703 × 10 ⁻⁵ ***	7.0419 × 10 ⁻⁷ ***
Owl Q/Owl H	7.5561 × 10 ⁻⁶ ***	0.16719	2.9436 × 10 ⁻⁹ ***	0.051723
Owl W/Owl H	0.44174	1.3702 × 10 ⁻⁵ ***	0.28379	1.1948 × 10 ⁻⁵ ***

The distribution of vector lengths was tested with a KS2D2S test for significant differences between trials with vs without a correction turn for each owl, as well as for differences between the three owls. The number of tested trials without a turn (nt) and with a turn (wt) is given in brackets. The distribution of vector angles was tested with a Kuiper's test. (A) The distributions were tested for each owl separately between trials with and without a correction turn. (B) The landing positions were compared between two owls (first column) separately for trials with and without a correction turn. Significant differences (*P*-values) are marked with asterisks depending on the significance level (**P*<0.05, ***P*<0.01, ****P*<0.0001). For further explanations see text.

Latencies for head turns

The flight time required to initiate a head turn varied between 60 and 500 ms, with a median latency of 180 ms. These data were in accordance with previous results from stationary sound-localization experiments (Knudsen et al., 1979; Wagner, 1993). Head turn latencies depended on the in-flight stimulus delay and on the distance between the speakers. In trials with short stimulus delays, the owl may have turned the head slowly because the turning angle was smaller (du Lac and Knudsen, 1990), as shown in Fig. 6A. This speculation is consistent with the finding that head turn latencies were smaller for the 50 cm speaker distance than for the 100 cm distance for all owls (cf. Fig. 4B), as the turning angle was smaller for adjacent than for distant target speakers (Fig. 6B). The latencies are also indicative of the sensory and motor capacities, which are similarly restricted in individual owls. They were not expected to decrease with increasing stimulus delay or decreasing distance between target speakers, but the owls might react faster to in-flight

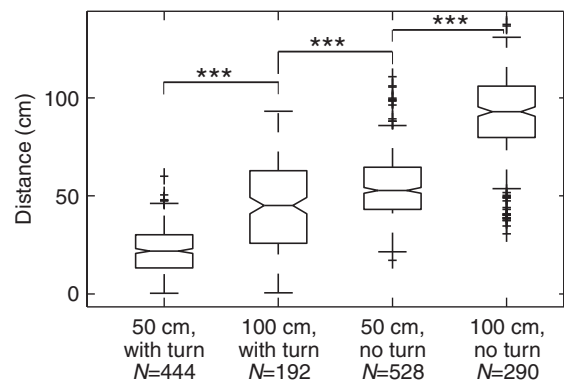


Fig. 8. Landing precision. The distance to the target loudspeaker was pooled for all stimulus delays. Trials with a correction turn (left two rows) and without a correction turn (right two rows) were analyzed separately. The first and third rows from the left present trials with adjacent target speakers (50 cm distance), the second and fourth rows from the left those with a 100 cm distance. Significant differences between stimulus delays are marked with asterisks (***) (*P*<0.001). The number of trials (*N*) included in the analysis is given below the *x*-axis.

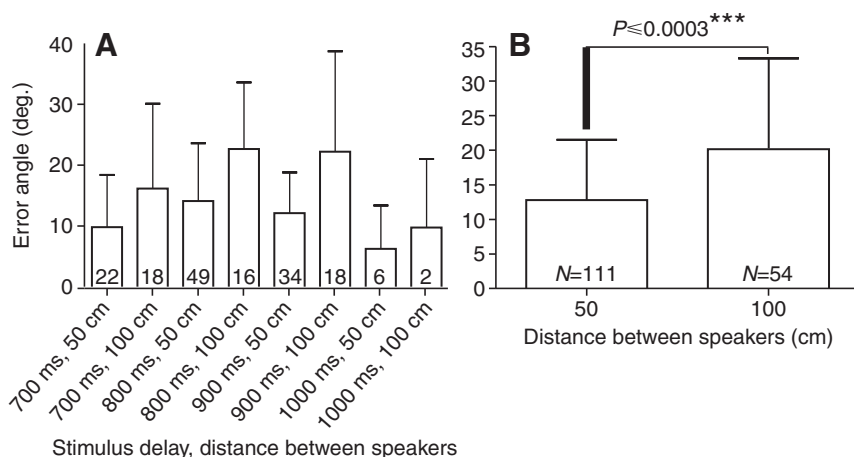


Fig. 9. Error angles. (A) The remaining angle β (in degrees) between the actual turning angle and the extended line between the owl's flight path and the center of the in-flight target speaker was measured, as shown in Fig. 2J. The error angle did not depend on the in-flight stimulus delay. Plotted is the mean \pm s.d. Due to technical limitations, only in-flight stimulus delays larger than 700 ms were considered for the analysis, as far as the owl's turn was visible from above on the video recording. The number of trials, N , is given at the base of each column. (B) For pooled data from all owls and delays, the error angles are significantly larger (t -test, $P \leq 0.0003$) for the 100 cm distance between speakers than for the 50 cm distance.

stimuli in the late flight phase, prior to initiation of the target strike. The relatively large variability of head turn latencies suggests that these might be influenced by factors other than pure reaction time, such as by arousal or attentiveness.

Turning angles and landing precision

Striking a target with equal precision requires a minimum turning angle, which increases with increasing stimulus delays (Fig. 5). Our data matched this explanation, in that striking precision was independent of stimulus delay. A similar situation is given when the distance between the initial and the in-flight target increases from 50 to 100 cm. In this case, the turning angles for the 100 cm distance were larger than those measured for 50 cm distance (Fig. 6B). The increase in turning angle, however, was not large enough, therefore the error angle also increased (Fig. 9B). Hence, barn owls can react to changing target positions to an extent that is subjected to larger errors if the target is farther displaced.

Two factors mainly influence the landing precision, namely the turning angle or the error angle, and the distance that the owl flew in the direction of the in-flight target before landing. The landing precision was correlated with the error angle, suggesting that striking precision mainly depends on the angular error. This is further supported by the observation that the landing precision in trials with a correction turn lay in a range comparable to that of control trials (cf. Fig. 7). Hence, undershooting occurred irrespective of whether the sound source was stationary or moving. A general undershooting in the localization behavior of barn owls was also reported in stationary experiments (Poganiatz et al., 2001). Stationary or translating human observers who had to approach a stationary sound source, which emitted a 20 Hz pulse train, overshoot near targets (2 m distance) and undershot distant targets (4 m distance) (Speigle and Loomis, 1993). Apparently, misestimating the sound source distance is not limited to barn owls. For the owl, it might be more beneficial to land short of the target instead of overshooting it, as this provides the opportunity to swoop again on the prey with no need for large-amplitude turns.

The switching between loudspeakers in our setup corresponds to sidewise motion of a target. Shiffman and Eilam reported an inability or at least severe impairment of tested owls to strike a target as it was moved sideways (or backwards), compared with a forward or forward/diagonal motion (Shiffman and Eilam, 2004). This held true even though the target, a dead mouse or chick, was pulled by a string and allowed both ongoing visual and auditory feedback. Our data suggest that this holds true if the sidewise motion occurs

late during an attack flight, as short in-flight stimulus delays correspond to a forward/diagonal rather than a sideways target motion. This is also corroborated by Konishi's observations (Konishi, 1973b). He reported that barn owls were able to strike a distant target as precisely as with ongoing noise stimulation if only three bursts of 50 ms duration each were presented during a flight time similar to the one used in the present study (i.e. about 1200–1400 ms). The noise bursts in his experiments were evenly distributed during the flight time. If, in darkness, the owl did not receive further feedback during the following 1000 ms of flight time, the striking precision decreased dramatically (Konishi, 1973b). We found this to be consistent with our data, because the precision was clearly reduced if the owl did not perform a correction turn (Fig. 7). Interestingly, the time span of 1000 ms seems to be shorter than the maximum temporal extent of the spatial working memory (0.1–2 s), as tested by Knudsen and Knudsen (Knudsen and Knudsen, 1996). Konishi's as much as our data suggest that the owl requires (intermittent, albeit possibly short) stimuli throughout most of its attack flight to precisely hit a target in darkness. Apparently, the owl's striking precision is influenced by the temporal pattern (inter-stimulus interval) of the in-flight stimuli, rather than by the absolute stimulus duration.

Comparison with other species

In contrast to barn owls, mammals use interaural time differences (ITD) and interaural level differences (ILD) for localization in the horizontal plane, and spectral shapes for localization in the vertical plane (Tollin and Yin, 2003). Studies on sound localization during which animals had to fixate or approach a sound source to indicate the perceived location have been conducted in several species [cat (Casseday and Neff, 1973; Casseday and Neff, 1975; Jenkins and Merzenich, 1984; Populin and Yin, 2007); bat (Aytekin et al., 2004); ferret (Kavanagh and Kelly, 1987; Kavanagh and Kelly, 1992; Parsons et al., 1999); rat (Kavanagh and Kelly, 1986); mouse (Ehret and Dreyer, 1984); and seal (Bodson et al., 2006)], whereas others have used conditioned reflexes (Ebert et al., 2008). Most of these species localize sound sources with similar or inferior accuracy when compared with the barn owl, even though many similarities in localization behavior can be found. For example, cats, as much as barn owls, orient their heads towards broadband sound sources in comparable saccadic movements (Beitel and Kaas, 1993). The localization acuity in stationary two-choice experiments with cats is with 4–7 deg. somewhat inferior to in barn owls (Heffner and Heffner, 1988), although other measurements indicate a better

performance, with localization errors as small as 0.16 ± 0.97 deg. (mean signed error \pm s.d.) in stationary experiments (Tollin et al., 2005). Casseday and Neff carried out experiments in which the cat had to approach the loudspeaker that emitted a sound (Casseday and Neff, 1973). The minimum detectable angle for pure tone localization was found in the range of about 5–15 deg. for frequencies below 4 kHz; this strongly increased to 35 deg. at 4 kHz and then decreased again for higher frequencies.

Localization performance varies depending on the species-specific requirements, but often is subjected to similar physical and physiological restrictions. Jenkins (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984) demonstrated that midline localization was better than peripheral localization, which can be explained by the higher spatial resolution in the frontal field. Albino rats were tested in a similar localization task, involving sound sources in the peripheral left and right hemifield (± 60 deg. from the midline) (Kavanagh and Kelly, 1986). The rats had minimum audible angles of about 12 deg. in the frontal field, similar to those of the house mice (Ehret and Dreyer, 1984), but performed poorly when the sound sources were peripherally displaced.

The localization precision in other species is clearly inferior to what has been observed in the barn owl, which can aim at a sound source with 2 deg. accuracy, and detect changes of 3 deg. in its location (Bala et al., 2003). The ability of the barn owl to localize auditory targets with a higher accuracy than most mammalian species is a consequence of the highly directional facial ruff (Campenhausen and Wagner, 2006; Coles and Guppy, 1988; Knudsen and Konishi, 1979), which allows using interaural time and level differences (ITD and ILD) for the localization of azimuth and elevation, independently. Together with the ability to adapt its trajectory to a sound stimulus appearing during flight, barn owls can strike a distant auditory target with high accuracy without auditory feedback, even if these targets expose sudden displacements.

However, natural conditions do not provide auditory feedback only. In fact, visual feedback improves localization acuity. Populin and Yin demonstrated that cats performed eye and head saccades to auditory targets with less accuracy than to visual targets (Populin and Yin, 2007). The cats in that study were impaired in their localization accuracy when stimulated with single clicks instead of click trains. This parallels what Konishi observed in the barn owl with 50 ms bursts of sound (Konishi, 1973b). A similar result was found for ferrets approaching a sound source: the ferrets were significantly better at localizing noise bursts of 500 ms duration than those of 40 ms duration (Parsons et al., 1999). Bodson et al. have tested the sound-localization performance of swimming seals (Bodson et al., 2006). The animal had to swim towards the sound source and touch the board of a half circle at the assumed position. The seals were better at localizing continuous noise than two pulses of noise. Although the last stimulus paradigm closely resembles our paradigm, to our best knowledge no one has carried out experiments with freely moving animals in which the sound source switched between loudspeakers in other animal species.

In nature, adaptive changes of the owl's behavior in response to altered target positions are required for striking moving prey. In-flight stimuli improve the barn owl's striking precision as long as they do not appear too late in the target approaching behavior. We assume that flight maneuvers may occur during early flight, but not in the final flight phase. In this respect it is interesting that the prey, through its movements, typically provides short intermittent auditory information to the predator. One of the avoidance strategies of the prey is to freeze, i.e. not make any

noise, and then jump to the side and flee shortly before the owl attempts to capture it (Edut and Eilam, 2004; Ilany and Eilam, 2008). Similar observations were made for peregrine falcons (Howland, 1974). These birds swoop at prey animals from the air at extremely high velocities. Prey animals were able to escape with a high probability if they ceased fleeing at a constant velocity and instead made a turn at an optimal time point, which was defined by the maneuverability of the falcon. Starting the turn too soon allowed for correction turns of the falcon, whereas turning too late did not leave enough time for the prey's turn.

The data presented here show that barn owls succeed in striking horizontally displaced targets under laboratory conditions by matching the extent of the corrective movement to the target position. Nevertheless, striking precision is dependent upon several physiological restrictions, such as reaction time and localization accuracy. Taken together, barn owls are well adapted to nocturnal hunting, even though potential prey animals may exploit the mentioned restrictions in the owl's striking ability in order to escape (Ilany and Eilam, 2008).

LIST OF ABBREVIATIONS

ILD	interaural level difference
ITD	interaural time difference
LS	loudspeaker
SPL	sound pressure level

REFERENCES

- Aytek, M., Grassi, E., Sahota, M. and Moss, C. F. (2004). The bat head-related transfer function reveals binaural cues for sound localization in azimuth and elevation. *J. Acoust. Soc. Am.* **116**, 3594-3605.
- Bala, A. D., Spitzer, M. W. and Takahashi, T. T. (2003). Prediction of auditory spatial acuity from neural images on the owl's auditory space map. *Nature* **424**, 771-774.
- Bala, A. D., Spitzer, M. W. and Takahashi, T. T. (2007). Auditory spatial acuity approximates the resolving power of space-specific neurons. *PLoS ONE* **2**, e675.
- Bala, A. D. S. and Takahashi, T. T. (2000). Pupillary dilation response as an indicator of auditory discrimination in the barn owl. *J. Comp. Physiol. A* **186**, 425-434.
- Beitel, R. E. and Kaas, J. H. (1993). Effects of bilateral and unilateral ablation of auditory cortex in cats on the unconditioned head orienting response to acoustic stimuli. *J. Neurophysiol.* **70**, 351-369.
- Bodson, A., Miersch, L., Mauck, B. and Dehnhardt, G. (2006). Underwater auditory localization by a swimming harbor seal (*Phoca vitulina*). *J. Acoust. Soc. Am.* **120**, 1550-1557.
- Brainard, M. S., Knudsen, E. I. and Esterly, S. D. (1992). Neural derivation of sound source location: resolution of spatial ambiguities in binaural cues. *J. Acoust. Soc. Am.* **91**, 1015-1027.
- Campenhausen, M. and Wagner, H. (2006). Influence of the facial ruff on the sound-receiving characteristics of the barn owl's ears. *J. Comp. Physiol. A* **192**, 1073-1082.
- Casseday, J. H. and Neff, W. D. (1973). Localization of pure tones. *J. Acoust. Soc. Am.* **54**, 365-372.
- Casseday, J. H. and Neff, W. D. (1975). Auditory localization: role of auditory pathways in brain stem of the cat. *J. Neurophysiol.* **38**, 842-858.
- Coles, R. B. and Guppy, A. (1988). Directional hearing in the barn owl (*Tyto alba*). *J. Comp. Physiol. A* **163**, 117-133.
- Damos, D. (1991). *Multiple Task Performance*. London: Taylor and Francis.
- Du Lac, S. and Knudsen, E. I. (1990). Neural maps of head movement vector and speed in the optic tectum of the barn owl. *J. Neurophysiol.* **63**, 131-146.
- Ebert, C. S., Blanks, D. A., Patel, M. R., Coffey, C. S., Marshall, A. F. and Fitzpatrick, D. C. (2008). Behavioral sensitivity to interaural time differences in the rabbit. *Hear. Res.* **235**, 134-142.
- Edut, S. and Eilam, D. (2004). Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. *Behav. Brain Res.* **155**, 207-216.
- Ehret, G. and Dreyer, A. (1984). Localization of tones and noise in the horizontal plane by unrestrained house mice (*Mus musculus*). *J. Exp. Biol.* **109**, 163-174.
- Haresign, T. and Moiseff, A. (1988). Early growth and development of the common barn owls facial ruff. *Auk* **105**, 699-705.
- Heffner, R. S. and Heffner, H. E. (1988). Sound localization acuity in the cat: effect of azimuth, signal duration, and test procedure. *Hear. Res.* **36**, 221-232.
- Howland, H. (1974). Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333-350.
- Ilany, A. and Eilam, D. (2008). Wait before running for your life: defensive tactics of spiny mice (*Acomys cahirinus*) in evading barn owl (*Tyto alba*) attack. *Behav. Ecol. Sociobiol.* **62**, 923-933.
- Jenkins, W. M. and Masterton, R. B. (1982). Sound localization: effects of unilateral lesions in central auditory system. *J. Neurophysiol.* **47**, 987-1016.
- Jenkins, W. M. and Merzenich, M. M. (1984). Role of cat primary auditory cortex for sound-localization behavior. *J. Neurophysiol.* **52**, 819-847.
- Kavanagh, G. L. and Kelly, J. B. (1986). Midline and lateral field sound localization in the albino rat (*Rattus norvegicus*). *Behav. Neurosci.* **100**, 200-205.

- Kavanagh, G. L. and Kelly, J. B.** (1987). Contribution of auditory cortex to sound localization by the ferret (*Mustela putorius*). *J. Neurophysiol.* **57**, 1746-1766.
- Kavanagh, G. L. and Kelly, J. B.** (1992). Midline and lateral field sound localization in the ferret (*Mustela putorius*): contribution of the superior olivary complex. *J. Neurophysiol.* **67**, 1643-1658.
- Keller, C. H., Hartung, K. and Takahashi, T. T.** (1998). Head-related transfer functions of the barn owl: measurement and neural responses. *Hear. Res.* **118**, 13-34.
- Knudsen, E. I. and Konishi, M.** (1979). Mechanisms of sound localisation in the barn owl (*Tyto alba*). *J. Comp. Physiol. A* **133**, 13-21.
- Knudsen, E. I. and Knudsen, P. F.** (1996). Disruption of auditory spatial working memory by inactivation of the forebrain archistriatum in barn owls. *Nature* **383**, 428-431.
- Knudsen, E. I., Blasdel, G. G. and Konishi, M.** (1979). Sound localization by the barn owl (*Tyto alba*) measured with the search coil technique. *J. Comp. Physiol. A* **133**, 1-11.
- Knudsen, E. I., Esterly, S. D. and Knudsen, P. F.** (1984). Monaural occlusion alters sound localization during a sensitive period in the barn owl. *J. Neurosci.* **4**, 1001-1011.
- Konishi, M.** (1973a). Locatable and nonlocatable acoustic signals for barn owls. *Am. Nat.* **107/958**, 775-785.
- Konishi, M.** (1973b). How the owl tracks its prey. *Am. Sci.* **61**, 414-424.
- Parsons, C. H., Lanyon, R. G., Schnupp, J. W. and King, A. J.** (1999). Effects of altering spectral cues in infancy on horizontal and vertical sound localization by adult ferrets. *J. Neurophysiol.* **82**, 2294-2309.
- Payne, R.** (1962). How the barn owl locates prey by hearing. In *The Living Bird First Annual Of The Cornell Lab Of Ornithology*, pp. 151-159. Ithaca, NY: The Laboratory of Ornithology at Cornell University.
- Poganiatz, I. and Wagner, H.** (2001). Sound-localization experiments with barn owls in virtual space: influence of broadband interaural level difference on head-turning behavior. *J. Comp. Physiol. A* **187**, 225-233.
- Poganiatz, I., Nelken, I. and Wagner, H.** (2001). Sound-localization experiments with barn owls in virtual space: influence of interaural time difference on head-turning behavior. *J. Assoc. Res. Otolaryngol.* **2**, 1-21.
- Populin, L. and Yin, T. C.** (2007). Behavioral studies of sound localization in the cat. *J. Neurosci.* **18**, 2147-2160.
- Saberi, K., Takahashi, Y., Farahbod, H. and Konishi, M.** (1999). Neural bases of an auditory illusion and its elimination in owls. *Nat. Neurosci.* **2**, 656-659.
- Shiffman, E. and Eilam, D.** (2004). Movement and direction of movement of a simulated prey affect the success rate in barn owl *Tyto alba* attack. *J. Avian Biol.* **35**, 111-116.
- Speigle, J. M. and Loomis, J. M.** (1993). Auditory distance perception by translating observers. *Proceedings of IEEE Symposium on Research Frontiers in Virtual Reality*, San Jose, CA, October 25-26, 1993.
- Tollin, D. J. and Yin, T. C.** (2003). Spectral cues explain illusory elevation effects with stereo sounds in cats. *J. Neurophysiol.* **90**, 525-530.
- Tollin, D. J., Populin, L. C., Moore, J. M., Ruhland, J. L. and Yin, T. C.** (2005). Sound-localization performance in the cat: the effect of restraining the head. *J. Neurophysiol.* **93**, 1223-1234.
- Wagner, H.** (1993). Sound-localization deficits induced by lesions in the barn owl's auditory space map. *J. Neurosci.* **13**, 371-386.
- Wagner, H.** (2002). Directional hearing in the barn owl: psychophysics and neurophysiology. In *Genetics and the Function of the Auditory System* (ed. L. Tranebjaerg, J. Christensen-Dalsgaard, T. Andersen and T. Poulsen) **19**, pp. 331-351. Denmark: Holmens Trykkeri.