

Sound-Localization Experiments with Barn Owls in Virtual Space: Influence of Interaural Time Difference on Head-Turning Behavior

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ABSTRACT

Specific cues in a sound signal are naturally linked to certain parameters in acoustic space. In the barn owl, interaural time difference (ITD) varies mainly with azimuth, while interaural level difference (ILD) varies mainly with elevation. Previous data suggested that ITD is indeed the main cue for azimuthal sound localization in this species, while ILD is an important cue for elevational sound localization. The exact contributions of these parameters could be tested only indirectly because it was not possible to generate a stimulus that contained all relevant spatial information on the one hand, and allowed for a clean separation of these parameters on the other hand. Virtual auditory worlds offer this opportunity. Here we show that barn owls responded to azimuthal variations in virtual space in the same way as to variations in free-field stimuli. We interpret the increase of turning angle with sound-source azimuths (up to $\pm 140^\circ$) such that the owls did not experience front/back confusions with virtual stimuli. We then separated the influence of ITD from the influence of all other stimulus parameters by fixing the overall ITD in virtual stimuli to a constant value ($+100 \mu\text{s}$ or $\pm 100 \mu\text{s}$) while leaving all other sound characteristics unchanged. This manipulation influenced both azimuthal and elevational components of head turns. Since the owls' azimuthal head-turn amplitude always resembled the value signified by the ITD,

these data demonstrated that azimuthal sound localization is influenced only by ITD both in the frontal hemisphere and in large parts of the rear hemisphere. ILDs did not have an influence on azimuthal components of head turns. While response latency to normal virtual stimuli was found to be largely independent of stimulus position, response delays of the head turns became longer if the ITD information pointed into a different hemisphere as the other cues of the sounds.

Keywords: psychophysics, spatial hearing, auditory, acoustic, HRTF

INTRODUCTION

To locate potential prey, barn owls turn their head toward the direction of faint, broadband sounds. In many studies, these head turns were measured under controlled laboratory conditions to investigate different aspects of sound-localization behavior in a free-field environment (Knudsen et al. 1979; Knudsen and Konishi 1979; Knudsen and Knudsen 1986; Wagner 1993) or with a closed-field system by inserting earphones into the ear canals of the birds (Moiseff and Konishi 1981; Moiseff 1989a; Wagner 1991; Saberi et al. 1998). The experiments with dichotic stimulus presentation demonstrated that barn owls are able to lateralize sounds and that interaural time difference (ITD) is the main stimulus parameter for azimuthal sound localization, whereas interaural level difference (ILD) is the prime cue for elevation (Moiseff and Konishi

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1981; Olsen et al. 1989; Moiseff 1989a). These results correspond well to neurophysiological findings which revealed that the tuning of the space-specific neurons (Knudsen and Konishi 1978) is due to their selectivity to ITD and ILD, and that ITD and ILD are processed independently in anatomically separate auditory pathways (Moiseff and Konishi 1983; Takahashi et al. 1984; Takahashi and Konishi 1988; Adolphs 1993; Mogdans and Knudsen 1994; Mazer 1998) up to the lateral shell of the central nucleus of the inferior colliculus.

Free-field stimuli contain all spatial cues that are available to the auditory system, but with free-field stimulation it is not possible to separate the contribution of the different single cues to sound perception. In previous closed-field experiments with barn owls, one or two parameters (ITD or ILD or both) were varied systematically. However, other possible cues that originate from the direction- and frequency-dependent filter characteristics of the external ear were ignored.

Such restrictions on stimulus presentation can be overcome with the virtual space technique. If sounds are filtered with the individual transfer functions of the external ears—the so-called head-related transfer functions (HRTFs)—before they are played to a human listener over headphones, the sounds can be externalized and heard at the simulated position outside the head (Plenge 1974; Buffer and Belendiuk 1977). Under optimal conditions, these virtual stimuli are indistinguishable from free-field sounds (Hartmann and Wittenberg 1996; Kulkarni and Colburn 1998), reflecting the fact that the HRTFs contain all relevant spatial cues of a sound.

Stimulation with virtual sounds offers the possibility of manipulating monaural or binaural parameters of an acoustic stimulus while leaving other cues as they occur in a natural free-field sound. Virtual auditory worlds have been used in psychophysical experiments with humans for many years. Most studies investigated the influence of features in the magnitude spectra of the complex HRTFs on sound localization in humans (e.g., Butler and Belendiuk 1977; Middlebrooks 1992; Blauert 1997). Other reports also dealt with the analysis of the HRTF phase spectra and their manipulation (Wightman and Kistler 1992; Kistler and Wightman 1992; Hartmann and Wittenberg 1996; Kulkarni et al. 1999).

Recently, the virtual space method has also been used in electrophysiological experiments with animals (cat: Poon and Brugge 1993; Brugge et al. 1994, 1998; guinea pig: Sterbing and Hartung 1999; barn owl: Keller et al. 1998). Interaural time or phase differences (ITD or IPD) and interaural level differences (ILD) appearing at the ears of barn owls were already measured in previous studies (Knudsen et al. 1991; Brainard et al. 1992; Keller et al. 1998) for sound positions

in the frontal hemisphere. Here we present spatial patterns of ITDs in the frontal hemisphere and in parts of the rear hemisphere of two owls that were calculated from their HRTFs. These data were used in psychophysical experiments with animals. By using normal virtual stimuli and by manipulating the broadband ITD in these stimuli while the direction-dependent monaural cues and ILDs were unchanged, we analyze the contribution of ITD to azimuthal and elevational sound-localization behavior.

METHODS

HRTF measurements and behavioral experiments were conducted with two captive-bred, adult barn owls. The initials of the owls' names (W and X) will be used for identification. HRTFs had been recorded about two months before the behavioral experiments with virtual stimuli started. All experiments were carried out in accordance with German law and the NIH guidelines for the care and use of laboratory animals and were approved by the Regierungspräsidium (Köln).

HRTF measurement

For the creation of a virtual acoustic space it was necessary to record HRTFs of each owl individually. Birds were anesthetized with diazepam (Valium, 1 mg/kg/h) and ketamin (4–20 mg/kg/h). A metal post was cemented to the skull of each bird as described in Wagner (1993). This holder enabled us to fix the head of the bird during the recordings in a constant position. The animal was placed in the center of a sound-attenuating chamber (2.4 m × 2.1 m × 2.7 m, IAC double wall, lined with pyramidal foam) in a natural posture. The tip of a 4-cm-long plastic tube that was fixed to a Sennheiser KE 4-211-2 microphone was positioned 15 mm inside the ear canal of each ear. We decided to measure at this position because no directional information was lost when measuring deeper than 7 mm inside the 17-mm-long ear canal of barn owls (Keller et al. 1998), and there was no danger of injury to the eardrum.

Computer-generated clicks with a duration of 12 μ s, amplified by a hi-fi amplifier (Denon PMA-S10), were used to measure HRTFs. The clicks were presented from a loudspeaker (TW6NG, 2–12 kHz: flat within ± 3 dB) 95 cm from the center of the owl's head. The speaker could be moved in elevation and azimuth on a semicircular vertical track. Microphone signals were preamplified by custom-built amplifiers, low-pass filtered (FT6, Tucker Davis Technologies, Gainesville, Florida, USA, corner frequency 20 kHz) and converted to a digital signal (sampling rate 50

kHz) by a computer board (DT2821, Data Translation, Marlboro, Massachusetts, USA).

Recordings of 1000 clicks were averaged for each of the 377 positions in space from -60° (lower hemisphere) to 60° elevation (upper hemisphere) and from -140° (left side of the animal) to 140° azimuth (right side) with 10° resolution. Elevation of 0° and 0° azimuth of the spherical coordinate system was in front of the owl. With this method, a signal-to-noise ratio of approximately 55–60 dB was reached for recordings in the front and of 35–40 dB for the positions at $\pm 140^\circ$ azimuth in the rear. The smallest signal-to-noise ratio measured at any position in frequency bands at least 3-kHz wide was 31 dB. Thus, although a single click has little energy, signal-to-noise ratios in the averaged signals were high enough for further analysis.

Additionally, a first reference measurement was made with earphones (SONY MDR-E831LP) in front of the ear canals while the microphone tubes were still inside the ear canals. A second reference measurement was made with the microphones fixed in the center of the sound-attenuating chamber without the owl, and clicks were played via the loudspeaker. Finally, we determined the loudspeaker's transfer function using a spectrum analyzer (DSP Technology SigLab, Fremont, California, USA) combined with a Brüel & Kjær microphone (No. 4135).

Calculation of virtual stimuli

Reflections from the hoop and other objects in the sound chamber that could be detected in the impulse responses as a delayed echo of the original transient signal were cut off by windowing with a Hanning window (length = 6 ms). HRTFs were calculated by dividing the complex spectrum of the recording in the ear canal by the spectrum of the second reference without owl. Since there were no notches in the first reference measurements, filter functions for virtual stimuli could be prepared by dividing the complex spectrum of the signal measured in the ear canal by the complex spectrum of the first reference measurement outside the ear canal. Such a calculation corrects for the transfer function of the microphones, the SONY earphones, and the ear canal. The last manipulation is necessary because the virtual stimuli are presented via the Sony earphones during the behavioral experiments at the entrance of the ear canal. We did not compensate for the loudspeaker characteristics because the loudspeaker's transfer function was flat within ± 3 dB and its influence was the same for all positions in space and for both ears. The resulting transfer functions were band-pass filtered (2–12 kHz) and then used to create a set of virtual stimuli by convolving 50-ms noise bursts with the impulse responses.

Manipulation of HRTFs

To manipulate the virtual stimuli, the time-domain equivalent of the HRTFs—the head-related impulse responses (HRIRs)—were used. We calculated the time shift of the maximum of the cross correlation function between the HRIRs of the right and left ear for each position in space (Fig. 1c). This time shift in the HRIRs represents the (broadband) overall interaural time difference that is produced by a sound source at the respective position (Fig. 1a α , b). We did not interpolate the HRIRs, so the accuracy of the fixation was limited to multiples of $20 \mu\text{s}$ according to the sampling rate. By shifting the HRIRs of the two ears against each other on the time scale, we fixed the ITD for each of the behaviorally tested positions in space to $-100 \mu\text{s}$ (left ear leading right ear, called FixT $_{-100}$ stimuli, Fig. 1a γ) or to $100 \mu\text{s}$ (right ear leading left ear, called FixT $_{100}$ stimuli, Fig. 1a β) for two further sets of filter functions. This manipulation affects temporal features but not the amplitude spectra of the HRTFs, including the frequency-dependent interaural level differences. Since time adjustment was performed as a pure temporal delay, small frequency-dependent phase differences that do not exactly match this delay may still occur in the phase spectra. To avoid distortion of the HRIR shape, we preferred to keep these phase differences, since they exist also in the unmodified HRTFs.

Two additional sets of virtual stimuli were generated in which the HRTFs were manipulated so that the overall interaural level difference was fixed to -6 dB and $+6$ dB. To minimize the effect of frequency ranges that would influence the calculation of ILD values but that are less important for sound localization in the owl, the stimuli were band-pass filtered from 4 to 10 kHz. This frequency range was chosen because it encompasses the frequencies important for sound localization in the barn owl (Konishi 1973).

For the manipulation of filter functions, the energy between 4 and 10 kHz was calculated (in dB) from the amplitude spectrum of the HRTF for each ear. Then the averaged energy of each ear was adjusted so that the overall interaural level difference was either 6 dB (right ear louder than left ear, called FixL $_6$ stimuli) or -6 dB (left ear louder than right ear, called FixL $_{-6}$ stimuli) after that step. With this manipulation the overall ILD was changed, but not the monaural spectral shape and the phase spectrum of the HRTFs. Stimuli were calculated by filtering 50-ms white noise bursts with the manipulated HRTFs.

Training procedures and psychophysical experiments

In the owl, head turning is a natural reaction to faint sounds. We exploited this reaction and trained two

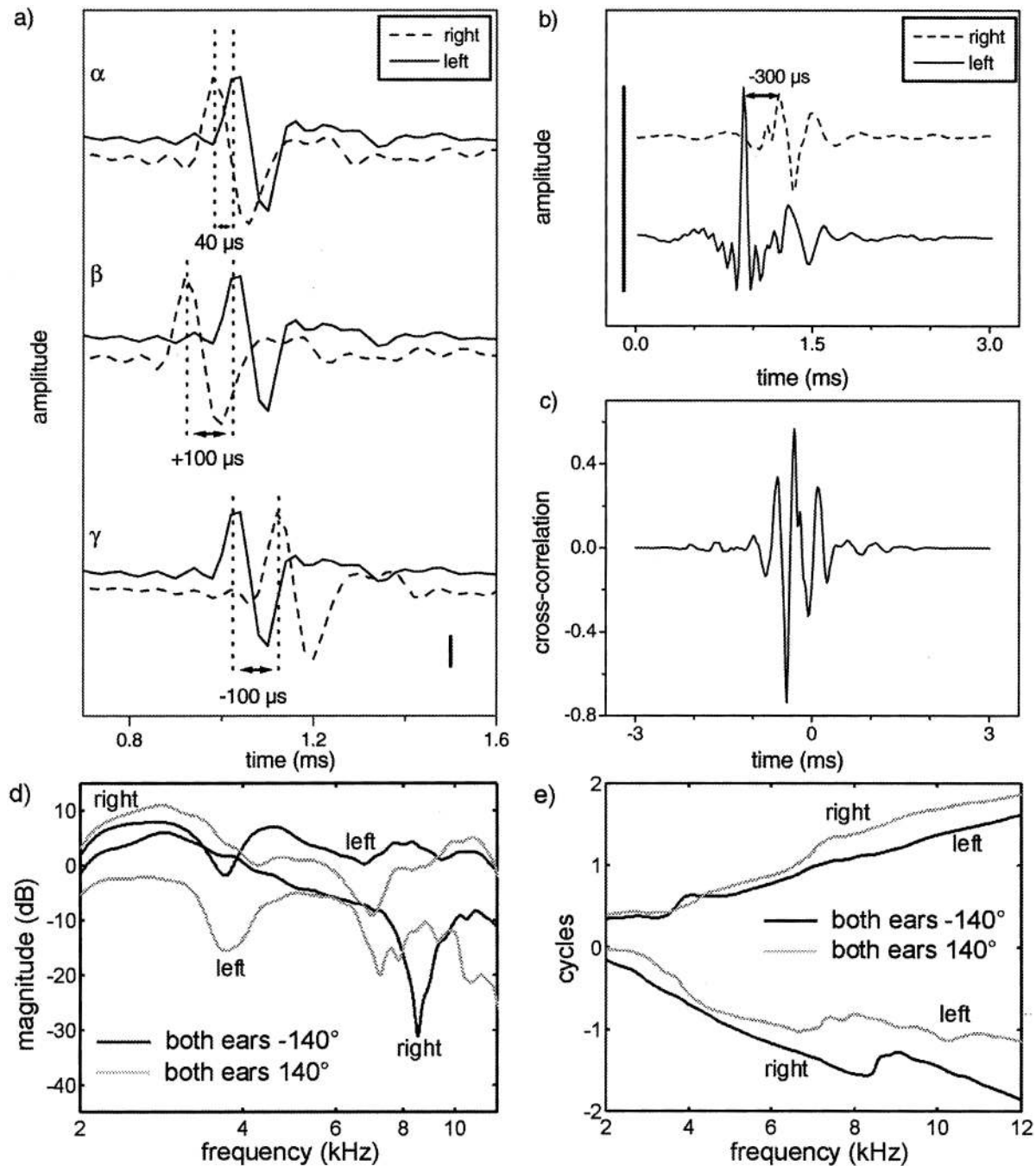


FIG. 1. Calculation of ITDs, manipulation of head-related impulse responses (HRIR), and HRTFs in the rear. **a, b.** HRIRs of both ears for two of the positions in space at which virtual stimuli were used in the behavioral experiments (**a** azimuth: 20° , elevation: 0° ; **b** azimuth: -140° , elevation 0°). The curves of the different ears were slightly shifted in the vertical direction for a clearer presentation. The vertical scale bars denote the same relative amplitude (in V) in both subplots. Note that signals in the front of the owl are about a factor 4–8 larger than in the rear. **a.** The time shift of the unmanipulated HRIRs (dotted lines) represents the naturally occurring ITD (α). **b.** For the manipulation, HRIRs were shifted on the time scale so that an ITD of $100 \mu\text{s}$ (FixT₁₀₀ stimuli, β) or $-100 \mu\text{s}$ (FixT₋₁₀₀ stimuli, γ).

c. Normalized cross-correlation function of the HRIRs presented in **b.** For the calculation of virtual FixT stimuli, the exact position of the peak of the HRIRs' cross-correlation function was calculated to determine the necessary shift of the HRIRs. Note that the cross-correlation function has a clear peak even for a position in the rear where large differences in the shape of the HRIRs of both ears were found and the signal-to-noise ratio was smaller than in the front. **d.** Amplitude spectra of the HRTFs at $\pm 140^\circ$ azimuth and 0° elevation for both ears. **e.** Corresponding phase spectra of the HRTFs presented in **d.** For a clearer presentation, phase spectra were unwrapped, hence phase angles are given in multiples of 2π .

owls to reliably turn their heads in the direction of sounds under free-field conditions for many trials. During the experiments the bird was sitting on a perch in a sound-attenuating chamber with a head tracker fixed at its head holder (search coil system described in Wagner 1993). If the owl had turned its head to a forward direction ($0^\circ \pm 10^\circ$ azimuth, $0^\circ \pm 10^\circ$ elevation) that was marked with a LED, a 50-ms noise burst was presented from one of two stimulus loudspeakers that were positioned at different sides and azimuthal angles to the animal. The azimuthal and elevational component of the animal's head position was recorded for 1 s (200 samples per second) starting with the beginning of the stimulus. The short duration of the stimuli ascertained that the animal operated under open-loop conditions (Wagner 1993), i.e., the stimulus ended before the head turn started. To mask the background noise of the stimulus loudspeakers, which would also destroy the open-loop conditions in the free-field experiments, six more loudspeakers were positioned around the owl. The same continuous white noise was delivered through these speakers during the whole experimental free-field session.

If the bird reacted to the stimulation with a head turn into the direction of the stimulus speaker, it received a piece of meat as a reward. If the bird did not react at all or showed only a twitch to the side followed by a head turn to the feeder, it was not rewarded and the same stimulus was repeated until the animal reacted correctly (repetition trials). Using this method, about 70%–90% of all trials led to a rewarded reaction. After a few weeks the birds performed well and worked for some 50–150 trials per day. We collected sound-localization data under free-field conditions with stimuli at 0° elevation and various azimuthal angles for both birds. To maintain the animals' interest in the task, their weight was reduced to 85%–90% of the normal weight. The weight was checked every time before a session started.

After the animals responded reliably to free-field stimuli, they were exposed to normal virtual stimuli without additional background noise. We used a head-phone holder that could be attached to the animal's head holder to position the earphones in front of the ear canals. The earphones had a slightly larger diameter than the ear canal which allowed for reproducible and exact positioning. Virtual sounds were presented via a computer-controlled sound-generating system (System II, Tucker Davis Technologies, Gainesville, Florida, USA).

The animals needed about a week to get accustomed to the earphones. During this period and the following few weeks, only normal virtual stimuli were presented. Manipulated stimuli with fixed ITD were then interspersed between the normal virtual stimuli in 20% of all trials. Manipulated stimuli were rewarded

randomly at the same rate as the normal stimuli (72% of the cases). Responses to manipulated stimuli were not reinforced by repetition trials, which means that the stimulus was not repeated, independent of the reaction of the bird.

In a first series of experiments with virtual stimulation, normal and FixT stimuli were presented at 18 positions in space in the frontal hemisphere at azimuth angles of -60° , -40° , -20° , 20° , 40° , and 60° and at elevations of -30° , 0° , and 30° . The order of the stimuli was varied pseudorandomly. Over a period of about 2 months each manipulated stimulus was presented 20 times for each tested position.

In a second series of experiments, we tested normal and manipulated virtual stimuli with fixed ITD at four different positions in space, including two positions in the back (azimuth: 40° , 140° , -40° , -140° ; elevation: 0° for all stimuli). For these experiments another, head tracker (Ascension Minibird, Ascension Technology, Burlington, Vermont, USA; sampling rate 100 Hz) was used which enabled us to record head turns that were greater than 90° azimuth angle. The output of this head tracker was influenced by magnetic objects. This influence was determined by a calibration procedure and was eliminated by correcting the recorded data accordingly. We increased the rate of manipulated stimuli to 40% for the second series of experiments because test sessions revealed that 60% of normal stimuli was sufficient to keep the animals under stimulus control.

After these experiments with virtual stimulation, we again collected free-field data with two loudspeakers. Speaker positions were changed for every session between $\pm 40^\circ$ and $\pm 140^\circ$ azimuth and 0° elevation.

In the last series of experiments, normal virtual stimuli and stimuli with fixed ILDs were presented to the owls at 18 different positions in space (azimuth: $\pm 40^\circ$; elevation: 0° , $\pm 10^\circ$, $\pm 20^\circ$, $\pm 30^\circ$, $\pm 40^\circ$). In 40% of all trials, FixL stimuli were interspersed between normal virtual stimuli. The manipulated stimuli were again rewarded randomly in 72% of the presentations. In 25 sessions per bird and about 100 trials per session, each manipulated stimulus in space was presented 20 times.

Data analysis

The head tracks were processed using software routines written in MATLAB. First, the starting point of each track that was induced with virtual stimulation was set to 0° azimuth or elevation because the owl always hears a simulated virtual stimulus relative to its own head-centered coordinate system independent of the head position during the presentation of the stimulus. It had been shown before that the initial head position does not influence head turning (Wagner

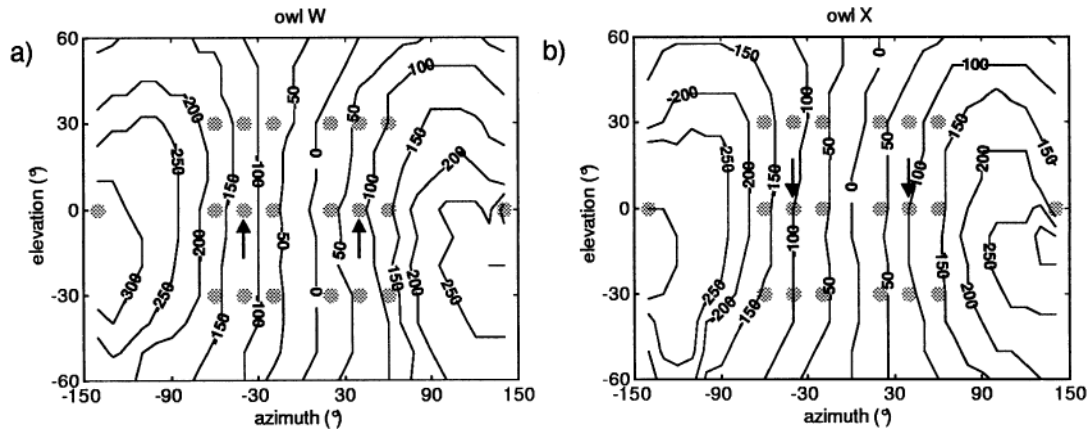


FIG. 2. Spatial pattern of ITD values calculated from the HRIRs of both owls (**a**: owl W; **b**: owl X). The iso-ITD contour lines are drawn at intervals of $50 \mu\text{s}$. Positive numbers indicate that the signal at the right ear is leading. The arrows mark the space positions at $\sim 40^\circ$ azimuth and 0° elevation. Note that ITDs were determined only in

steps of $20 \mu\text{s}$. Spatial positions are given in spherical coordinates. 0° elevation and 0° azimuth is in front of the owl, negative angles mean lower or left hemisphere, respectively. The gray dots mark the positions in space where virtual stimuli were simulated in the behavioral experiments.

1993). Second, the angle of the head position after the reaction was calculated. Third, the response delay of the reaction was measured. Statistical tests were carried out with the professional software packages JUMP or SPSS.

RESULTS

HRTFs in the rear hemisphere

Since HRTFs of barn owls for the rear hemisphere have not been published as yet, we present the amplitude and phase spectra of the transfer functions for the rear positions that were used in the behavioral experiments in this study (Fig. 1d, e). HRTFs measured for rear positions often had spectral notches in the amplitude spectrum of one ear (e.g., see solid gray line at 8.5 kHz in Fig. 1d). Phase spectra of the HRTFs were approximately linear after they were unwrapped by the algorithm provided by MATLAB (Fig. 1e). Distortions of the linear course typically appeared at frequencies where notches of the amplitude spectrum were observed.

Spatial pattern of ITD

Since the HRIRs for a specific position in space contain all relevant acoustical information that is available to the auditory system when a subject is listening to free-field sounds, they could be used to calculate the ITDs in the frontal hemisphere and in parts of the rear hemisphere of the two owls (owl W and owl X, Fig. 2). The time difference of the HRIRs of the right and the left ears represents the time shift that a sound

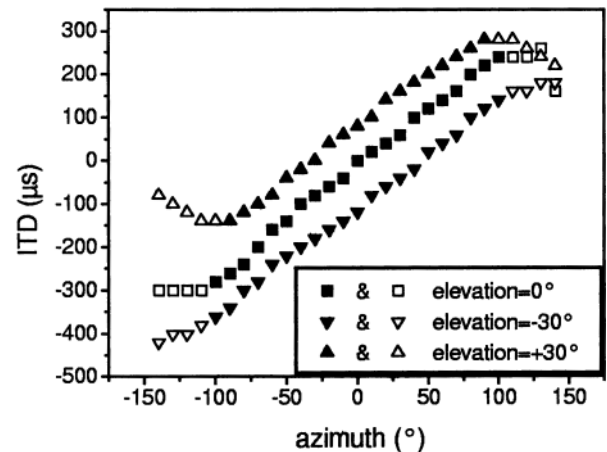


FIG. 3. Dependence of ITD calculated from the HRIRs on azimuth for owl X at elevation 0° and $\pm 30^\circ$. For clarity, the symbols for elevation $\pm 30^\circ$ were shifted by $\pm 100 \mu\text{s}$ in vertical direction. The filled symbols indicate which data points were included when linear fits were calculated. Note that ITDs are increasing in the rear hemisphere at elevation 0° and -30° .

source evokes at the ears. The HRIRs for both ears of owl X that were measured at 20° azimuth and 0° elevation—one of the positions at which virtual stimuli were simulated in the behavioral experiments—revealed an ITD of $40 \mu\text{s}$ for this position (Fig. 1a α).

If we assume that the head is a sphere with symmetrical ears, ITD would be $0 \mu\text{s}$ along the vertical meridian passing through 0° azimuth. ITDs should increase from 0° to 90° azimuth and then decrease again from 90° to 180° , with the vertical meridian at 90° forming a symmetry axis. Such a change in ITD was not observed in our measurements. Instead, ITDs changed linearly with azimuth (azi) up to at least 100° (Figs. 2, 3). Therefore, data analysis was accomplished by simple

TABLE 1

Results from linear regression between ITD and azimuth ^a						
	Owl W at elevation			Owl X at elevation		
	-30°	0°	30°	-30°	0°	30°
Slope ± SD (°/μs)	0.40 ± 0.02	0.37 ± 0.01	0.44 ± 0.01	0.40 ± 0.01	0.38 ± 0.01	0.42 ± 0.01
Intercept ± SD (°)	8.4 ± 1.0	4.9 ± 0.6	15.7 ± 0.7	3.1 ± 0.7	4.7 ± 0.8	9.6 ± 0.8

^a $R > 0.997$, $p < 0.0001$ for all linear fits.

linear regression between ITD and azimuth and not by a sinusoidal model (Fig. 3). The resulting linear equations were transformed to express azimuth independence of ITD to allow a comparison of the data with earlier studies (Table 1).

The values of the intercepts (Table 1) demonstrated that an ITD of 0 μs was shifted by 3°–16° with respect to 0° azimuth in the external coordinate system, indicating an influence of owl positioning and elevation on the measured ITD. In owl W the ITD pattern was shifted by about 20 μs compared with owl X (Fig. 2). The slope in the regression lines (Table 1) revealed that an ITD change of 100 μs corresponds to an azimuth change of about 40°.

For assembling the contour plots in Figure 2, the actually calculated ITDs were used. Since ITDs were calculated only in steps of 20 μs, sometimes a slight mismatch between the ITD calculated from the regression lines and the ITDs appearing on the contour plots may be observed.

Although we did not measure ITDs in a full sphere, the contour plots (Fig. 2) and the data presented in Figure 3 demonstrate that there is no axis of symmetry at 90° and -90°. For azimuth angles from 100° to 140° and from -100° to -140°, respectively, ITDs did not change (elevation 0°) or even increased up to values of ±300 μs (Fig. 3 at elevation -30°). Only for positive elevations did we find declining ITDs in the rear hemisphere between 110° and 140°. The curved iso-ITD lines (Fig. 2) in the upper hemisphere indicate that ITDs will decrease again between 140° and 180° for lower elevations, which is also expected for the other elevations. While the ITD values increased beyond ±90° azimuth, the amplitudes of the HRIRs decreased compared with frontal positions (Fig. 1b), reflecting that there was a smaller signal-to-noise ratio for the HRIRs in the rear (35 dB) than in the front (55 dB).

Response to free-field and normal virtual stimuli

The reaction of barn owls to faint sounds is usually a single fast turn of the head in the direction of the sound source, followed by a prolonged period during which the bird fixates the source. Our head trackers

separated the response into an azimuthal and an elevational component (Fig. 4). Response latencies of azimuthal components were usually around 130 ms under both free-field and virtual conditions (Fig. 4a). For a given head turn, the response latencies of the elevational components were typically longer than that of the azimuthal component (Fig. 4b). The head turns were completed within some 200 ms (Fig. 4). Subsequently, the owl looked to the perceived sound position usually for more than 200 ms, resulting in a plateau of the azimuthal and elevational head track (Fig. 4 α, γ). If the owl turned its head but did not keep it fixed after the turn for at least 50 ms, the trial was not used in further analysis. Repetition trials were also not considered. If the owl moved its head less than 5° in azimuth, the trial was classified as no-reaction trial (Fig. 3 β).

As already mentioned, reactions to stimuli in the frontal hemisphere and in the rear hemisphere were investigated in a separate series of experiments. We did not pool the data of the two series but analyzed them separately for two reasons: First, we cannot exclude that there are long-term effects or effects caused by the daily variability that influences the owl's sound-localization performance. Second, different head tracker systems were used in the experiments.

Both owls responded to the free-field stimuli of varying azimuthal locations in the frontal hemisphere with a head turn in the direction of the speaker position in most trials. Four percent of the trials with owl W and 7% of the trials with owl X were classified as no-reaction trials in this experimental series. A head turn to the wrong side, i.e., a turn to the right although the stimulus was presented on the left side or vice versa, was observed only once for owl W. If the birds responded with a head turn, they usually undershot the target positions especially for more lateral azimuthal angles (Fig. 5a, b). In spite of intensive training, the accuracy of azimuthal localization could be only slightly improved. A linear regression of the data resulted in the following equations:

$$\text{Owl W: } \text{azi}_{\text{owl}} \text{ (in deg)} = 0.73 \pm 0.01$$

$$\times \text{azi}_{\text{stimulus}} \text{ (in deg)} + 4.5 \pm 0.3 \text{ deg} \quad (1)$$

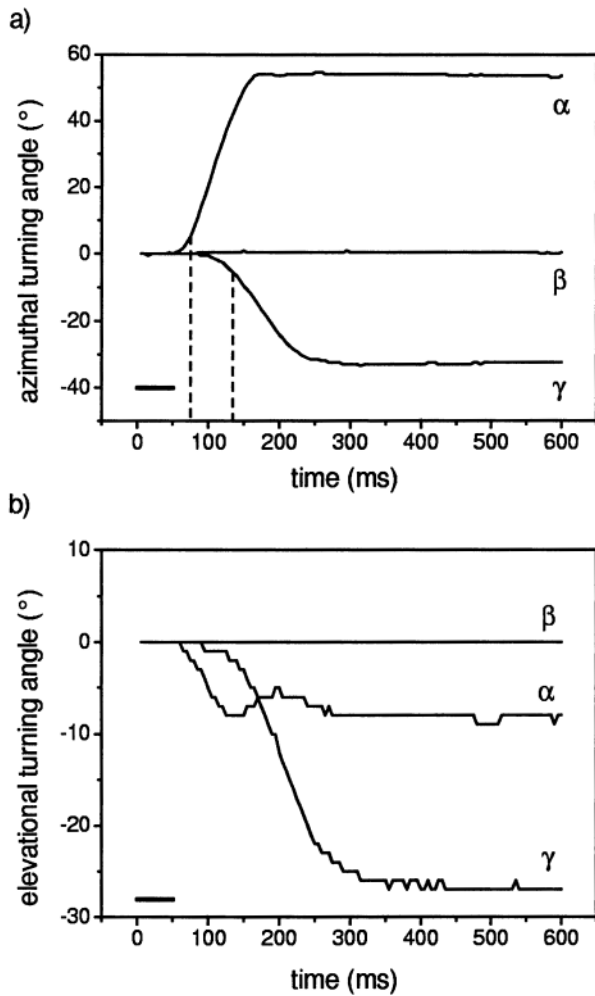


FIG. 4. **a** Azimuthal and **b** elevational components of three typical head turns (α , β , γ). When the owl looked to a position in the direction of $0^\circ \pm 10^\circ$ azimuth and $0^\circ \pm 10^\circ$ elevation, the virtual stimulus was presented. The duration of the stimulus is indicated by the bar above the time axis. The head position at stimulus onset was defined as 0° in the head-centered coordinate system. The owl turned its head with a latency of 75 ms in trial α and 135 ms in trial γ as indicated by the dotted lines. The criterion for the initiation of the turn was a change in azimuth of more than 5° . After the movement the animal kept its head still for a few hundred milliseconds, resulting in a plateau of the head track that allowed the measurement of an end position. The azimuthal stimulus positions for the presented trials were 60° (α), 40° (β), and -40° (γ), the elevational positions were 0° (α), 30° (β), and -30° (γ). Since the owl moved its head less than 5° in trial β , this trial was classified as no-reaction trial.

Owl X: azi_{owl} (in deg) = 0.66 ± 0.01

$$\times azi_{stimulus} \text{ (in deg)} + 2.0 \pm 0.4 \text{ deg} \quad (2)$$

Both owls responded to virtual acoustic stimuli in the frontal hemisphere with the same behavior as they did to free-field stimuli. The virtual stimuli elicited head turns to the simulated positions in space (Figs. 5c, d; 9a–d). When stimuli with positive azimuthal angles were presented, we expected a head turn to the right side (correct side), while a turn to the left

would reflect a response to the wrong side and vice versa. Azimuthal head turns to the wrong side rarely occurred. Owl W made 5 failures in 2769 trials (0.2%). Owl X never turned to the wrong side when normal virtual stimuli were presented. The turns to the wrong side in owl W did appear randomly as responses to different virtual stimuli and may be explained by a lack of attention. Additionally, we never observed signs of front/back confusions when stimuli in the frontal hemisphere were presented.

In both animals a linear relationship was found between the azimuthal position of the stimulus and the amplitude of the head turn (Fig. 5c, d). A linear regression of the data at 0° elevation resulted in the following equations:

Owl W: azi_{owl} (in deg) = 0.70 ± 0.01

$$\times azi_{stimulus} \text{ (in deg)} + 2.7 \pm 0.2 \text{ deg} \quad (3)$$

Owl X: azi_{owl} (in deg) = 0.55 ± 0.01

$$\times azi_{stimulus} \text{ (in deg)} + 4.5 \pm 0.2 \text{ deg} \quad (4)$$

Consistent with the free-field data, an increasing underestimation of target location was observed for more laterally presented stimuli also under virtual space conditions. A comparison of Eqs. (1) and (2) with Eqs. (3) and (4) demonstrates the similarity of the azimuthal localization performance under free-field and virtual conditions. This is underlined by a comparison of the variances for different azimuthal locations in space at elevation 0° under the two experimental conditions, which did not reveal significant differences (Wilcoxon signed ranks test, owl W: $p = 0.94$, owl X: $p = 0.13$).

Azimuthal reactions to virtual stimuli with fixed ITDs

The owls did not show signs of unusual reactions when manipulated virtual stimuli were presented. Both owls reacted to these stimuli with a head turn. If ITD had been fixed to $100 \mu\text{s}$, the birds turned their heads to the right side. If ITD had been fixed to $-100 \mu\text{s}$, they turned their heads to the left side, independent of the position in space that was encoded by other spatial cues of the acoustic signal (Figs. 5e, f; 6). Thus, the direction of the head turn was determined by the ITD value of the stimulus presented. This was true when the ITD and the other spatial cues pointed in the same direction (same-side configuration), as well as when the ITD and the other spatial cues of the stimulus pointed to different hemispheres (opposite-side configuration). Exceptions from this general result were observed in 0.5% of the trials for owl W and never for owl X. The mean amplitude of the azimuthal head

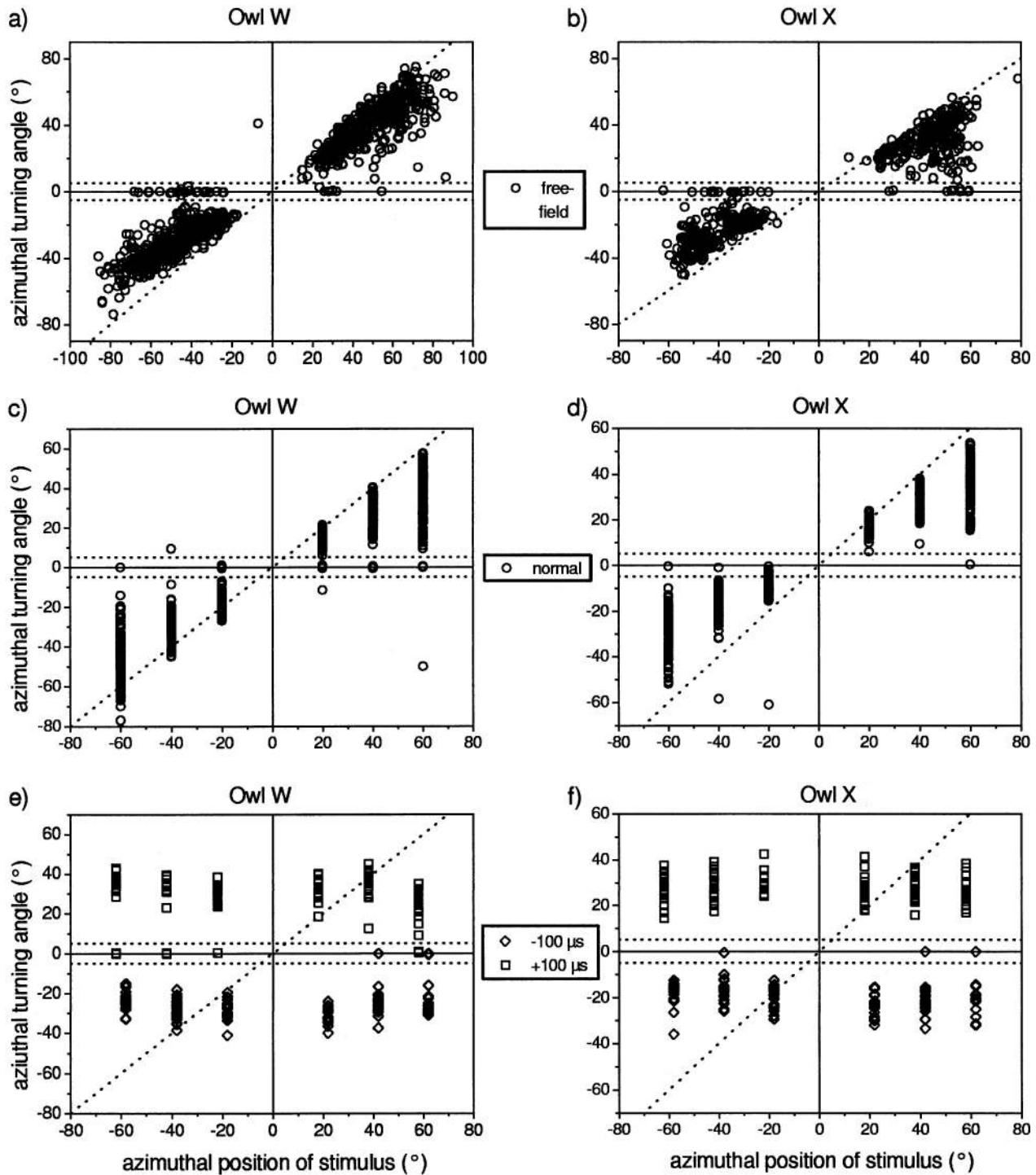


FIG. 5. Scatter diagrams of azimuthal components of head turns, **a, b.** Responses to free-field stimuli of owl W **a** ($N = 819$) and **b** X ($N = 485$). In the free-field experiments the azimuthal stimulus position was calculated as the azimuthal difference between the speaker position and the bird's initial head position. Since the initial head positions of the trials scattered about $\pm 10^\circ$ around 0° azimuth, the azimuthal stimulus position also scatters. Note the linear relation between the head-turning angle and the azimuthal position of the stimulus. The dotted lines at $\pm 5^\circ$ mark the thresholds for the classification of no-reaction trials. **c, d.** Responses to normal virtual stimuli of **c** owl W and **d** owl X. At each azimuth about 160 trials were presented. Since the direction of the virtual stimuli is given in head-

centered coordinates, there is no scatter of the stimulus position. Note the similarity to the data in **a, b, e, f.** Responses to manipulated virtual stimuli with fixed ITDs of **e** owl W and **f** Owl X. At each azimuth and for each stimulus type about 20 trials were conducted. In these two scatter diagrams the azimuthal stimulus position on the abscissa means that all spatial cues of the stimulus reproduced a sound at the specific position except for the ITD. For clarity, the data points representing FixT_{-100} stimuli (square symbols) are shifted slightly to the left, while the data points representing FixT_{+100} stimuli (diamond symbols) are shifted to the right on the x axis. Note that the head-turn amplitude is independent of the stimulus position for the manipulated stimuli. Elevation was 0° for all stimuli.

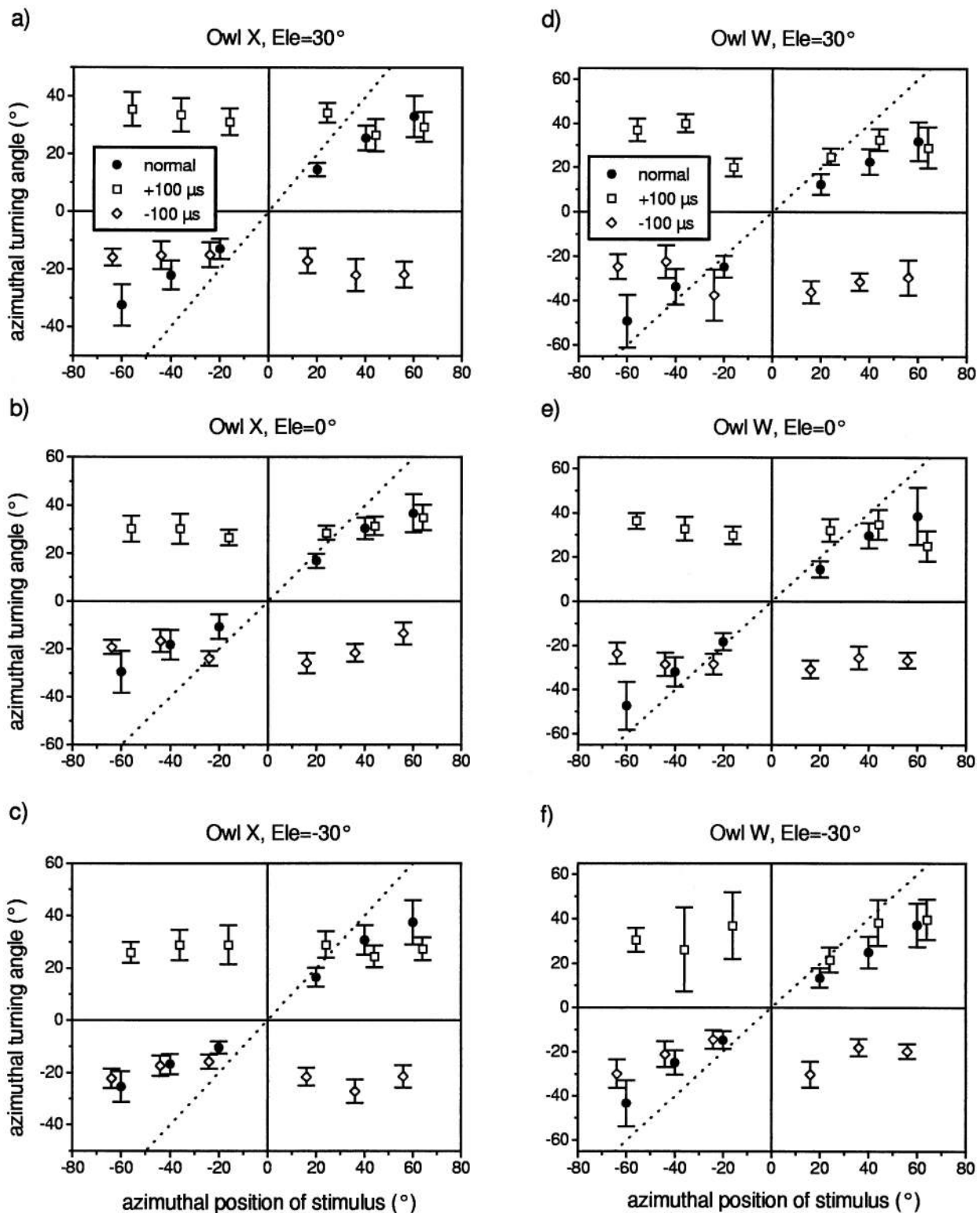


FIG. 6. Sound-localization behavior at three different elevations. Each diagram shows the mean turning angles to normal ($N = 150-170$) and manipulated virtual stimuli ($N = 15-20$) with fixed ITDs (see legend in upper plot). Error bars represent the standard deviations.

No-reaction trials and head turns to the wrong hemisphere were not included in the calculation of the mean values. For clarity, symbols for the different stimulus types are shifted as described in the legend to Fig. 5.

TABLE 2

Results from six covariance analyses of azimuthal turning amplitudes. Each column presents the results of one ANCOVA; the values represent the F statistics. Degrees of freedom = 1 and $R^2 > 0.95$ for all six tests

x factors of covariance analysis		Owl X at elevation			Owl W at elevation		
		-30	0	30	-30	0	30
FixT ₁₀₀	Stimulus type	727 ^e	452 ^e	1478 ^e	174 ^e	1002 ^e	230 ^e
vs.	Azimuth ^a	1.39	0.59	14.3 ^d	1.12	1.91	1.56
FixT ₋₁₀₀	Type ^a azimuth ^b	0.613	0.178	0.06	0.0795	0.86	0.0014

^a Cofactor of the ANCOVAs.

^b Interaction term.

^c $p < 0.05$.

^d $p < 0.01$.

^e $p < 0.001$.

turns for the different positions was similar to the mean amplitude of head turns to normal virtual stimuli at -40° and 40° , respectively. Since the responses of each owl to repetitions of the same stimulus clustered around one direction in space and were distributed normally (Kolmogorov–Smirnov test, $p > 0.05$) for the vast majority of the different stimuli tested, we present mean and not median values in Figure 6. The influence of ITD fixation depended somewhat on the elevational component of the stimulus (Fig. 6). For 0° elevation, response amplitudes seemed to be independent of azimuth in both owls (Fig. 6b, e). This held true also for the other two elevations tested in owl X and for 30° of elevation in owl W (Fig 6a, c, d). However, for an elevation of -30° , the responses of owl W to the manipulated stimuli seemed to be very similar to the reactions to the normal stimuli, if the ITD information and the other spatial cues of the manipulated stimuli pointed to the same hemisphere (Fig. 6f).

We compared the mean azimuthal turning amplitudes of the normal virtual stimuli with the mean amplitudes of the FixT stimuli as presented in Figure 6 separately for each elevation with a covariance analysis. This resulted in 9 ANCOVAs (3 elevations and 3 stimulus types) for each animal analogous to the presentation in Figure 6. A highly significant difference between the responses to normal virtual stimuli and FixT stimuli was observed for all elevations and for both owls ($p < 0.001$). The head turns evoked by the manipulated stimuli did not depend significantly on the azimuth of the stimulus in 5 of 6 tests (Table 2). They depended only on stimulus type, even for the data of owl W at -30° of elevation (Table 2). This means that the major determinant of the azimuthal angle is ITD, and that other factors play a much smaller role, if at all.

In another statistical analysis, we investigated whether localization precision differed between the different stimulus types. The reactions to the manipulated stimuli (Fig. 5e, f) gave rise to the assumption

that the owls perceived a spatially restricted and not a spatially diffuse sound source, because their head turns scattered around a distinct position in space. Hence, we performed a test between the standard deviations of the different stimulus types at each location in space. The localization of normal virtual stimuli was not significantly more precise than the localization of the stimuli with the fixed ITDs (one-sided Wilcoxon signed ranks test, owl X: normal vs. FixT₁₀₀: $p = 0.80$, normal vs. FixT₋₁₀₀: $p = 0.98$; owl W: normal vs. FixT₁₀₀: $p = 0.68$, normal vs. FixT₋₁₀₀: $p = 0.96$). This confirmed the impression that the owls perceive one spatially restricted sound source and not two sources or a diffuse sound image when stimulated with the manipulated virtual stimuli.

Latencies of azimuthal head turns

The unusual combination of spatial cues might influence characteristics of the head turn other than amplitude, specifically response latencies. The deviation of the head trajectory in azimuth of 5° from the start point was measured as response latency. With this criterion the measured values are about 5–10 ms longer than the exact latency of the behavioral reaction. Distributions of latencies were asymmetrical in most cases. Usually the distributions of latencies for different spatial directions had a steep rising flank and a steep falling flank, followed by a long tail (Fig. 7a). Only about 5% of the latencies were shorter than 85 ms. The shortest latency was 55 ms. The latency of 95% of all head turns was shorter than 300 ms. Since the latency distributions were asymmetric, the medians of the distributions were used in the comparisons. The latencies of the reactions to the normal stimuli were shorter than the latencies of the reactions to FixT stimuli, but only the difference to stimulus type FixT₋₁₀₀ was significant (Wilcoxon signed ranks test, FixT₁₀₀: owl X: $p = 0.72$, owl W: $p = 0.99$; FixT₋₁₀₀: owl X: $p = 0.004$, owl W: $p = 0.028$). A more detailed

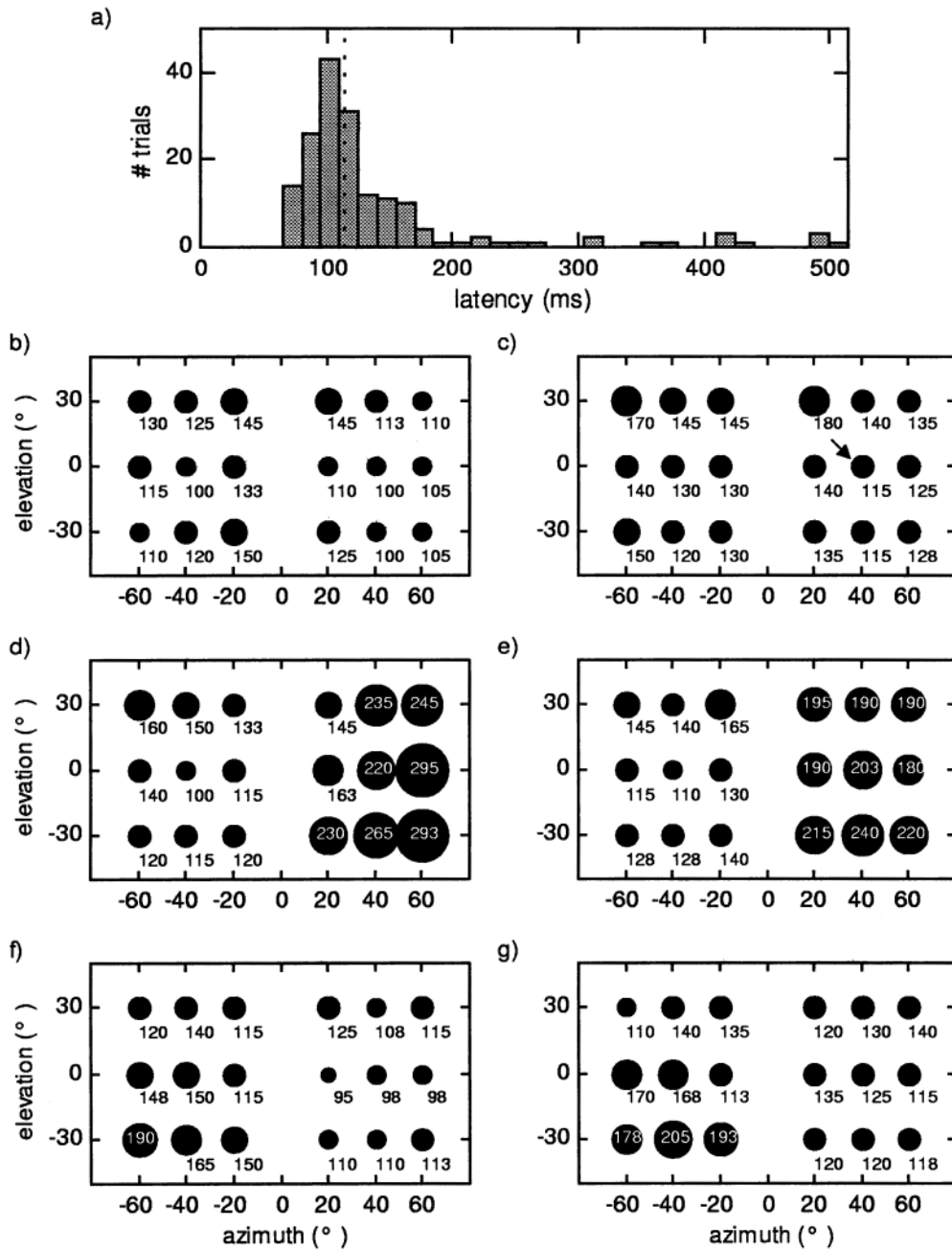


FIG. 7. Latencies of head turns, **a**. Example for a distribution of response latencies [owl W at 0° elevation and 40° azimuth (bin width: 20 ms)]. The dotted line marks the median of the distribution at 115 ms. **b–g**. Medians of response latency distributions measured for different stimulus positions and stimulus types for **b,d,f** X owl and **c,e,g** owl W. The median of each distribution is symbolized by the diameter of the dots in the bubble plots. The exact values of the

medians are printed next to or inside each bubble. The data point resulting from the distribution in **a** is marked by an arrow in **c**, **b**, **c**. Response delays measured with normal virtual stimuli (**d,e**: FixT₋₁₀₀ stimuli; **f,g**: FixT₁₀₀ stimuli). Note that the latencies for the opposite-side configuration are longer than the latencies for the same-side configuration.

analysis of the latencies showed that this difference is caused by the longer reaction time to the manipulated stimuli in the opposite-side configuration (Fig. 7d–g). If ITD information and other stimulus cues pointed to the same hemisphere, the latencies were similar to the values measured with normal virtual sounds. Latencies in the opposite-side configuration

were on average about 60 ms longer than for normal stimuli, especially for elevations at 0° and -30° . A comparison of latencies of the opposite-side and the same-side configurations revealed that the effect is significant for both owls and for each manipulated stimulus type (Wilcoxon-Mann-Whitney test: $p < 0.002$ for all tests).

No-reaction trials

As already described in previous studies, barn owls sometimes do not react to the acoustic stimuli presented. Such no-reaction trials occurred in 2.8% of the trials with normal virtual stimulation of owl X and in 7.9% of those trials of owl W. The proportion of no-reaction trials was not significantly higher for the FixT stimuli (χ^2 test: $df = 1$, $p > 0.05$, owl X: $\chi^2 = 3.837$; owl W: $\chi^2 = 0.069$). However, the owls responded less often to manipulated stimuli of the opposite-side configuration than to the stimuli of the same-side configuration (χ^2 test: $df = 1$, $p < 0.05$, owl X: $\chi^2 = 5.26$; owl W: $\chi^2 = 13.7$) indicating an influence of contradicting acoustical information on the behavior of the animals.

Elevational components of head turns in the frontal hemisphere

If the elevational component of a head turn was larger than 5° , the turning angle in the vertical direction of the trial was determined with the same method as already described for the azimuthal components. If the elevational component was smaller than 5° but the azimuthal component exceeded 5° , the elevational head-turning component was determined at the same instant in time as the azimuthal component.

Both owls responded to normal virtual stimuli at 0° elevation with head turns to about -10° elevation (Fig. 8, filled circles). This bias to lower elevations was also observed for source positions at $\pm 30^\circ$ elevation. Thus, the elevational position of the sound source was perceived to be shifted by about 10° to lower sound positions in the virtual experiments. This suggested that the elevational head position during the HRTF measurement did not exactly match the natural head position of the animal when looking to the front.

A linear relationship between the position of the stimulus and the amplitude of the head turn was also observed for the elevational components. Owls underestimated elevations more for stimuli from lateral positions than for stimuli from frontal locations. However, elevational components scattered a lot, probably because the training regimen did not reinforce elevational head turns.

To investigate the influence of the fixation of ITD on the elevational component, we compared the reactions of the animals to normal stimuli with those to manipulated stimuli at different elevations (Fig. 8a–d). At -40° azimuth the results of the normal stimuli and the data of the FixT₋₁₀₀ stimuli did not differ significantly (Fig. 8c, d, ANCOVA $p > 0.05$, $R^2 > 0.96$). This was not surprising, because the normal stimuli at -40° azimuth had a natural ITD of about $-100 \mu\text{s}$ (Fig. 2,a) and consequently were almost identical with the FixT₋₁₀₀ stimuli at this azimuth. In contrast, the

amplitudes of responses to FixT₋₁₀₀ stimuli were reduced compared with amplitudes of responses to the normal stimuli at -40° azimuth, especially for -30° and $+30^\circ$ of elevation (Fig. 8c, d). As described above, FixT₁₀₀ stimuli elicited azimuthal head turns to the side contralateral to 40° azimuth. Accordingly, in owl X at 40° azimuth, the elevational components of the head turns for normal and FixT₁₀₀ stimuli were similar and the turning amplitudes of FixT₋₁₀₀ stimuli were different (Fig. 8b).

Thus, the elevational component of the head turns also depends on ITD because the turning amplitude of the owls is different if the stimuli contain different ITD information while all other spatial cues are identical. This effect was significant for owl X but not for owl W (ANCOVA, $p < 0.05$, $R^2 > 0.96$).

For 0° elevation, there was not much change of the elevational head-turning component with azimuth in owl W (Fig. 8e). However, owl X turned its head to higher elevation positions if FixT₋₁₀₀ stimuli were presented in the opposite-side configuration (Fig. 8f, open diamonds).

Localization of stimuli in the rear hemisphere

The data presented in the following section were obtained in a separate series of experiments in which behavioral reactions to $\pm 40^\circ$ (control) and to $\pm 140^\circ$ were recorded with free-field and virtual stimulation. These values were chosen because they are symmetrical about the 90° axis of a spherical head model. The mean azimuthal head-turning amplitudes under virtual space conditions were not significantly different from the mean turning amplitudes under free-field conditions for the control directions at $\pm 40^\circ$ in 3 of 4 tests (Wilcoxon–Mann–Whitney tests, owl W: $p = 0.225$ at 40° , $p = 0.951$ at -40° owl X: $p = 0.353$ at 40° , $p < 0.001$ at -40°). When free-field stimuli were presented at $\pm 140^\circ$ of azimuth, the localization precision was worse than for stimuli presented in the frontal hemisphere. The means of the turning angles to stimuli at $\pm 140^\circ$ were 53° and -74° , respectively, for owl X and 63° and -74° , respectively, for owl W under free-field conditions. The maximal turning angles were 79° (-102°) for owl X and 84° (-106°) for owl W at 140° (-140°) (Fig. 9a, b). These values were much larger than the values obtained for stimuli at 40° , demonstrating that the owls were not confused and were able to discriminate 140° from 40° . The number of reactions in which the owls turned their heads to the side that was contralateral to the stimulus was low. Owl X made no errors, whereas owl W made 0.7% of the turns to the wrong side.

With virtual stimulation there was more scatter in the sample of head turns (Fig. 9c, d). The means of the turning amplitudes to the stimuli in the back

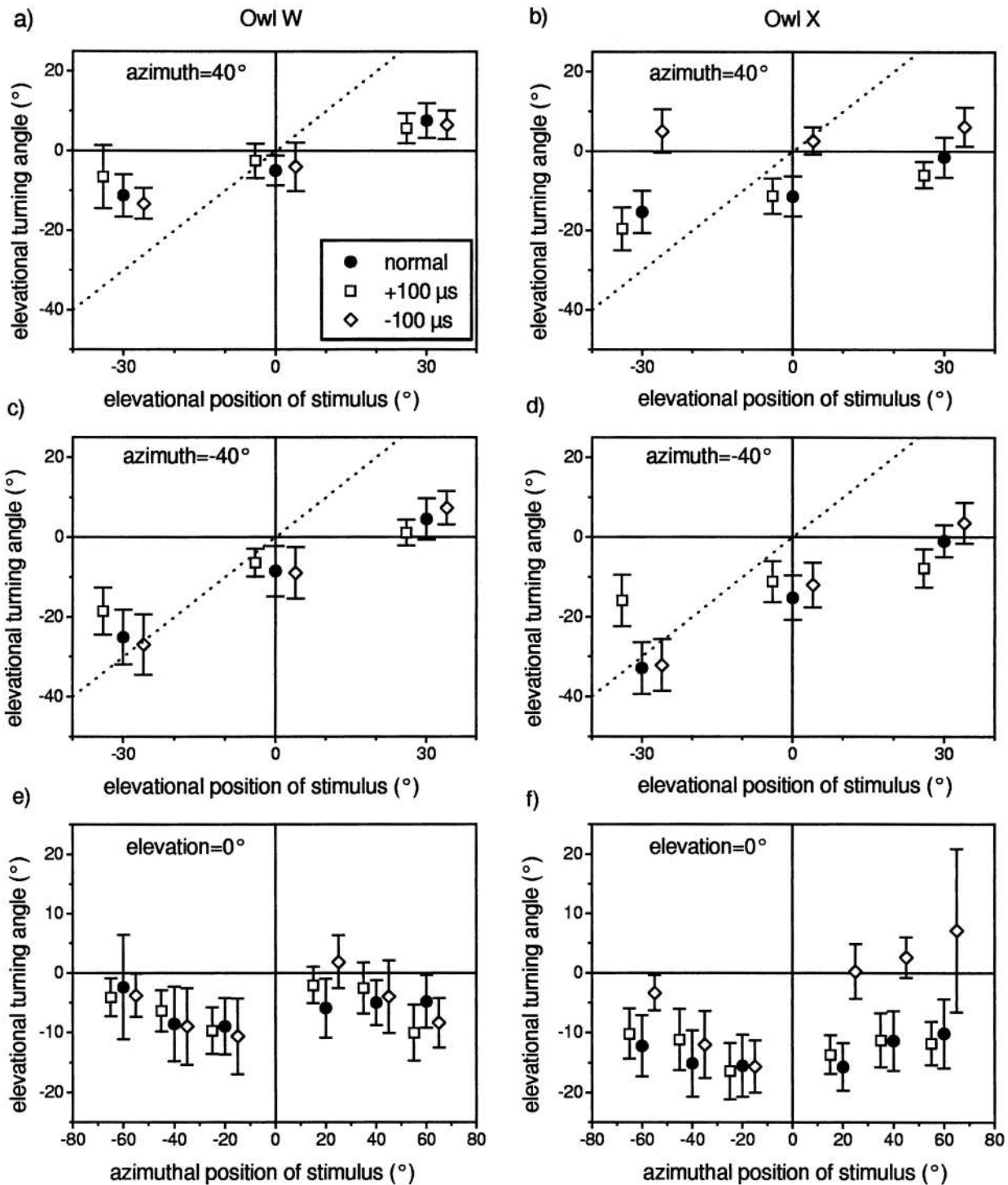


FIG. 8. Dependence of elevational sound-localization behavior on stimulus elevation **a–d** and on stimulus azimuth **e,f** at a constant azimuth or elevation, respectively. Means and standard deviations of the vertical head-turn components are presented separately for

stimulus position and stimulus type (see legend in **a**). For the normal virtual stimuli 150–170 trials were averaged; for the other stimulus types 15–20 trials were averaged. Left column: owl W, right column: owl X.

hemisphere were slightly smaller than the means in the free-field case except for the value at -140° for owl W, which was much smaller (owl X: 57° at 140° , -56° at -140° ; owl W: 60° at 140° , -42° at -140°). The maximal turning angles for the virtual stimuli at

$\pm 140^\circ$ were 82° (-90°) for owl X and 113° (-87°) for owl W, which were similar to the free-field values. In addition, in about 3% of the cases each owl turned to the wrong side when a virtual stimulus in the rear hemisphere was presented. In particular, owl W

seemed to have difficulty localizing the virtual sounds in the back at -140° . With these stimuli the bird under-shot the stimulus position often by a great amount. The smaller the azimuthal component of the head turn was, the further down the bird turned its head (inset of Fig. 9c, Spearman rho correlation, $R = -0.622$, $N = 70$, $p < 0.001$). The same tendency could also be observed with owl X (inset of Fig. 9d, Spearman rho correlation, $R = -0.487$, $N = 86$, $p < 0.001$).

ITD fixation in HRIRs of backward positions influenced the behavior in a way similar to that already shown for frontal positions. The owls turned their heads to the left side if the ITD was fixed to $-100 \mu\text{s}$ and to the right side if the ITD was fixed to $100 \mu\text{s}$ (Fig. 8e, f). The mean amplitude of the head turns was about 37° and -24° , respectively. However, the owls had difficulty localizing the stimulus at 140° with a fixed ITD value at $100 \mu\text{s}$. The azimuthal head-turn components were almost equally distributed between 61° and -19° for this condition in owl X (Fig. 9f).

The elevational component of the head turns was also influenced if the ITD was fixed for stimuli presented in the rear hemisphere (Fig. 9g, h). If the ITD was fixed to $\pm 100 \mu\text{s}$ in a stimulus presented at -140° , both owls turned their heads to significantly lower elevational positions than for the normal stimuli (Fig. 9g, h). If the ITD was fixed to $-100 \mu\text{s}$ in a stimulus presented at $+140^\circ$, the fixation caused a significant increase in the elevational turning angle in owl X. The elevational component was not affected in owl W in this condition, and also not for a fixation of ITD at $+100 \mu\text{s}$ in stimuli recorded at $+140^\circ$ in both owls (T tests, $p < 0.001$ for all significant tests).

Azimuthal responses to virtual stimuli with fixed ILDs

To investigate the influence of the overall ILD on horizontal localization, we compared the azimuthal components of head-turn responses to normal virtual stimuli with responses to stimuli with fixed ILDs for both owls (Fig. 10). Although there was a difference of 12 dB of the overall ILD between FixL_{-6} and FixL_6 stimuli, the mean azimuthal components for the FixL stimuli lie within the range of the standard deviations of the responses to normal virtual stimuli for both owls, both azimuth angles, and all elevations tested (Fig. 10, only data at elevation 0° are shown). A positional comparison of standard deviations of responses to different stimulus types did not show significant difference (Wilcoxon signed ranks test, owl X: normal vs. FixL_6 : $p = 0.702$, normal vs. FixL_{-6} : $p = 0.108$; owl W: normal vs. FixL_6 : $p = 0.099$, normal vs. FixL_{-6} : $p = 0.766$). This similarity between the data resulting from the normal and manipulated stimulus conditions

indicates that the ILD has no influence on azimuthal sound localization in owls.

DISCUSSION

The present study demonstrates that barn owls are able to localize sounds along the azimuth under open-loop conditions in a virtual acoustic environment. The owls responded to virtual stimuli with a head turn in the expected direction. The azimuthal components of head turns elicited by normal virtual stimulation were similar to those observed with free-field stimulation. When ITD was fixed, it became obvious that the owls rely only on ITD and not on other stimulus cues in the generation of the azimuthal amplitudes of head turns. However, response latency was influenced by ITD fixation in the opposite-side configuration. Elevational components of head turns were also influenced by ITD fixation. ILD fixation did not change azimuthal components of head turns. These findings are discussed below with respect to the spatial pattern of ITD, the general sound-localization performance of owls with virtual stimuli, the role of ITD in sound localization, and the influence of the manipulations on response latency and the reliability of the reaction.

HRTFs and spatial pattern of ITDs

We used individual HRTFs because Keller et al. (1998) found that intersubject variations of owl HRTFs are of comparable magnitude to those found in humans. This suggests that individual HRTFs might be necessary to create an adequate virtual environment for owls. General features of individual transfer functions of our owls were comparable to the characteristics of HRTFs described by Keller et al. (1998). This encouraged us to dispense with further acoustic validation.

The spatial pattern of ITD in the frontal hemisphere that was calculated from the transfer functions corresponded to earlier findings (Payne 1971; Coles and Guppy 1988; Olsen et al. 1989; Knudsen et al. 1991; Brainard et al. 1992). Interestingly, a symmetry axis at $\pm 90^\circ$ of azimuth was absent in the spatial patterns of ITDs for most elevations. Although the shape of the iso-ITD lines (Fig. 2) between -90° and -140° or 90° and 140° indicates that ITDs will decrease for even greater azimuth angles and go to zero again for an azimuth at 180° , ITDs increased beyond $\pm 90^\circ$ azimuth at least for some elevations. One possible explanation for the increase of ITDs beyond 90° lies in the fact that the owl's ruff is made out of sound-reflecting feathers. These feathers may increase the acoustic path of sounds from the rear and thus cause increasing instead of declining ITDs at least for some 10° – 30° beyond $\pm 90^\circ$ of azimuth. A comparison of the results

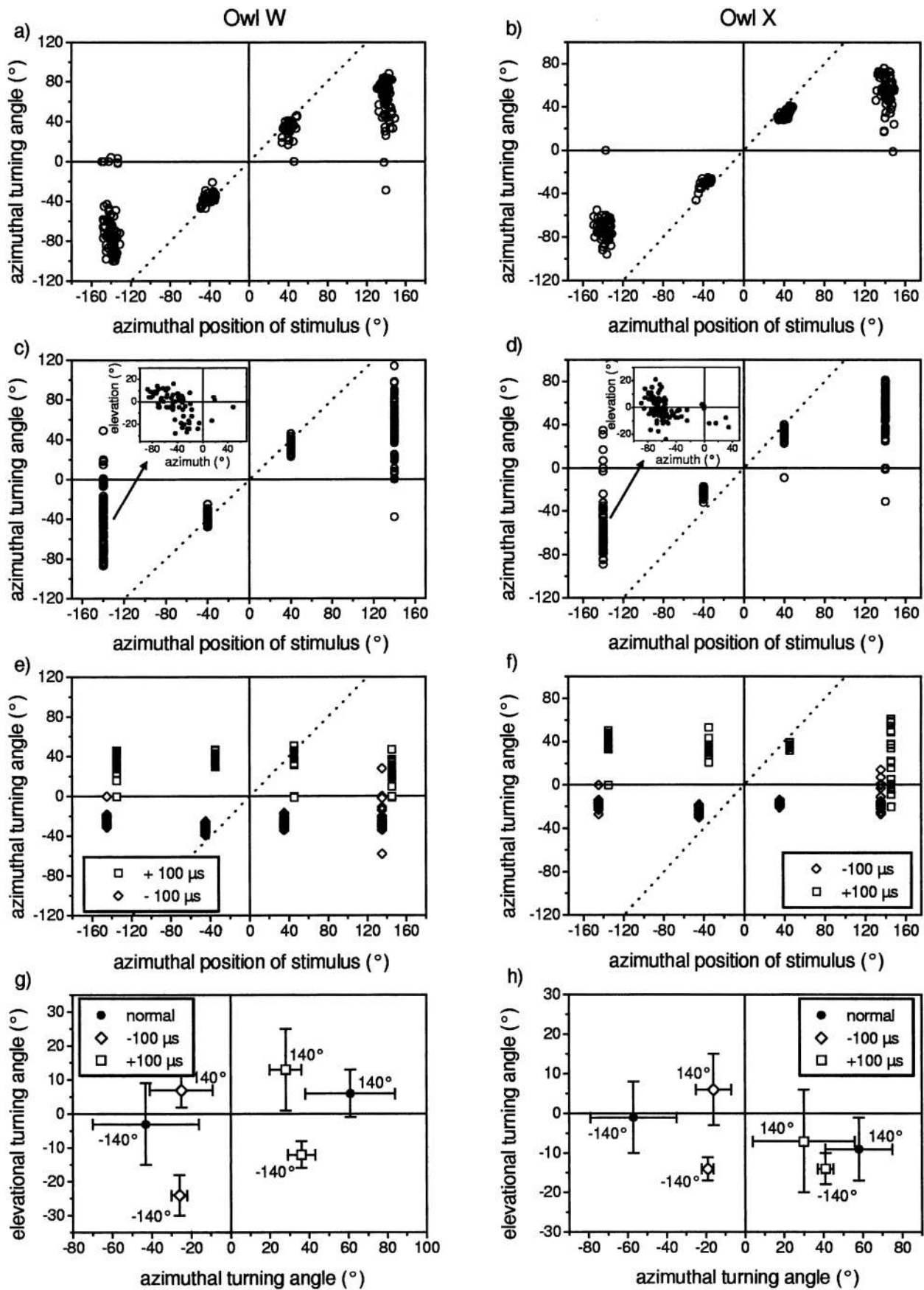


FIG. 9. Comparison of sound-localization behavior as response to stimuli in the rear hemisphere. Data of owl W: left column; data of owl X: right column. Elevational stimulus position was 0° for all trials, **a, b.** Localization of free-field sound sources at four different speaker positions, **c, d.** Localization of virtual stimuli at the same positions as in the free-field experiments. The inset shows the elevational turning amplitude as function of the azimuthal turning amplitude for stimuli

at -140°, **e, f.** Responses to manipulated stimuli with fixed ITDs. The manipulated stimuli were presented randomly between normal virtual stimuli, **g, h.** Mean values and standard deviations of azimuthal and elevational head turns for all virtual stimulus types but only for the backward stimuli. The azimuthal stimulus position is given next to each data point.

measured in the rear hemi-field with other owl studies was not possible because only data from the frontal hemisphere have been presented in other studies. We can exclude that the increase of ITD in the rear was due to errors of the cross-correlation algorithm that was used to calculate the ITDs because we checked the maximum of the cross-correlation function for each position in space thoroughly. If the cross-correlation function had a double peak, which was the case for only a few directions, we used the continuity of ITD change in space as a criterion to choose the correct peak. As a further control, we calculated the ITDs again from HRIRs that were converted into minimum-phase signals, but the resulting spatial pattern of ITDs was only slightly changed with this approach. From a physiological point of view, it is not likely that the auditory system of owls has access to minimum-phase signals. On the contrary, the auditory system rather uses a cross-correlation like neural computation (Keller and Takahashi 1996; Saberi et al. 1998; Rucci and Wray 1999). Thus, to understand the principles of processing in the auditory system of owls, the cross-correlation of HRIRs of both ears might be the appropriate method to calculate ITDs. This calculation revealed that the overall ITD in owls represents a reliable cue for the azimuthal position of a sound not only for the

frontal hemisphere but also for parts of the back hemisphere.

Sound-localization performance in virtual space

The azimuthal angle of the stimulus and the azimuthal component of the head turns were linearly related for stimuli in the frontal hemisphere under both free-field and virtual space conditions. Ideal localization performance would result in a slope of 1° turning angle per degree stimulus azimuth in this linear relationship. Barn owls often underestimated the target location. The slopes varied between 0.66 (owl X) and 0.73 (owl W) for the azimuthal direction in the experiments with free-field stimulation. We estimated the slope values from the figures or from the data tables in various free-field studies and found values between about 0.5 and 0.8 (Table 4 in Knudsen et al. 1979; Fig. 1b in Knudsen et al. 1993; Fig. 3 in Wagner 1993; Fig. 2 in Wagner 1995), demonstrating that our results were in the range of intersubject variability of free-field experiments. A direct comparison of slope values between the free-field and the virtual experiments showed that for owl X the slope was slightly smaller in the virtual experiments and for owl W the slopes

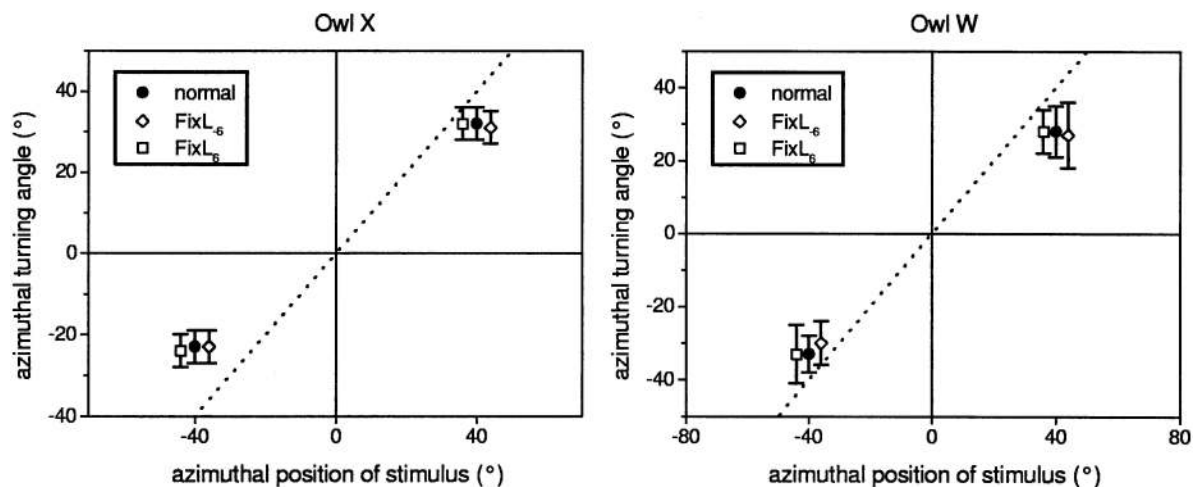


FIG. 10. Influence of the fixation of overall ITDs on azimuthal sound-localization behavior. Data are presented for both owls at azimuthal stimulus directions at 40° or -40° and 0° elevation. Means and standard deviations of the horizontal head turn components are

presented separately for stimulus position and stimulus type (see legend in a). For the normal virtual stimuli 60 trials were averaged, for the FixL stimuli 20 trials were averaged.

were almost identical. The small differences for owl X might be explained by long-term effects and daily variability which influenced the localization performance of the birds. Since the slope values in the experiments with virtual stimulation in general were very similar to free-field values, we conclude that our virtual stimuli provide an appropriate simulation of free-field sounds—at least for the azimuthal variations that we had tested with both the free-field and virtual-space stimuli.

The elevational position perceived by the owl was about 10° lower than expected. This was probably due to a slight difference in alignment of the birds when measuring HRTFs and when defining the origin of the head-centered coordinate system behaviorally. Payne (1971) compared the spectral filter characteristics at high frequencies in the sleeping posture with an alert posture of the ruff and found that the maximum sensitivity is shifted downward in the alert ruff posture. Since we recorded the HRTFs in anesthetized birds, this shift may have influenced our data. Furthermore, our data demonstrate a large scatter in elevational head turns and little tendency in the owls to fixate on virtual sounds from above. Knudsen and Konishi (1979), albeit reporting data with much less scatter than we do, also reported that birds only fixated targets in the upper hemisphere after extensive training. Our owls were never explicitly trained to localize accurately in elevation since we wanted to investigate mainly the azimuthal components of head turns. This may explain the larger scatter in the elevational data.

In humans the rate of front/back confusions and the number of errors in general is higher with virtual stimuli than with real sound sources (Bronkhorst 1995; Wightman and Kistler 1989, 1999), even if subjects are able to externalize the virtual targets. Even after intensive training the owls responded to stimuli in the rear with head turns that clustered around $\pm 60^\circ$ to $\pm 80^\circ$ (Fig. 9). This does not mean that they could not discriminate stimuli in the rear from frontal stimuli; the amplitudes of the head turns to stimuli from the rear were larger than to stimuli from the frontal hemisphere. The distributions did not exhibit double-peaks. We interpret these data such that the owls did not experience front/back confusions with virtual stimuli. Since the amplitudes of the head turns were smaller than 90° , an alternative explanation could be that the owl perceived the stimuli as lying in the frontal hemisphere. We regard this possibility as rather unlikely. Since the turning amplitudes increased linearly with sound-source azimuth, and head-turn amplitudes did not show a bimodal distribution that we would have expected, if the owls had experienced front/back confusions. A reason for the rare front/back confusions could be the extreme frontal directionality of the owl's facial ruff and the asymmetry of

the owl's ears. Both aspects contribute to the cancellation of ambiguities of spatial parameters. At the two spatial positions tested in the rear hemisphere, the number of head turns to the wrong side was higher (3%) under virtual stimulus conditions. This slight increase in confusion might be a result of a reduced signal-to-noise ratio for these virtual stimuli (Fig. 1b).

The role of ITD

The influence of ITD on azimuthal sound localization has also been the topic of earlier behavioral studies. By presenting binaurally time-shifted noise delivered through earphones, Moiseff and Konishi (1981) showed that an ITD cue is sufficient to evoke head turns in owls and that there is a linear relationship between the overall ITD of a stimulus and the azimuthal components of head turns. The slope of the regression between azimuth and ITD was $0.52^\circ/\mu\text{s}$ in their study. Moiseff (1989a, 1989b) demonstrated that the owl uses a bi-coordinate system to translate an acoustic signal into a spatial location. In this coordinate system, ITD is a strong determinant of azimuth of elicited head turns while ILD mainly influences elevation. The slope for the relation between azimuth and ITD was $0.38^\circ/\mu\text{s}$ in behavioral experiments and $0.44^\circ/\mu\text{s}$ in recordings of cochlear potentials (Moiseff 1989a, 1989b). These slope values correspond well to the slopes between $0.37^\circ/\mu\text{s}$ and $0.44^\circ/\mu\text{s}$ which we calculated from the azimuth-dependent ITD changes of the HRIRs at different elevations.

Describing the bi-coordinate system, Moiseff (1989a) showed that ITD and ILD contain information about azimuth. This result is somewhat at odds with the finding presented here that ITD alone determines the azimuthal localization behavior. The contribution of ILD to azimuthal head-turn components was based on the finding that dichotic stimuli with a broadband ILD elicited head turns which contained an azimuthal component. The ILDs tested ranged from -30 to 30 dB, but the natural range of ILDs in the frontal hemisphere lies between about -10 and 10 dB if only the overall ILD is considered, as in Moiseff's (1989a) study. Thus, at least part of the influence of ILD on azimuth might be explained by the use of supernormal stimulus parameters in his study.

While earlier studies suggested that ITD had a major influence on azimuthal sound localization, it was not possible to test the influence of other cues in those experiments because flat noise stimuli were used. In this study, the noise was convolved by HRIRs, thus generating natural virtual stimuli. The manipulation of the stimuli by fixing the ITD while leaving the other parameters as they occurred naturally allowed for a separation of the influence of ITD from the possible influences of all other cues. While in the experiments

with FixT stimuli the same ITD was combined with different frequency-specific ILDs and monaural cues that are contained naturally in the HRTFs at different positions, in the experiments with FixL stimuli the influence of overall ILDs on azimuthal localization was investigated directly. By combining these experiments, it could be demonstrated that barn owls base their judgment of the azimuthal position of a sound exclusively on the overall ITD of a binaural acoustic signal independent of other spatial cues. Even for stimulus positions of $\pm 140^\circ$ the ITD seems to be the only relevant cue for the azimuthal position of a sound source. This may be understandable since sound sources in parts of the rear hemisphere produce even greater ITDs at the owls' eardrums than sources originating from frontal positions. Thus, ITD is a reliable cue for the azimuthal position of a stimulus in a range of more than 220° , at least at elevations between 0° and -30° . For parts of the upper hemisphere, this range is slightly smaller but larger than 180° .

The results presented here are similar to those found in humans. Wightman and Kistler (1992) produced virtual stimuli in which ITD and ILD cues signaled different directions. They reported that subjects always followed the direction signaled by the ITD as long as low frequencies were included. Hartmann and Wittenberg (1996) described that contradictory ITD and ILD information in virtual sounds led to inside-the-head locatedness and lateralization of the sound at the side to which the ITD points. Since barn owls are able to process interaural phase differences up to frequencies of 9 kHz (Sullivan and Konishi 1984; Köppl 1997), the dominant role of ITD for horizontal localization need not be restricted to low frequencies. However, a behavioral test to prove this hypothesis has still to be done.

Some variations in the means of azimuthal head-turn components for different space positions were observed (Fig. 6). These variations might—at least to a large extent—be explained by methodological aspects. The fixation of the ITD was carried out by calculating the maximum of the cross-correlation function of both ears' HRIRs. At a sampling rate of 50 kHz the maximum was detected with an accuracy of 20 μ s. A difference of 20 μ s corresponds to about 8° of azimuth in barn owls (Fig. 2). Most of the observed variation lie in this range.

The present study also demonstrated an influence of ITD on the elevational component of head turn. On the one hand, this might be a hint that ITD contains information about azimuth and elevation, as already suggested by Moiseff (1989a). On the other hand, the effects reported here might reflect only an indirect influence of ITD. As mentioned before, there is evidence that the ILD of a sound is a strong determinant of elevation (Knudsen and Konishi 1979; Moiseff

1989a; Olsen et al. 1989). Changes of ILD in space are not as regular as for ITDs (Keller et al. 1998) resulting, for example, in different ILD values at -30° elevation and 40° or -40° azimuth. Assuming that the spatial location of a sound is determined by a combination of ITD and ILD, different elevational head-turn amplitudes to different manipulated virtual FixT stimuli would be expected. We speculate that frequency-dependent ILDs are responsible for the elevational effects, especially for the different results for both owls, but this has to be investigated in further studies.

Latencies and no reaction trials

Response latencies to normal virtual stimuli had median values between 100 and 180 ms. As in earlier studies the response latencies were independent of the spatial position of the stimulus (Wagner 1993). Knudsen et al. (1979) recorded median latencies of 100 ms when 75-ms free-field noise was presented to owls, but to calculate this value only the first ten trials of the daily sessions were used to assure a high level of motivation of the animals. We observed a consistent localization behavior for more than 100 trials. Hence, we used all trials for the calculation of median latencies. However, this methodological difference might explain the slightly different results compared with data presented by Knudsen et al. (1979). Mean latencies of 90–130 ms can also be estimated from experiments described in Wagner (1993). These values correspond well with our findings with virtual stimulation.

If the ITD and the other spatial cues of the manipulated virtual stimuli point to different hemispheres in space, the numbers of no-reaction trials and mean response latencies were increased. In the opposite-side configuration, the sounds contain a binaural combination of spatial information that never occurs under natural conditions. This combination of unusual spatial cues might require a more complex processing of sound location, especially in the forebrain, leading to longer response latencies. Such pathways have been studied and a contribution to sound localization has been demonstrated (Knudsen et al. 1993; Knudsen and Knudsen 1996; Cohen et al. 1998). Interestingly, the increase of 60 ms in latency in the opposite-side configuration was very close to what others have seen when invalid cues were presented to barn owls in a cueing paradigm (Johnen and Gaese, personal communication). A similar value was implied to reflect the difference between detection and discrimination in a study using the pupillary dilation response to determine minimum audible angle (Bala and Takahashi 2000).

This article implies that the virtual space technique is a valid method for studying the acoustic basis of

sound localization, as opposed to within-the-head lateralization, in barn owls. Although barn owls react to noise bursts with ITD, and although the relationship between ITD and head-turning angle is essentially identical for full virtual space stimuli and for simple noise bursts with ITD, virtual space stimuli bring additional information about the behavioral relevance of different cues.

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REFERENCES

- ADOLPHS R. Bilateral inhibition generates neuronal responses tuned to interaural level differences in the auditory brainstem of the barn owl. *J. Neurosci.* 13:3647–3668, 1993.
- BALA ADS, TAKAHASHI, TT. Pupillary dilation response as an indicator of auditory discrimination in the barn owl. *J. Comp. Physiol. A* 186:425–434, 2000.
- BLAUERT J. *Spatial Hearing*. MIT Press Cambridge, MA, 1997.
- BRAINARD MS, KNUDSEN EI, ESTERLY SD. Neural derivation of sound source location: resolution of spatial ambiguities in binaural cues. *J. Acoust. Soc. Am.* 91:1015–1027, 1992.
- BRONKHORST AW. Localization of real and virtual sound sources. *J. Acoust. Soc. Am.* 98:2542–2553, 1995.
- BRUGGE JF, REALE RA, HIND JE, CHAN JCK, MUSICANT AD, POON PWF. Simulation of free-field sound sources and its application to studies of cortical mechanisms of sound localization in the cat. *Hear. Res.* 73:67–84, 1994.
- BRUGGE JF, REALE RA, HIND JE. Spatial receptive fields of primary auditory cortical neurons in quiet and in the presence of continuous background noise. *J. Neurophysiol.* 80:2417–2432, 1998.
- BUTLER RA, BELENDIUK K. Spectral cues utilized in the localization of sound in the median sagittal plane. *J. Acoust. Soc. Am.* 61:1264–1269, 1977.
- COHEN YE, MILLER GL, KNUDSEN EI. Forebrain pathway for auditory space processing in the barn owl. *J. Neurophysiol.* 79:891–902, 1998.
- COLES RB, GUPPY A. Directional hearing in the barn owl (*Tyto alba*). *J. Comp. Physiol. A* 163:117–133, 1988.
- HARTMANN WM, WITTENBERG A. On the externalization of sound images. *J. Acoust. Soc. Am.* 99:3678–3688, 1996.
- JEFFRESS LA, TAYLOR RW. Lateralization versus localization. *J. Acoust. Soc. Am.* 33:482–483, 1961.
- KELLER CH, TAKAHASHI TT. Binaural cross-correlation predicts the responses of neurons in the owl's auditory space map under conditions simulating summing localization. *J. Neurosci.* 16:4300–4309, 1996.
- KELLER CH, HARTUNG K, TAKAHASHI TT. Head-related transfer functions of the barn owl: measurement and neural responses. *Hear. Res.* 118:13–34, 1998.
- KISTLER DJ, WIGHTMAN FL. A model of head-related transfer functions based on principal components analysis and minimum-phase reconstruction. *J. Acoust. Soc. Am.* 91:1637–1647, 1992.
- KNUDSEN EI, KONISHI M. A neural map of auditory space in the owl. *Science* 200:795–797, 1978.
- KNUDSEN EI, BLASDEL GG, KONISHI M. Sound localization by the barn owl (*Tyto alba*) measured with the search coil technique. *J. Comp. Physiol. A* 133:1–11, 1979.
- KNUDSEN EI, KONISHI M. Mechanisms of sound localization in the barn owl (*Tyto alba*). *J. Comp. Physiol. A* 133:13–21, 1979.
- KNUDSEN EI, KNUDSEN PF. The sensitive period for auditory localization in barn owls is limited by age, not by experience. *J. Neurosci.* 6:1918–1924, 1986.
- KNUDSEN EI, ESTERLY SD, DULAC S. Stretched and upside-down maps of auditory space in the optic tectum of blind-reared owls; acoustic basis and behavioral correlates. *J. Neurosci.* 11:1727–1747, 1991.
- KNUDSEN EI, KNUDSEN PF, MASINO T. Parallel pathways mediating both sound localization and gaze control in the forebrain and midbrain of the barn owl. *J. Neurosci.* 13:2837–2852, 1993.
- KNUDSEN EI, KNUDSEN PF. Contribution of the forebrain archistriatal gaze fields to auditory orienting behavior in the barn owl. *Exp. Brain Res.* 108:23–32, 1996.
- KONISHI M. How the owl tracks its prey. *Am. Sci.* 61:414–424, 1973.
- KÖPPL C. Phase locking to high frequencies in the auditory nerve and cochlear nucleus magnocellularis of the barn owl, *Tyto alba*. *J. Neurosci.* 17:3312–3321, 1997.
- KULKARNI A, COLBURN HS. Role of spectral detail in sound-source localization. *Nature* 396:747–749, 1998.
- KULKARNI A, ISABELLE SK, COLBURN HS. Sensitivity of human subjects to head-related transfer-function phase spectra. *J. Acoust. Soc. Am.* 105:2821–2840, 1999.
- MAZER JA. How the owl resolves auditory coding ambiguity. *Proc. Natl. Acad. Sci. USA* 95:10932–10937, 1998.
- MIDDLEBROOKS JC. Narrow-band sound localization related to external ear acoustics. *J. Acoust. Soc. Am.* 92:2607–2624, 1992.
- MOGDANS J, KNUDSEN EI. Representation of interaural level difference in the VLVp, the first site of binaural comparison in the barn owl's auditory system. *Hear. Res.* 74:148–164, 1994.
- MOISEFF A, KONISHI M. Neuronal and behavioral sensitivity to binaural time differences in the owl. *J. Neurosci.* 1:40–48, 1981.
- MOISEFF A, KONISHI M. Binaural characteristics of units in the owl's brainstem auditory pathway: precursors of restricted spatial receptive fields. *J. Neurosci.* 3:2553–2562, 1983.
- MOISEFF A. Bi-coordinate sound localization by the barn owl. *J. Comp. Physiol. A* 164:637–644, 1989a.
- MOISEFF A. Binaural disparity cues available to the barn owl for sound localization. *J. Comp. Physiol. A* 164:629–636, 1989b.
- OLSEN JF, KNUDSEN EI, ESTERLY SD. Neural maps of interaural time and intensity differences in the optic tectum of the barn owl. *J. Neurosci.* 9:2591–2605, 1989.
- PAYNE RS. Acoustic location of prey by barn owls (*Tyto alba*). *J. Exp. Biol.* 54:535–573, 1971.
- PLENGE G. On the differences between localization and lateralization. *J. Acoust. Soc. Am.* 56:944–951, 1974.
- POON PW, BRUGGE JF. Virtual-space receptive fields of single auditory nerve fibers. *J. Neurophysiol.* 70:667–676, 1993.
- RUCCI M, WRAY J. Binaural cross-correlation and auditory localization in the barn owl: a theoretical study. *Neural Networks* 12:31–42, 1999.
- SABERI K, FARAHBOD H, KONISHI M. How do owls localize interaurally phase-ambiguous signals? *Proc. Natl. Acad. Sci. USA* 95:6465–6468, 1998.
- STERBING SJ, HARTUNG K. Effects of sound pressure level, stimulus duration, and binaural correlation on virtual sound source coding in the inferior colliculus of the guinea pig. In Dau T, Hohmann V, Kollmeier B (eds) *Psychophysics, physiology and models of hearing*. World Scientific Publishing Singapore 1999. 27–30.
- SULLIVAN WE, KONISHI M. Segregation of stimulus phase and intensity coding in the cochlear nucleus of the barn owl. *J. Neurosci.* 4:1787–1799, 1984.

- TAKAHASHI T, MOISEFF A, KONISHI M. Time and intensity cues are processed independently in the auditory system of the owl. *J. Neurosci.* 4:1781–1786, 1984.
- TAKAHASHI TT, KONISHI M. Projections of the cochlear nuclei and nucleus laminaris to the inferior colliculus of the barn owl. *J. Comp. Neurol.* 274:190–211, 1988.
- WAGNER H. A temporal window for lateralization of interaural time difference by barn owls. *J. Comp. Physiol. A* 169:281–289, 1991.
- WAGNER H. Sound-localization deficits induced by lesions in the barn owl's auditory space map. *J. Neurosci.* 13:371–386, 1993.
- WAGNER H. Sound-localization experiments in owls. In Klump GM, Dooling RJ, Fay R, Stebbins WC (eds) *Methods in Comparative Psychoacoustics*. Birkhäuser Verlag Basel 1995. 183–195.
- WIGHTMAN FL, KISTLER DJ. Headphone simulation of free-field listening II. Psychophysical validation. *J. Acoust. Soc. Am.* 85:868–878, 1989.
- WIGHTMAN FL, KISTLER DJ. The dominant role of low-frequency interaural time differences in sound localization. *J. Acoust. Soc. Am.* 91:1648–1661, 1992.
- WIGHTMAN FL, KISTLER DJ. Resolution of front-back ambiguity in spatial hearing by listener and source movement. *J. Acoust. Soc. Am.* 105:2841–2853, 1999.