

## Mechanisms of Sound Localization in the Barn Owl (*Tyto alba*)

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**Summary.** 1. We investigated the mechanisms by which the barn owl (*Tyto alba*) determines the azimuth and elevation of a sound source. Our measure of localizing ability was the accuracy with which the owl oriented its head to a sound source.

2. When localizing tonal signals, the owl committed the smallest errors at frequencies between 4 and 8 kHz. The azimuthal component of these errors was frequency independent from 1 to 8 kHz, but the elevational component increased dramatically for frequencies below 4 kHz.

3. The owl's mean error when localizing wide band noise was nearly three times less than its mean error when localizing the optimal frequency for tonal localization (6 kHz).

4. Occluding the right ear caused the owl to orient below and to the left of the sound source; occluding the left ear caused it to orient above and to the right of the sound source.

5. With ruff feathers (facial ruff) removed, the owl continued to localize sounds accurately in azimuth, but failed to localize sounds in elevation.

6. We conclude from these results that the barn owl uses interaural comparisons of sound spectrum to determine the elevation of a sound source. Both interaural onset time and interaural spectrum are used to identify the azimuth of the sound source. If onset time is not available (as in a continuous sound), the owl can derive the azimuth of the source from interaural spectrum alone, but its spatial resolution is poorer.

### Introduction

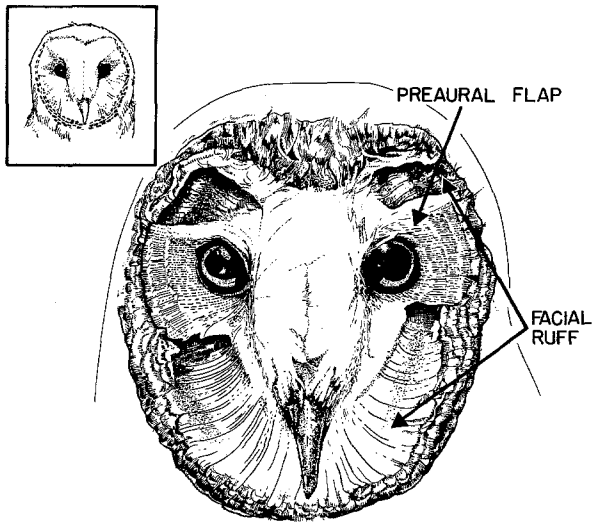
The barn owl (*Tyto alba*) localizes sound with extreme accuracy in both azimuth and elevation without moving its head (Knudsen et al., 1979). To identify

the location of a sound source in two dimensions, the owl's auditory system must make independent measurements on at least two different, space-variant parameters of the auditory stimulus. Which auditory parameters might the owl exploit as cues for sound localization? Excluding cues provided by head movement (not required by the owl), the cues that do not demand an a priori knowledge of the spectral composition of the original sound are derived from a binaural comparison of a sound's arrival time, phase, intensity and spectrum. Interaural arrival time ( $\Delta T$ ) refers to the delay in the onset of a sound at the two ears; interaural phase ( $\Delta\Phi$ ) is the relative phase shift in the ongoing waveforms at the two ears. Both  $\Delta T$  and  $\Delta\Phi$  depend on the difference in the path lengths that sound must travel to reach each ear, and therefore vary as a function of the azimuth of the sound source. Interaural intensity ( $\Delta I$ ) refers to the difference in the amount of sound energy reaching each ear; interaural spectrum ( $\Delta S$ ) is the difference in the distribution of sound energy as a function of frequency (power spectrum) in each ear. Direction-dependent  $\Delta I$  and  $\Delta S$  cues are caused by changes in the sensitivity of each ear as a function of sound direction (ear directionality).

In mammals, and particularly in man, the contribution of each of these binaural cues to sound localization has been well documented. Man for example uses  $\Delta T$ ,  $\Delta\Phi$ , and  $\Delta I$  to determine the azimuth of a sound source, and  $\Delta S$  (as well as monaural spectrum) to deduce its elevation (Searle et al., 1976). In contrast, none of the cues that the barn owl, or any other bird, uses in sound localization has been firmly established, although the potential use of each has been proposed on theoretical grounds by several authors (Pumphrey, 1948; Norberg, 1968, 1978; Payne, 1971; Knudsen, in press).

The only behavioral data on this issue are from localization experiments by Konishi (1973b) on the barn owl, in which the accuracy of the owl's strike at a sound target was measured before and after plug-

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**Fig. 1.** Facial ruff and asymmetrical ears of the barn owl (*Tyto alba*). This illustration depicts the face of the owl as it would appear if the owl's facial disc feathers were removed. The owl's normal appearance is shown in the upper left corner. The owl's ear openings lie behind the preaural flaps

ging one ear. With the right ear plugged the owl struck to the left and short of the target; with the left ear plugged, it struck to the right and beyond the target. Since an ear plug attenuates sound without significantly altering its rate of propagation, such an experiment demonstrates the importance of either  $\Delta I$  or  $\Delta S$ , although it does not distinguish between them.

The frequency-dependent, directional sensitivity of the barn owl's ears suggests that  $\Delta S$  is likely to be the important cue (Payne, 1971; Knudsen and Konishi, 1978, unpublished). The ear openings and preaural flaps of the barn owl are asymmetrically positioned within the facial ruff, a structure composed of tightly packed, dense feathers that forms two vertical troughs behind each ear opening (Fig. 1). The barn owl's left ear opening and flap are located high in the left trough, whereas the right ear opening and flap are centered in the right trough. At low frequencies ( $< 4$  kHz), where the wavelength of the sound is greater than the dimensions of the ruff (6–8 cm), the directionalities of the ears are not substantially affected by the ruff: the left ear is more sensitive to the left, and the right ear is more sensitive to the right (personal observation). However, at frequencies greater than or equal to 4 kHz, the facial ruff becomes an effective sound reflector and the asymmetrical positions of the ears in the ruff causes a vertical disparity in the directionalities of the two ears: the left ear becomes more sensitive to regions of space below the owl's horizontal plane ( $0^\circ_{el}$ ), and the right ear to regions above the horizontal plane (Payne, 1971). Thus, as sound frequency increases

above 3 kHz, the plane of equal sensitivity for the two ears rotates from vertical to horizontal. Hence the owl could determine the azimuth of a source by comparing interaural intensity at low frequencies, and its elevation from interaural intensity at high frequencies. Such a mechanism would be sound localization by interaural spectrum ( $\Delta S$ ). In theory the owl could determine both the azimuth and elevation of a noise source from  $\Delta S$ , therefore Pumphrey (1948) and Norberg (1968, 1978) proposed that  $\Delta S$  is likely to be the cue for sound localization in the owl.

In this study we investigate the contributions of various binaural cues to sound localization by the barn owl. Based on the owl's performance in localizing tonal targets, and on the effects of perturbing the peripheral auditory apparatus, we conclude that the barn owl uses both  $\Delta T$  and  $\Delta S$  to localize sounds.

## Methods

Details of the behavioral paradigm, measurement techniques, and stimulus conditions were given in the preceding paper (Knudsen et al., 1979). In short, we trained two barn owls (*Tyto alba*), Dini and Roger, to sequentially fixate on the sources of two sounds presented in succession: an initial zeroing sound to align the owl's head, and a target sound to test the accuracy of the saccade and fixation. The experiments were conducted in a darkened anechoic chamber. The zeroing speaker was permanently suspended directly in front of the owl; the target speaker moved, under computer control, in azimuth and elevation around the owl.

The azimuth and elevation of the owl's head orientation were monitored continuously by using a modification of the search coil technique (Robinson, 1963; Knudsen et al., 1979) and were expressed in degrees using a double polar coordinate system (Fig. 2).

We began a test session by instructing the computer to move the target speaker to one of 8 standard locations (Fig. 2C). The sequence of target locations was chosen arbitrarily. Once the target speaker reached the designated location a 100 ms noise burst was presented through the zeroing speaker. After the owl had fixated on the zeroing speaker to within  $5^\circ$ , a single test sound was presented through the target speaker. If the owl turned its head quickly in response to the target sound, whether accurate or not, it was rewarded with food and the data were stored. Following each trial the target speaker moved to a new location and the trial procedure repeated.

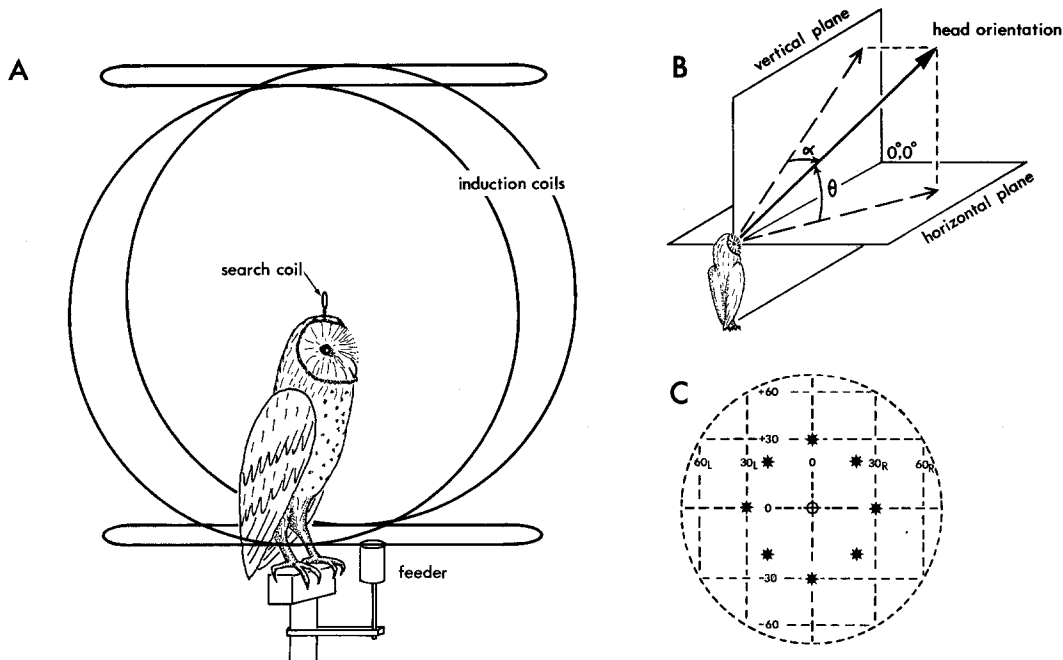
Target sounds included noise and tone bursts. The bursts were either 75 ms or 1,000 ms in duration with 2.5 ms rise and decay times.

## Definitions

**Vertical plane:** the plane that runs vertically and dorsoventrally through the middle of the owl's head when it faces the zeroing speaker.

**Horizontal plane:** the plane that is horizontal with respect to the ground and contains the owl's ear canals when it faces the zeroing speaker.

**Azimuth ( $\alpha$ ):** left-right direction; measured in degrees relative to the vertical plane.



**Fig. 2A.** The owl is shown perched within the induction coil array and facing the zeroing speaker. The magnetic fields generated by the induction coils induced a current in the search coil, the magnitude of which depended upon the orientation of the search coil. The signal from the search coil was demodulated and used to compute the orientation of the owl's head. **B** The azimuth ( $\alpha$ ) and elevation ( $\theta$ ) of the owl's head orientation (heavy arrow) were defined with respect to the owl's vertical and horizontal planes. **C** The contour lines of this coordinate system, viewed from  $[0^\circ_{\text{az}}, 0^\circ_{\text{el}}]$  appear as perpendicular sets of parallel lines on a unit sphere. The target locations at which data were compiled are represented by stars

Elevation ( $\theta$ ): up-down direction; measured in degrees relative to the horizontal plane.

Total error: the angle defined by the target location, the center of the search coil (origin), and the owl's final fixation point.

Open-loop localization: orientation to a sound that terminated prior to head movement.

Closed-loop localization: orientation to a sound that persisted throughout the orienting response.

Coordinate notation: spatial locations are defined by their coordinates in the double polar system as  $[\alpha^\circ_{\text{az}}, \theta^\circ_{\text{el}}]$ .

Interaural arrival time ( $\Delta T$ ): the time delay between the arrival of a distinct acoustic event at the left and right ears.

Interaural phase ( $\Delta\Phi$ ): the relative phase shift in the ongoing waveforms at the two ears.

Interaural intensity ( $\Delta I$ ): the difference in the total sound intensity detected by the two ears. In mathematical terms:

$$\Delta I = [i_{f1} + i_{f2} + \dots + i_{fn}]_{\text{Left}} - [i_{f1} + i_{f2} + \dots + i_{fn}]_{\text{Right}}$$

where  $i_{f1}$  equals the intensity of sound at a frequency,  $f_1$ , in one ear. Note that interaural intensity yields a single value.

Interaural spectrum ( $\Delta S$ ): the difference in the intensity of sound at each frequency at the two ears. In mathematical terms:

$$\Delta S = [i_{L f1} - i_{R f1}], [i_{L f2} - i_{R f2}] \dots [i_{L fn} - i_{R fn}]$$

where  $i_{L f1}$  equals the sound intensity at frequency  $f_1$  in the left ear and  $i_{R f1}$  the sound intensity at the same frequency in the right ear. Note that interaural spectrum yields a set of values.

## Results and Discussion

**Localization of Tones.** Interaural time, phase and intensity can be readily derived from a tonal stimulus. Interaural spectrum, on the other hand, is reduced to a comparison of intensity at a single frequency band. If interaural spectrum is crucial to sound localization, then the owl's ability to localize a tonal target should be dramatically worse than its ability to localize a noise target. With this in mind, the accuracy of the owl's localization of 1–10 kHz tonal targets was measured. Tone frequencies were presented in a random order and were interspersed with noise burst trials. The target sound and location were changed after every trial. The tone and noise bursts had durations of 75 ms (open-loop localization) or 1000 ms (closed-loop localization). The intensity of each frequency was adjusted to compensate for the frequency-response of the speaker and the auditory sensitivity of the owl (Konishi, 1973b), so that the stimulus intensity ranged between 20 and 40 dB above hearing threshold.

The targets were presented at eight standard speaker locations, each of which was approximately  $30^\circ$  from  $[0^\circ_{\text{az}}, 0^\circ_{\text{el}}]$  (Fig. 2C). Equal numbers of trials were conducted at each location for a given frequency.

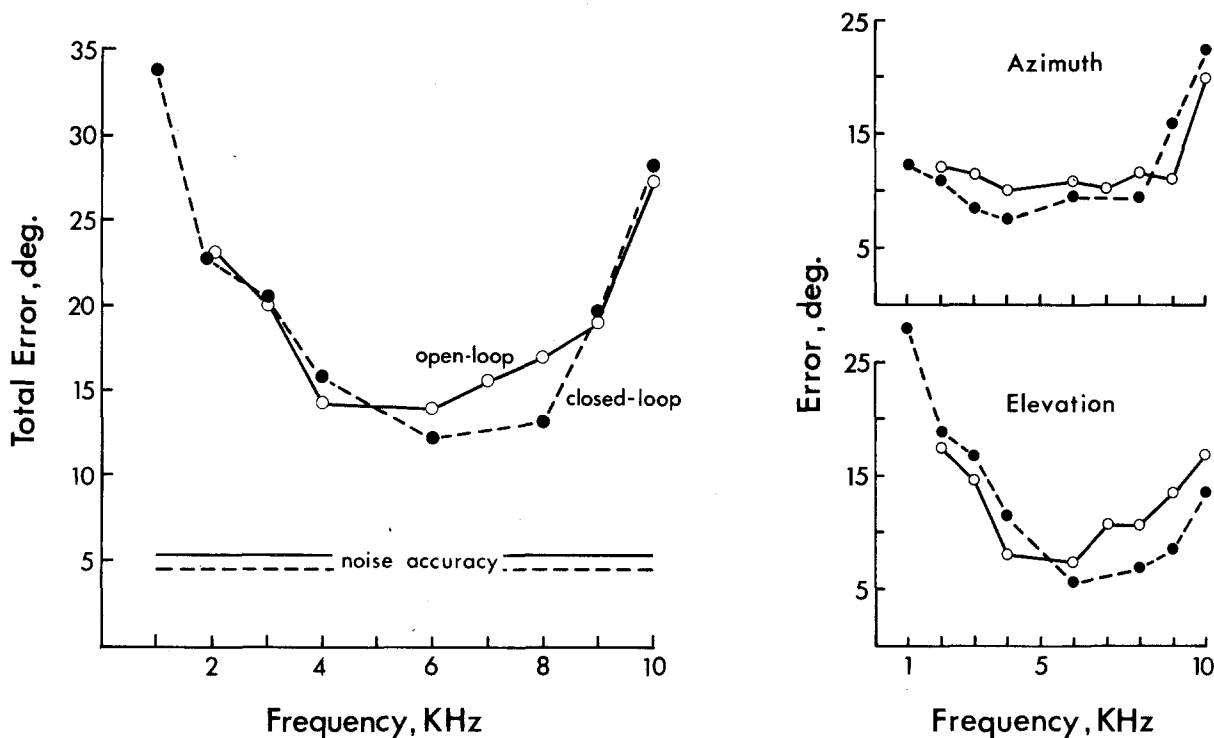


Fig. 3. Frequency dependence of sound localization. Head orientation error to tonal targets measured under open-loop (open circles) and closed-loop (closed circles) conditions, is plotted as a function of tone frequency. The owl's mean total errors are plotted on the left; the azimuthal and elevational components of these errors are plotted separately on the right

To achieve a sufficient sample size for each frequency, the error data for all locations were pooled. Trials in which the owl made no movement in response to a tone were discarded. No movement was typical for 1 and 10 kHz trials; the owls responded somewhat more reliably to 2 and 9 kHz tones. However, even after pooling the data, the owls' reluctance to respond to frequencies below 3 kHz and above 8 kHz resulted in only 9–18 successful trials at these extreme frequencies compared with 24–45 trials for all other frequencies.

The median localization errors for one owl (Dini) to short and long tone bursts are plotted as a function of frequency in Figure 3. These data demonstrate three important points: 1) the owl was maximally accurate to frequencies between 4 and 8 kHz (this finding agrees well with the best frequency range of 5 to 9 kHz reported by Konishi (1973b), who measured target striking accuracy); 2) even at the optimal tone frequency of 6 kHz, the owl's error was almost three times greater than when it localized noise targets (Table 1); 3) the owl localized tones under open- and closed-loop conditions with equal accuracy (no significant difference at the  $P > 0.05$  level, Mann-Whitney U-test).

Clearly the owl required signals with sufficiently wide bandwidths (undetermined) in order to maxim-

Table 1. Closed-loop localization of tones<sup>a</sup>

Target frequency (kHz)	Localization error ( $X^{\circ} \pm$ S.D.)		
	Total	Azimuth	Elevation
1	34.1 $\pm$ 22.6	11.9 $\pm$ 11.8	28.2 $\pm$ 23.9
2	21.9 $\pm$ 10.0	10.4 $\pm$ 9.9	18.7 $\pm$ 9.3
3	20.4 $\pm$ 9.4	8.4 $\pm$ 5.7	16.6 $\pm$ 10.7
4	15.9 $\pm$ 9.9	7.9 $\pm$ 9.4	11.4 $\pm$ 7.7
6	12.2 $\pm$ 6.2	9.5 $\pm$ 6.1	5.8 $\pm$ 5.1
8	13.2 $\pm$ 7.9	9.4 $\pm$ 6.4	7.8 $\pm$ 6.6
9	19.6 $\pm$ 12.9	15.7 $\pm$ 10.2	8.5 $\pm$ 10.4
10	28.4 $\pm$ 17.4	22.3 $\pm$ 14.6	13.1 $\pm$ 12.8
Noise	4.5 $\pm$ 1.8	3.6 $\pm$ 1.8	2.2 $\pm$ 1.5

<sup>a</sup> 1 s tone bursts. The data are from Dini

ize its localization accuracy. However, it can be noted from the scatter plots in Figure 4, that at 6 kHz, although errors were sometimes large, the owl was obviously succeeding in localizing the tone in both azimuth and elevation. This implies that the owl could still measure two different space-dependent parameters of the tonal signal. Since a tone contains only a single frequency band, the spatial information that the owl could have gained from  $\Delta I$  or  $\Delta S$  would have been the same:  $\Delta I = \Delta S = [i_{L6\text{kHz}} - i_{R6\text{kHz}}]$ . Assuming that the owl used  $\Delta i_{6\text{kHz}}$  to determine the

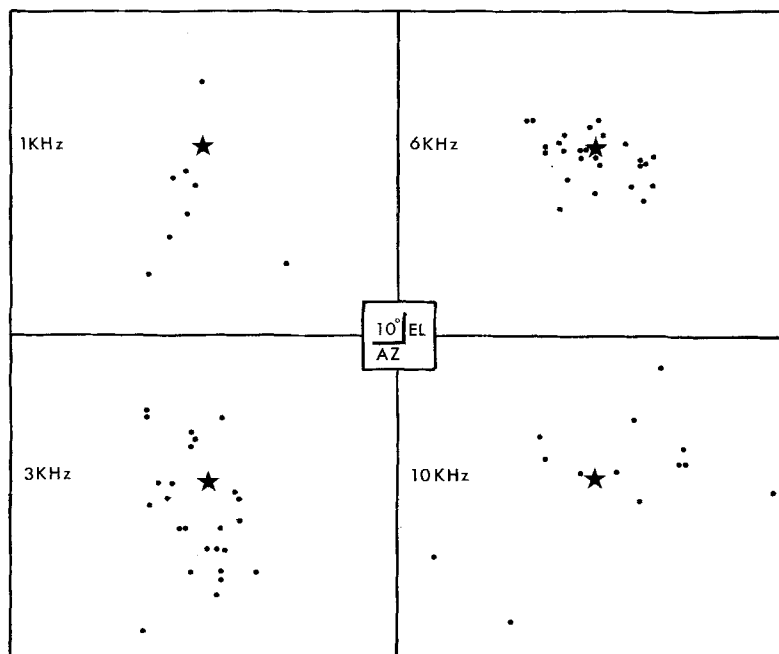


Fig. 4. Individual fixation points in response to 1,000 ms tonal targets of 1, 3, 6 and 10 kHz. The spatial scale is shown in the center. The target's location is designated by a star. Data are from Dini

elevation of the 6 kHz target (see Introduction), which cue did it use to identify the target's azimuth? The only cues left are  $\Delta T$  and  $\Delta\phi$ .

Evidence that implicates  $\Delta T$  can be found in the frequency dependence of the owl's azimuthal error (Fig. 3). Since  $\Delta T$  is a property of the onset of the sound envelope, its spatial resolution is independent of the tone's frequency as long as the rise time of the burst is slower than the period of the tone.

In contrast, the spatial resolution of  $\Delta\phi$  is frequency-dependent. The  $\Delta\phi$  cue affords unambiguous spatial information only if the wavelength ( $\lambda$ ) of the tone is at least twice as long as the distance between the owl's ears (for the barn owl this means  $\lambda > 10$  cm or  $f \leq 3$  kHz); at shorter wavelengths the owl cannot distinguish between its leading and lagging ears and therefore loses the laterality of the source. At very low frequencies, i.e., as the wavelength becomes long compared to the distance between the owl's ears, the shift in phase with sound direction becomes small and causes the spatial resolution of  $\Delta\phi$  to deteriorate. According to these theoretical considerations, there exists a frequency window, determined by interaural separation, within which  $\Delta\phi$  offers high resolution, unambiguous spatial information.

These considerations predict that if the owl localized the tones in azimuth by using  $\Delta T$ , its azimuthal error should be frequency independent, whereas if it used  $\Delta\phi$ , its azimuthal error should be frequency dependent and smallest for frequencies up to about 3 kHz. The experimental results, given in Table 1 and Figure 3, show that the owl's azimuthal errors were

largely independent of frequency up to 8 kHz, above which localization performance deteriorated in general.

The difference between the owl's azimuthal error when localizing noise versus tonal targets (Table 1) indicates the importances of signal bandwidth either for precise measurement of  $\Delta T$ , or for additional azimuthal information contained in  $\Delta S$ , or both.

In contrast to the relative frequency independence of the owl's azimuthal errors, elevational errors decreased sharply from 1 kHz to 4 kHz, reached a minimum at about 6 kHz, and increased again near 10 kHz (Fig. 3).

The discrepancy in the owl's azimuthal versus elevational errors for low frequency tones was evident in the vertically elongate distribution of its fixation points at 1 kHz (Fig. 4). As the owl's elevational accuracy improved at higher frequencies, the distribution of fixation points became smaller and nearly circular, surrounding the target location. The inability of the owl to determine the elevation of a 1 kHz sound source was also apparent in the path that the head followed prior to fixation. Instead of a rapid head saccade and abrupt fixation, characteristic of responses to noise targets (Knudsen et al., 1979), the owl (when it responded at all) made relatively slow scanning movements that were approximately in line with the target's azimuth, but that terminated at seemingly arbitrary points in elevation. One characteristic of vertical errors to 1 kHz tones was that the owl never oriented upwards to a target, i.e., regardless of the target's elevation, upon hearing a 1 kHz tone,

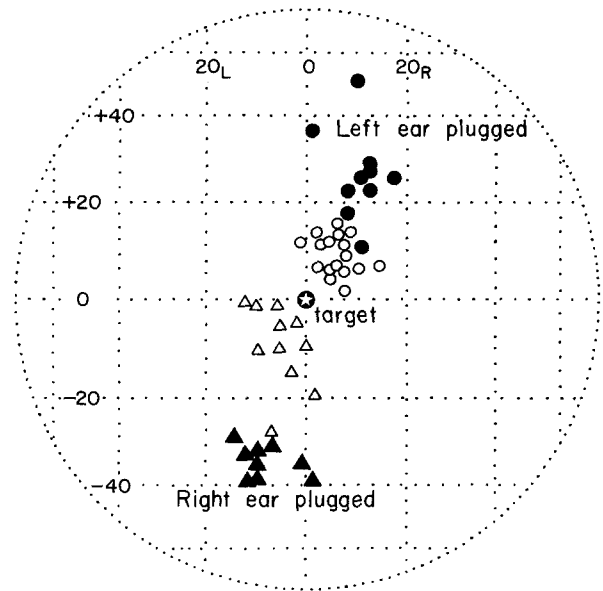
the owl always oriented to a location that was below the horizontal plane.

At 2 kHz the owl began to respond reliably to tonal stimuli but the pattern of head movement was qualitatively the same as for 1 kHz. At 3 kHz the owl began to orient properly to upward targets. At 4–6 kHz, the owl's responses were quick, straight head saccades with final fixations that were often very accurate in both azimuth and elevation at all target positions (Fig. 4). The responses at 7 and 8 kHz continued to be crisp and accurate, however a new phenomenon appeared: when the target was placed at  $[30^{\circ}_L, 0^{\circ}]$ , the owl often oriented to  $[30^{\circ}_R, 0^{\circ}]$ . This left-right confusion, seen in both owls, was only elicited by  $[30^{\circ}_L, 0^{\circ}]$  targets, and was more prevalent at 8 kHz (Dini: 11 out of 14 trials) than at 7 kHz (Dini: 3 out of 9 trials). Prolonging the tones to 1,000 ms did not eliminate this confusion. The left-right errors were precise, but to the wrong side, and as such could not be combined with normal errors (these trials were excluded from the error calculations). No evidence of left-right confusion remained at 9 kHz, but the owl's unwillingness to respond began to re-emerge. At 10 kHz responses were sporadic, and errors were large and unsystematic (Fig. 4).

The frequency dependence of elevational errors (Fig. 3) is expected if the owl used  $\Delta S$  to localize sounds in elevation. As described in the Introduction, the directionalities of the barn owl's ears change their mutual plane of symmetry away from the median sagittal plane at 3 kHz, towards the horizontal plane at 6 kHz (Knudsen, in press). Thus, as frequency increases from 3 to 6 kHz, the spatial information offered by  $\Delta i_r$  changes from azimuthal to elevational. The closer the axis of  $\Delta i_r$  change comes to being vertical, the greater will be its spatial resolution in elevation. Furthermore, as frequency increases over this same range, the magnitude of  $\Delta i_r$ , and therefore its spatial resolution, increases due to the increasing directionality of the owl's ears at higher frequencies (Payne, 1971; Knudsen, in press). Both of these physical trends anticipate the decrease in the owl's elevational error with increasing tone frequency.

#### *The Effect of Ear Occlusion on Sound Localization.*

In free field experiments,  $\Delta T$  cannot be manipulated as a single variable. However,  $\Delta S$  (and  $\Delta I$ ) can be perturbed without affecting  $\Delta T$  by occluding either ear. We measured the effect of occluding the owl's left or right ear on its ability to localize 75 ms noise bursts (open-loop). The ear was occluded just prior to the test session each day. A "tight plug" was a ball of beeswax that fitted snugly into the ear canal; a "mild plug" was a thin layer of silicone cement covering the ear opening. The difference in the behav-



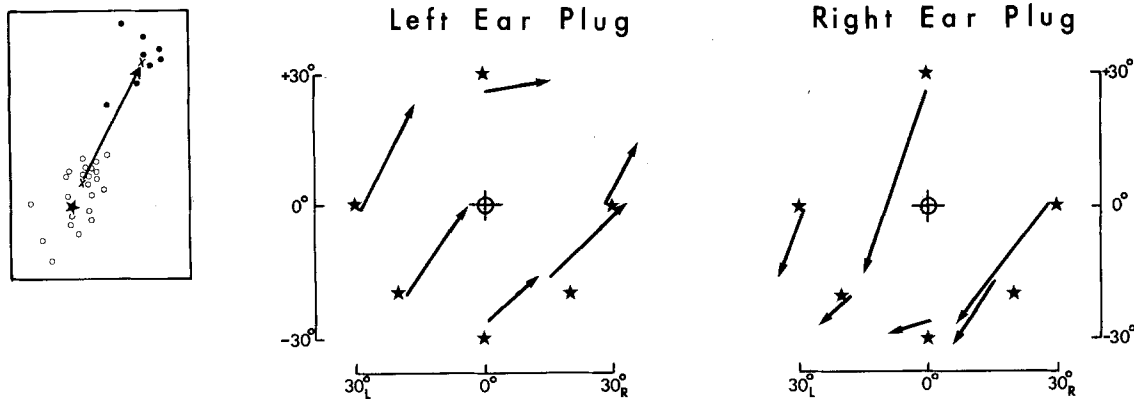
**Fig. 5:** Effect of ear occlusion on open-loop sound localization. Individual fixation points in response to a wide-band noise target located at  $[0^{\circ}, 0^{\circ}]$  (star) are plotted for four conditions of ear occlusion: 1) left ear, tight plug (closed circles); 2) left ear, mild plug (open circles); 3) right ear, tight plug (closed triangles); and 4) right ear, mild plug (open triangles). Left ear occlusion causes the owl to miss up and to the right; right ear occlusion, down and to the left. Data are from Dini

ioral effects of the tight and mild plugs was readily apparent, but the actual attenuation factors of each was not measured.

After ear occlusion the owl was placed in the test chamber and its localization accuracy at six (Roger) or seven (Dini) different target locations was measured. The smaller number of target locations used in these experiments stemmed from the need to gather complete data on a given plug in a single test session, since the effectiveness of the plug may have changed from day to day. The target speaker was moved after every trial until a total of at least nine trials had been accumulated at each location.

The dramatic effect of even a mild ear occlusion on the owl's ability to localize sound necessitated a modification in our testing paradigm. Since the owls no longer zeroed their heads in response to the zeroing speaker (Fig. 5), we abandoned our use of the initial zeroing sound and waited until the owl zeroed to criterion level spontaneously. The overtraining of the owls by this time made this strategy possible. Thus, in these experiments, a trial consisted of only a single target sound to which the owl oriented.

The results from these experiments are presented in Fig. 6. The data for each target location are presented in the form of a vector. The origin of the vector corresponds to the median of the fixation



**Fig. 6.** Effect of a tight ear plug on open-loop localization of various target positions. The systematic localization errors caused by a tight, left or right ear plug are displayed in vector form for six target locations (stars). Vectors were derived as shown in the box on the left. The tail of the vector indicates the median of the owl's fixation points under normal conditions (open circles). The head of the vector corresponds to the median of the fixation points following ear occlusion (closed circles). Thus each vector represents the magnitude and the direction of the effect of ear occlusion. Data are from Roger

points measured under normal conditions (Knudsen et al., 1979). The head of the vector marks the median of the fixation points under the designated condition of ear occlusion.

The general effect of ear occlusion can be seen best in the owl's errors to a target located at  $[0^{\circ}_{az}, 0^{\circ}_{el}]$  (Fig. 5): left ear occlusion caused the owl to fixate above and to the right of the target; right ear occlusion resulted in the owl fixating below and to the left. The tighter the plug, the greater were the owl's errors.

The magnitude of the owl's errors also depended upon the location of the target (Fig. 6). When their left ears were plugged, their largest errors were committed to targets located below and to the left; when their right ears were plugged, their largest errors were to targets above and to the right. Notice that errors were never strictly elevational, but always included an azimuthal component. This implies that the owl gains some azimuthal as well as elevational information from  $\Delta S$ .

*The Effect of Removing the Facial Ruff on Sound Localization.* The converse experiment to ear occlusion, which increases  $\Delta S$ , is to eliminate  $\Delta S$  as a spatial cue. Removing the owl's facial ruff feathers (Fig. 1) accomplishes this to some degree by depriving the owl of the principal, acoustically reflective component at the auditory periphery. In theory, the consequences of ruff removal must be due primarily to the change in ear directionality particularly for frequencies greater than 3 kHz for which the ruff is an effective sound reflector. Of course the owl still has its head to create a sound shadow, and its preaural flaps and ear openings that are asymmetrically located on the thickened skin which previously supported the

ruff (postaural fold). However, to the extent that the ruff is responsible for the highly directional and vertically disparate sensitivities of the two ears, removal of the ruff reduces  $\Delta S$ .

An owl without its ruff should hear sounds with normal  $\Delta T$ , but the magnitudes of  $\Delta i_r$  should tend toward zero. Under normal conditions (with ruff intact),  $\Delta i_r = 0$  for the higher frequencies occurs only when the sound source is located in the owl's horizontal plane (Payne, 1970; Knudsen, in press). Thus one might expect that the owl without its ruff would not only make substantial errors in elevation, but that these errors would be towards the horizontal plane.

In a final experiment, we removed the ruff feathers from Dini and Roger. Normal testing conditions were used, i.e., a zeroing sound followed by a target sound. The target was a 75 ms wide-band noise burst (band-pass = 0.8 to 12 kHz). Following ruff removal, the owls were less sensitive to sound, therefore the sound level from the speakers was increased to 30–50 dB SPL. Between 10 and 13 trials were run at each of the target locations indicated in Fig. 7.

The qualitative effect of ruff removal was immediately apparent. When we snapped our fingers behind the owl, it would turn and orient quite well in azimuth, but would miss completely in elevation. This qualitative impression was confirmed by the performance of the owls in the test paradigm (Fig. 7). The data are again presented as vectors, pointing from the median value under normal conditions (Knudsen et al., 1979) to the median value after ruff removal.

Two properties of these vectors are conspicuous: 1) they are vertically oriented indicating that the owls made little or no azimuthal errors while committing large elevational errors; and 2) they are directed toward the horizontal plane  $[0^{\circ}_{el}]$  signifying that the

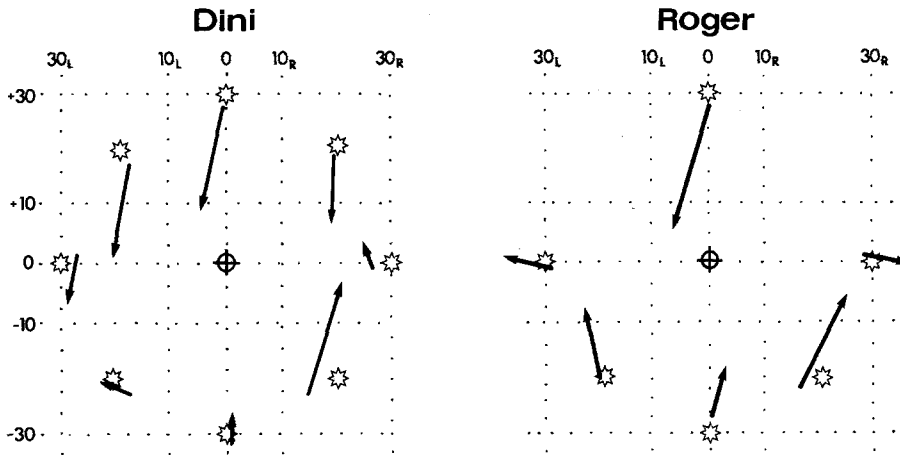


Fig. 7. Effect of ruff removal on sound localization. The ability of Dini and Roger to orient to 75 ms noise bursts presented at various locations was tested before and after their ruff feathers were removed. The data are presented in vector form as described in Fig. 6. Each vector represents the magnitude and direction of the error caused by ruff removal for a given target location (designated by stars). Azimuthal accuracy is largely unaffected by the absence of the ruff, whereas in most cases elevational accuracy is significantly worse

owls responded as though the targets had converged upon the horizontal plane. For example, note Dini's responses to targets at  $[20^{\circ}_{\text{R}}, +20]$  and  $[20^{\circ}_{\text{R}}, -20]$ ; these locations differed in elevation by  $40^{\circ}$ , but the responses to the respective targets differed in elevation by only  $15^{\circ}$  (Fig. 7).

Although the azimuthal components of the owls' errors were small, and usually not significantly different from those measured under normal conditions, the errors were consistent in that the owls overestimated most target locations compared to control performances. This is probably explained by the altered directionality of the ears and the azimuthal component associated with  $\Delta S$  (Fig. 6).

When the target was on the owl's left, and ostensibly somewhat louder in the left ear, the owl fixated lower than when the target was on its right. This result is also expected from the ear occlusion results (Fig. 6).

Removing the facial ruff had little effect on the accuracy of either owl when localizing targets at  $[30^{\circ}_{\text{L}}, 0^{\circ}]$  or  $[30^{\circ}_{\text{R}}, 0^{\circ}]$ . That is, the presence or absence of the ruff had little effect on the owl's ability to localize targets in the horizontal plane. The small errors committed by Dini to targets at  $[20^{\circ}_{\text{L}}, -20^{\circ}]$  and  $[0^{\circ}, -30^{\circ}]$  were peculiar to this bird. Roger made large and statistically significant errors ( $P < 0.01$ ) in elevation at these locations (Fig. 7).

In summary, removing the owl's ruff feathers, which in theory diminished the magnitude of  $\Delta S$ , but left  $\Delta T$  undisturbed, caused a decrease in elevational accuracy but did not significantly affect azimuthal accuracy.

In the following sections, the behavioral evidence that the owl uses  $\Delta T$  and  $\Delta S$  to localize sound is

reviewed. For a more detailed discussion of this evidence, refer to Knudsen (in press).

*$\Delta S$  as a Localization Cue.* The ear occlusion experiments (Figs. 5 and 6) demonstrate directly the importance of binaural intensity differences for sound localization by the barn owl. However, these experiments do not distinguish whether the owl uses  $\Delta S$  or  $\Delta I$ , since both cues are affected by ear occlusion. Evidence for  $\Delta S$  as the localization cue is seen in the owl's need for a wideband signal to maximize its localization accuracy; the owl's error when localizing tonal targets, even at the best frequency (6 kHz) was about three times greater than its error to noise targets (Fig. 3). Previously Konishi (1973a) demonstrated that the barn owl was able to localize a 1 kHz bandwidth of noise (centered at 7.5 kHz) no better than a 7 kHz pure tone. Furthermore the owl's accuracy improved rapidly with an increase in noise bandwidth from 2 kHz up to 4 kHz (the widest band tested). Responses to 4 kHz bandwidth noise were approximately four times more accurate than responses to tones or 1 kHz bandwidth noise.

The requirement for a wide signal bandwidth is not expected if the owl were using  $\Delta I$ . On the other hand, a dramatic improvement in localization accuracy with bandwidth is to be expected if the owl were using  $\Delta S$ . This expectation relies on the rotation of the plane of symmetry of the ears' directionalities with increasing frequency (see Introduction). When the sound is a tone,  $\Delta S$  comprises only one  $\Delta i_t$  value, which localizes the source to a particular spatial plane with some degree of error. A substantial increase in the owl's accuracy should not occur until the signal includes frequencies which define significantly differ-



ent spatial planes. The wider the sound bandwidth, the greater will be the diversity in the orientations of the  $\Delta i_t$  planes, and the more restricted will be their region of intersection, which defines the location of the sound source in space (Knudsen, in press).

*$\Delta T$  as a Localization Cue.* The necessity of including  $\Delta T$  as a localization cue for the barn owl comes from several lines of evidence. First, the owl's azimuthal errors were frequency independent up to 8 kHz (Fig. 3). Second, the owl's azimuthal errors were equal under open- and closed-loop conditions when localizing tones (Fig. 3). If the owl were using  $\Delta\phi$ , closed-loop errors should have been smaller at frequencies below 3 kHz (see Localization of Tones), since it had the opportunity to turn toward the ongoing sound and thereby improve the spatial resolution derived from  $\Delta\phi$ . The similarity of open- and closed-loop errors is consistent with the use of a  $\Delta T$  cue, which could only have been measured at the beginning of each tone burst (open- or closed-loop), and therefore was equal in both stimulus conditions.

A third piece of evidence favoring  $\Delta T$  as a localization cue is found in the owl's performance when localizing wide band noise under closed-loop conditions (Fig. 7 in Knudsen et al., 1979). For all azimuthal target angles of  $30^\circ$  or more the accuracy of the owl's localization was fairly constant; since the continuing sound afforded an opportunity to correct major errors. However, even with correction, the owl could not localize the target as accurately as when the target was located at azimuthal angles of less than  $30^\circ$ . The target needed to be at a small azimuthal angle at the onset of the sound in order for the owl to achieve its maximum accuracy.  $\Delta T$  is the only localization cue that is derived exclusively from the onset of a sound. Furthermore,  $\Delta T$  provides maximum spatial resolution when the sound comes from a small azimuthal angle ( $\alpha$ ), since the magnitude of  $\Delta T$  follows a sine function of the incident angle of the sound (Woodworth, 1962).

The arguments above assume that the owl requires a substantial discontinuity in the sound envelope in order to make a  $\Delta T$  measurement, since no apparent use was made of the transients present within noise bursts to maximize azimuthal accuracy.

In sum, according to our interpretation of the data, the owl uses  $\Delta S$  to determine the elevation of a sound source, and both  $\Delta T$  and  $\Delta S$  to localize the azimuth of the source. If the sound is continuous and begins when the owl is facing away from the source, the spatial resolution provided by  $\Delta T$  will be poor (for example, as in the closed-loop trials at  $[70^\circ, 0^\circ]$ ; Knudsen et al., 1979). In this situation the owl can derive both azimuth and elevation from  $\Delta S$  alone, but its accuracy in azimuth will be worse than when an onset cue from a small azimuthal angle is available.

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## References

- Knudsen, E.I.: Sound localization in birds. In: Comparative studies of hearing in vertebrates. Popper, A.N., Fay, R.R. (eds.). New York: Springer (in press)
- Knudsen, E.I., Blasdel, G.G., Konishi, M.: Sound localization by the barn owl *Tyto alba* measured with the search coil technique. *J. Comp. Physiol.* **133**, 1-11 (1979)
- Knudsen, E.I., Konishi, M.L.: Space and frequency are represented separately in the auditory midbrain of the owl. *J. Neurophysiol.* **41**, 870-884 (1978)
- Konishi, M.: Locatable and nonlocatable acoustic signals for barn owls. *Am. Natl.* **107**, 775-785 (1973 a)
- Konishi, M.: How the owl tracks its prey. *Am. Sci.* **61**, 414-424 (1973 b)
- Norberg, A.: Physical factors in directional hearing in *Aegolius funereus* (Linné) (Strigiformes), with special reference to the significance of the asymmetry of the external ears. *Arkiv. Zool.* **20**, 181-204 (1968)
- Norberg, R.A.: Skull asymmetry, ear structure and function, and auditory localization in Tengmalm's owl, *Aegolius funereus* (Linné). *Philos. Trans. R. Soc. Lond. (Biol.)* **282**, 325-410 (1978)
- Payne, R.S.: Acoustic location of prey by barn owls (*Tyto alba*). *J. Exp. Biol.* **54**, 535-573 (1971)
- Pumphrey, R.J.: The sense organs of birds. *Ibis* **90**, 171-199 (1948)
- Robinson, D.A.: A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans. Biomed. Electron.* **10**, 137-145 (1963)
- Searle, C.L., Braid, L.D., Davis, M.F., Colburn, H.S.: Model for auditory localization. *J. Acoust. Soc. Am.* **60**, 1164-1175 (1976)
- Woodworth, R.S.: *Experimental Psychology*, pp 349-361. New York: Holt, Rinehart and Winston 1962