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Bi-coordinate sound localization by the barn owl

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Summary. 1. Binaurally time-shifted and intensity-unbalanced noise, delivered through earphones, induced owls to respond with a head-orienting behavior similar to that which occurs to free field auditory stimuli.

2. Owls derived the azimuthal and elevational coordinates of a sound from a combination of interaural time difference (ITD) and interaural intensity difference (IID).

3. IID and ITD each contained information about the azimuth and elevation of the signal. Thus, IID and ITD formed a coordinate system in which the axes were non-orthogonal.

4. ITD was a strong determinant of azimuth, and IID was a strong determinant of elevation, of elicited head turn.

Introduction

Barn owls turn their heads toward the source of a sound. This behavior has been studied under controlled, laboratory conditions, allowing the accuracy of sound localization to be measured as a function of free-field acoustic parameters and target location (Knudsen et al. 1979; Knudsen and Konishi 1979). Similar behavioral responses can be elicited by dichotic sounds delivered to owls through earphones (Moiseff and Konishi 1981). Under these conditions, the owl still performs stereotyped sound localization behavior and localizes a phantom target. Presumably, the localization of the phantom target is accomplished through the external projection of an internal sound image produced by the particular set of binaural parameters that have been presented. The ability to externalize phantom targets is dependent upon binaural fusion of the dichotic stimuli and has been reported, and exploited extensively in psychophysical experiments (Blauert 1983; Durlach and Colburn 1978; Levy and Butler 1978; Mills 1972; Sayers and Cherry 1957).

The position of the ear opening, that of the preaural flap, and the orientation of the two halves of the facial ruff are asymmetrical in the barn owl (Payne 1971). These asymmetries, coupled with the spatial separation between the ears cause interaural time and interaural intensity differences to vary along different spatial coordinates (Knudsen 1980; Payne 1971; Moiseff 1989).

Behavioral evidence indicates that the barn owl uses interaural time difference mainly for localization in azimuth, and interaural intensity difference mainly for elevation. Interaural time difference was shown to be an important cue for azimuthal localization by presenting dichotic stimuli with controlled interaural time differences (Moiseff and Konishi 1981). The role of interaural intensity difference as a cue for localization in the vertical plane was inferred from the effects of ear-plugging on sound localization behavior (Knudsen and Konishi 1979, 1980). Behavioral and neurophysiological evidence revealed that plugging one ear of an owl, which primarily altered interaural intensity differences, resulted in a large shift in the perceived elevation of free-field stimuli (Knudsen and Konishi 1979, 1980). The effects of plugging one ear were not confined to shifting the apparent elevation of the stimulus, but also resulted in a small shift (6°–10°) in apparent azimuth (Knudsen and Konishi 1980). The shift in azimuth might have been the result of phase shifts induced by the ear plugs or these shifts might suggest that interaural intensity difference is also a cue for azimuth.

Abbreviations: IID Interaural intensity difference; *ITD* Interaural time difference

These facts suggest that the owl can determine location of a sound from the combination of interaural time differences and interaural intensity differences; the owl uses a bicoordinate system. The present paper describes the characteristics of the owl's bicoordinate system.

Materials and methods

Training of owls. The two tame barn owls (*Tyto alba*) used in this study were removed from their parents approximately one week after hatching and raised by hand. At about 3 months of age the owls began to receive daily training to stand still on a perch in an anechoic room. The room was illuminated solely by infrared light enabling us to monitor the owls with an infrared video system. The owls responded to sound, delivered by a loudspeaker in free field, by rapidly turning their heads towards it and fixating at this position; the speaker could be moved to any location around the owl's head at a constant distance of 1 m (Knudsen et al. 1979). Although the owls performed the head turning and fixation behavior without any training, their response eventually waned unless it was periodically reinforced. Therefore, responses were reinforced by rewarding with a small piece of meat delivered from a feeder that was controlled from outside the room. Reinforcement was not contingent upon the accuracy of the sound localization behavior, but rather was contingent upon the proper behavioral sequence, i.e., rapid head-turn followed by fixation for several seconds.

After training, we tested the behavioral response elicited by dichotic auditory stimulation, with the earphones. Hollow, stainless steel cylinders, 5 mm long and 8 mm diameter and threaded on the inside, were sutured into the ear canals of the owls under Ketamine anesthesia (Moiseff and Konishi 1981). The owl was allowed to recover from anesthesia fully before behavioral experiments were performed. The cylinders, once implanted, remained in place for as long as two weeks, obviating the need for frequent anesthetization and surgery. The earphones used in the dichotic experiments were miniature condenser microphones (Knowles model 1759 used in an earphone mode) encased in a stainless steel cylinder whose exterior was threaded to match the cylinder sutured into the ear canal. The earphone assembly could be screwed into the threaded interior of the cylinder that was sutured into the ear canal. The earphones could be easily installed or removed with this system without the need to restrain the owl.

Stimulus generation and delivery. Stimuli were generated and delivered by procedures similar to those published previously (Moiseff and Konishi 1981). Briefly, stimuli were a single burst of noise (15 dB/octave bandpassed filter, centered at 7 kHz) 50–100 ms in duration and 5 ms in rise and fall time. An analog delay circuit was used to split the stimulus into 2 channels, i.e., for the left and right earphones, that were identical except for the interaural time difference. The two outputs of the delay circuit were independently attenuated and delivered to the earphones. The delay circuit was routinely tested both for the accuracy of time shift and for the lack of interference with signal intensity. Interaural time difference (ITD) was varied over the range of -150 µs (left ear leads right ear) to $+150$ µs (right ear leads left ear) in 30 µs steps. Interaural intensity difference (IID) was varied over the range of -30 dB (left side louder than right side) to $+30$ dB (right side louder than right side) in 10 dB steps. The range of ITDs presented was well within the biologically significant range of binaural parameters that an adult owl would experience (Payne 1971; Knudsen 1980; Moiseff 1989). The range of IIDs was as much as 10 dB greater than might be expected under normal conditions (Moiseff 1989). For each trial ITD and IID were randomly chosen from a table of stimulus parameters. The minimum sound intensity that elicited the head-turning response was determined empirically and was approximately 0 dB SPL. The owl is more motivated to respond to faint sound than to loud sound. The average binaural intensity used in most trials was 20 dB (SPL).

Measuring localization. The movement and orientation of the owl's head was measured with a modified version of the search coil technique (Knudsen et al. 1979). A set of orthogonally oriented electromagnetic coils surrounded the owl's head. The head carried an orthogonal pair of small search coils (about 25 mm in diameter). The cables to the earphones and those from the search coils were fastened together on a metal post that was permanently cemented to the skull under anesthesia at an earlier date. The search coil system in conjunction with a PDP 11/40 computer could measure the angular position of the owl's head to a resolution of 0.5°. Before each test session the search coil system was calibrated by setting it to known angular positions and measuring the detected angles. These data were used to determine any corrections that needed to be applied to the measurements. Only unambiguous responses were included in the analysis of the data. Unambiguous responses were defined by three distinct attributes: first, the owl was alert, not moving, and facing directly ahead; second, the head-turning began and ended abruptly; third, the owl fixated its head in a particular direction for at least 3 s. Angular displacements used in various calculations are the differences between the initial and the final angular position assumed by the head.

Data analysis. Simple or multiple linear regression analysis was performed between the dependent variables (azimuth and elevation components of the head-turn behavior) and the independent variables (ITD and IID) depending on whether one, or both, of the independent variables were varied. Analysis was confined to linear relationships due to their analytical simplicity. No attempt was made to test non-linear relationships to see if they would better explain the data because the linear analyses were found to be satisfactory.

Results

Time course of head-turn

A head-turn behavior similar to that described by Knudsen et al. (1979) was elicited when a noise was presented through earphones (Fig. 1). The angular rotations of the head-turn were separated into elevation and azimuth components by the measurement technique. The magnitude and direction of the azimuth and elevation components could be predicted from the parameters of the dichotic stimulus, specifically, the combination of interaural time and interaural intensity differences that were presented to the animal.

Time difference alone

Stimuli in this series ($n=68$) were produced with interaural time differences ranging from -90 µs

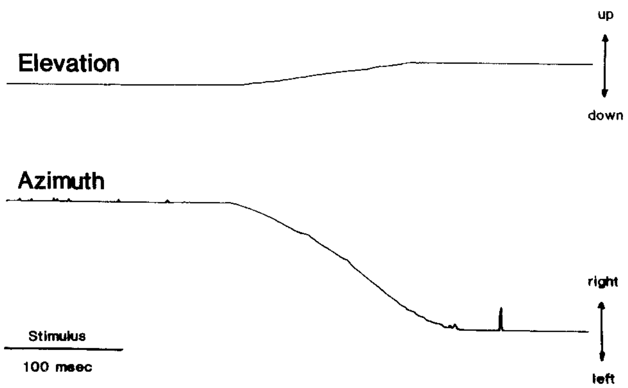

Fig. 1. Time course of head orienting response. Response to single 100 ms noise burst (ITD = −120 μs, IID = 0). In response to this stimulus the bird moved its head up 0.1° and turned 53.2° to the left. Time calibration = 100 ms

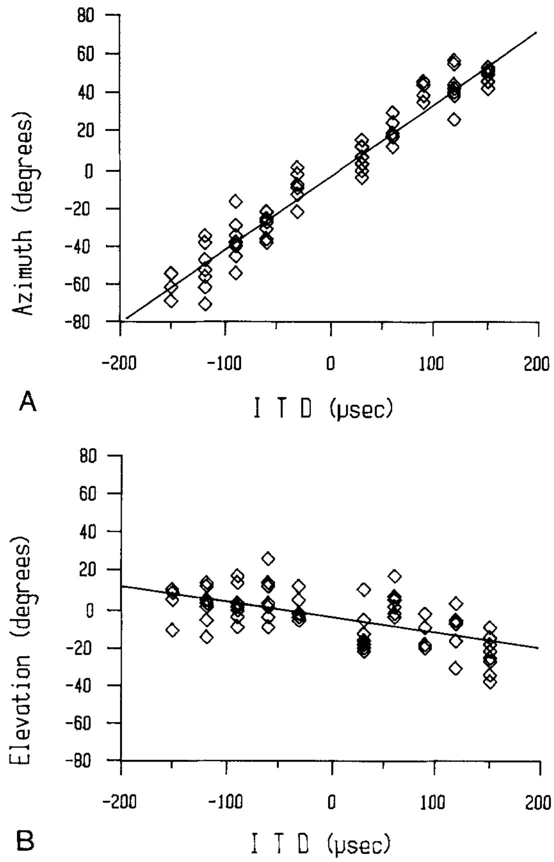

Fig. 2A, B. Interaural time differences (ITD) and spatial locations. Azimuth (**A**) and Elevation (**B**) positions associated with ITD when IID = 0 dB. Negative values of ITD indicate that the left ear's signal leads the right ear's signal. Total number of responses was 68. Equations describing these data are detailed in the text

to +90 μs, while the interaural intensity difference was kept at 0 dB. Although the IIDs were equal to 0 dB, the average binaural intensities varied over a 30 dB range, the average binaural intensity being the product of the summed sound pressure level of the two ears divided by 2. Since only one independent variable was varied during this series (i.e., ITD was varied while IID was kept constant) data analysis was accomplished by simple linear regression between each behavioral component (movement in azimuth and movement in elevation) and ITD.

Interaural time difference was a good predictor of the azimuthal angle to which the owls turned their heads (Fig. 2A). This relationship was fit well by the linear equation ($r = 0.98$, $P < 0.0001$):

$$\text{azimuth} = 0.38°\text{Az}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} - 3.74°.$$

Interaural time difference also affected orientation in elevation (Fig. 2B). The owl turned its head slightly above eye level when the left ear led the right ear and below eye level when the right ear led the left ear. The correlation between ITD and elevation angle of the head turn was weaker than above ($r = 0.59$, $P < 0.001$) but still statistically significant. The slope of the linear equation relating ITD and elevation was much smaller than that relating ITD and azimuth:

$$\text{elevation} = -0.081°\text{El}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} - 4.48°.$$

Intensity difference alone

The results contained a total of 55 responses to interaural intensity differences varying from −30 dB to +30 dB. The average binaural intensity varied over a 30 dB range and was not included in the analysis. Again, only one independent variable was varied during this series (IID was varied while ITD was kept constant at 0 μs) so linear regression between each behavioral axis (azimuth and elevation) and IID was calculated. Interaural intensity differences caused the owls to turn their heads in elevation (Fig. 3A). The owls turned their head upward when sound was louder in the right ear (IID > 0) and downward when the left ear was louder (IID < 0). Both owls showed a wider range of downward movement (0 to 45°) than upward movements (0 to 20°). In spite of this nonlinearity, a linear approximation of this relationship yielded highly significant results ($r = 0.90$, $P < 0.0001$):

$$\text{elevation} = 1.34°\text{El/dB} \cdot \text{IID(in dB)} - 12.8°.$$

Interaural intensity difference was also correlated with the azimuthal component of the head turn, though, more weakly ($r = 0.76$, $P < 0.0001$). The owls tended to turn their heads toward the side of louder sound (Fig. 3B):

$$\text{azimuth} = 0.55°\text{Az/dB} \cdot \text{IID(in dB)} - 2.0°.$$

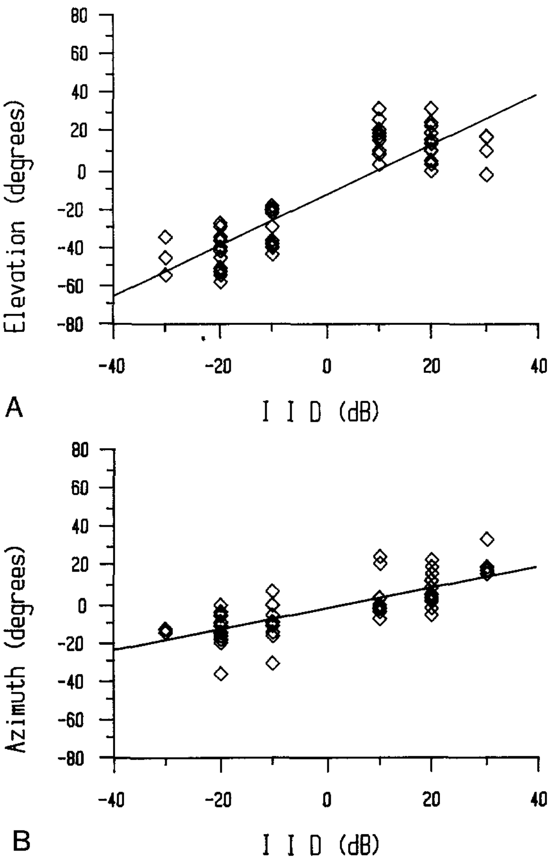

Fig. 3A, B. Interaural intensity differences (IID) and spatial locations. Elevation (**A**) and Azimuth (**B**) positions associated with IID when ITD = 0 μs. Negative values of IID indicate that the left ear's signal is louder than the right ear's signal. The total number of responses was 55. See text for detailed equations

Combination of non-zero interaural time and intensity differences

Stimuli containing non-zero values of both interaural time difference and interaural intensity difference were presented 32 times. These data were analyzed by multiple linear regression between each of the behavior components (i.e., azimuth and elevation) and the two independent variables IID and ITD (Fig. 4). The regression analysis revealed that ITD and IID were both important in predicting the azimuthal component of the behavior.

Inspection of Fig. 4B revealed 4 points, located at the lower right of the graph, that did not seem to follow the general trend set by the majority of the data. These 4 data points appeared to be inconsistent with the rest of the results, but they were not arbitrarily discounted since they met the same criteria for acceptance as the other responses. To avoid the possibility of adversely biasing the interpretation of the rest of the data, analysis of this data set was performed with, and without these deviant points.

When all points ($n = 31$), including the apparently deviant ones, were included in the analysis, the results were

$$\text{azimuth} = 0.18°\text{Az}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} + 0.62°\text{Az/dB} \cdot \text{IID(in dB)} - 1.8°$$
$$(r = 0.73,\ P < 0.0001),$$
$$\text{elevation} = -0.045°\text{El}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} + 1.2°\text{El/dB} \cdot \text{IID(in dB)} - 2.1°$$
$$(r = 0.92,\ P < 0.0001).$$

Although included in the latter equation, the ITD variable was not a significant predictor of elevation ($P > 0.1$, slope was not significantly different from 0°El/μs); all of the other slopes were significantly different from 0 ($P < < 0.01$).

Removal of the 4 points that seemed to be deviant yielded the following results ($n = 27$).

$$\text{Azimuth} = 0.31°\text{Az}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} + 0.21°\text{Az/dB} \cdot \text{IID(indB)} + 2.23°$$
$$(r = 0.89,\ P < 0.0001),$$
$$\text{Elevation} = -0.055°\text{El}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} + 1.23°\text{El/dB} \cdot \text{IID(in dB)} - 2.2°$$
$$(r = 0.93,\ P < 0.0001).$$

In the above relationships both ITD and IID were important determinants of both azimuth and elevation. However, these equations mask the fact that ITD was a better predictor than IID for azimuth, and that IID was a better predictor than ITD for elevation. This was evident in the statistical significance of the slopes for each of these component relationships (i.e., the probability that the particular slope was different from 0). The 'better' predictor had a $P < < 0.01$, whereas the 'lesser' predictor had a $P = 0.09$, in each case.

Pooled data

For completeness, multiple linear regression analyses were performed for all of the results obtained with noise stimuli, pooled together ($n = 155$). The pooled data included the 4 outlying points described earlier and yielded the following relationships:

$$\text{Azimuth} = 0.36°\text{Az}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} + 0.56°\text{Az/dB} \cdot \text{IID(in dB)} - 2.8°$$
$$(r = 0.92,\ P < 0.0001),$$
$$\text{Elevation} = -0.075°\text{El}/\mu\text{s} \cdot \text{ITD(in } \mu\text{s)} + 1.29°\text{El/dB} \cdot \text{IID(in dB)} - 6.9°$$
$$(r = 0.84,\ P < 0.0001).$$

In these equations, all of the slopes were significantly different from 0 ($P < < 0.01$).

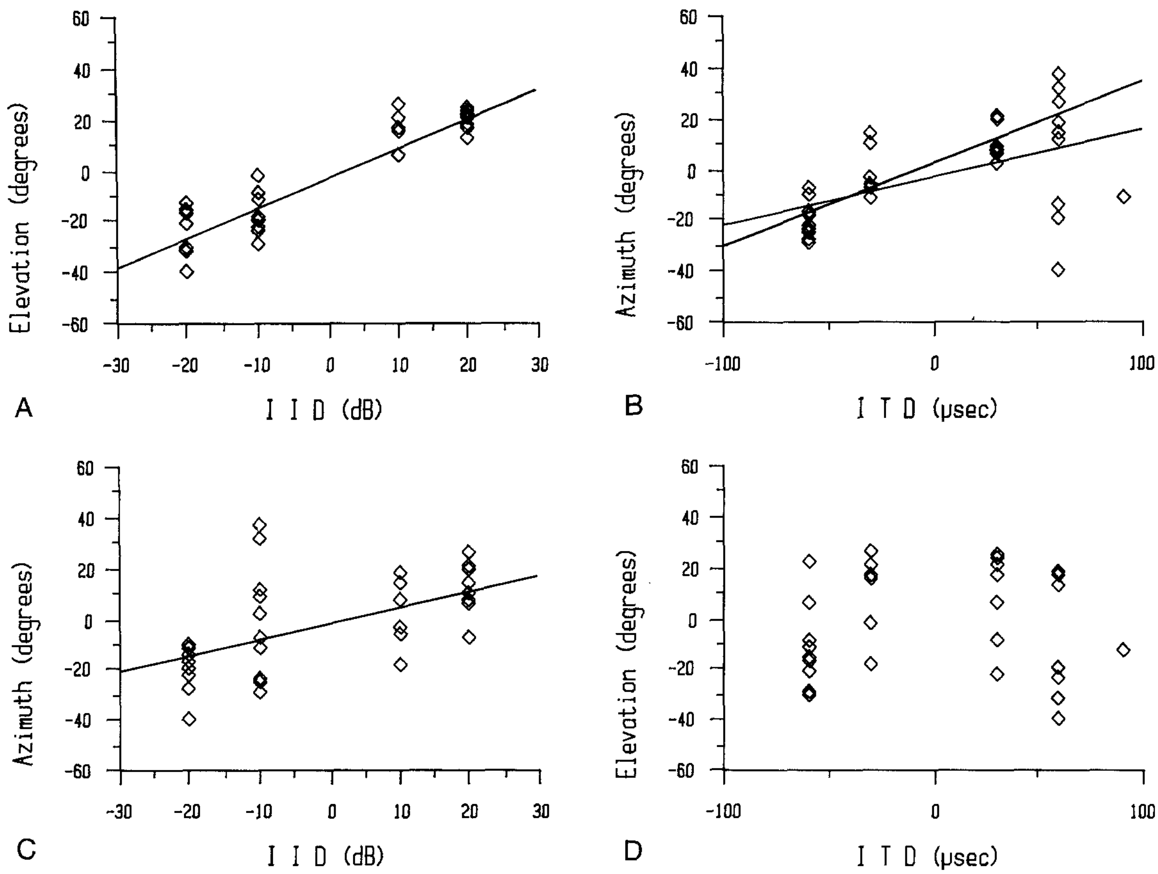

Fig. 4A–D. Spatial locations associated with combinations of non-zero ITD and IID. Total number of responses was 32. **A** Elevation was related to IID ($r^2=0.85$) by the equation: Elevation $=1.20°/\mathrm{dB} \cdot \mathrm{IID}-2.24°$. **B** The relatively weak correlation between azimuth and ITD ($r^2=0.28$) is largely the result of the deviant points at the lower right. If these apparently deviant points are removed, the correlation improves dramatically ($r^2=0.78$). The lines shown, are the linear equations with, and without the deviant points (without: Azimuth $=0.33°/\mu s \cdot \mathrm{ITD}+2.70°$). The linear equation fitting all the data points is Azimuth $=0.19°/\mu s \cdot \mathrm{ITD}-2.6°$. **C** Azimuth is correlated with IID ($r^2=0.30$), Azimuth $=0.66°/\mathrm{dB} \cdot \mathrm{IID}-1.07°$. **D** Elevation is not correlated with ITD ($r^2=0.002$, Elevation $=-0.02°/\mu s \cdot \mathrm{ITD}-3.70°$)

The reproducibility of the head-turn response to the binaural earphone stimuli was addressed by determining the scatter in the elevation and azimuth components of the head turn for each set of binaural parameters. Specifically, for each pair of binaural parameters that were repeated 3 or more times the mean and standard deviation for the amount of head turn in azimuth and elevation were calculated (Table 1). The average standard deviation of azimuth was 8.2°. This was very similar to the average standard deviation of elevation which was 8.4°. In calculating these average standard deviations, each set of parameters was given equal weighting (i.e., those derived from $n=3$ were weighted the same as those derived from greater n). Values of standard deviation ranged from as little as 0.8° to a maximum of 13.6°. There was no systematic relationship between the amount of reproducibility and the magnitude of either of the binaural cues. Similarly, the reproducibility was not dependent upon the magnitude of the head turn.

A non-orthogonal coordinate system

The results of the pooled data described above indicated that the final position of the owls head-turn response was uniquely defined by a pair of ITD and IID. The relationship between the two binaural parameters (ITD and IID) and the two spatial coordinates (azimuth and elevation) were shown in Fig. 5. This graph was generated using the equations derived from the pooled data, reported above. The ordinate and abscissa represent the behavioral response (azimuth and elevation components, respectively). The family of lines indicate the loci of azimuth and elevation coordinates resulting from varying one binaural parameter when the other parameter was kept constant. This graphic representation shows a unique, though

Table 1. Head-turn repeatability, for $n >= 3$

ITD	IID	*n*	AZ AVG	EL AVG	AZ SDEV	EL SDEV
−150	0	4	−60.2	2.6	6.2	9.8
−120	0	7	−52.0	1.2	12.4	10.0
−90	0	8	−37.8	2.7	11	8.6
−60	−20	4	−19.4	−21.0	7.6	6.4
−60	−10	3	−25.7	−16.4	2.9	11.4
−60	0	8	−28.5	6.8	6.3	11.3
−30	0	6	−9.7	−0.1	8.1	6.6
−30	10	3	1.2	20.8	10.8	5.6
0	−30	3	−14.5	−45.3	0.8	10.5
0	−20	14	−12.6	−42.9	9.1	9.4
0	−10	11	−9.6	−30.5	9.8	10.0
0	10	9	3.9	16.7	11.3	9.2
0	20	14	7.3	13.6	8.4	8.9
0	30	4	20.7	9.9	8.8	9.3
30	0	9	5.8	−13.8	6.3	9.9
30	20	4	13.5	21.6	7.9	3.9
60	−20	3	−24.5	−34.5	13.6	4.9
60	−10	3	26.6	−21.2	13.2	2.6
60	0	7	19.3	3.5	5.9	6.9
90	0	4	41.1	−13.1	4.7	8.3
120	0	7	43.5	−10.6	10.5	10.9
150	0	8	48.2	−24.3	4.1	9.8

Negative values of ITD indicate left ear leads right ear. Units of ITD are μs. Negative values of IID indicate that stimulus delivered to right ear is louder than stimulus delivered to left ear. Units of IID are dB. Azimuth is in units of degrees, where negative values indicate directions towards the left. Elevation is in degrees, where negative values indicate downward directions. *n* number of repetitions; *AVG* average; *SDEV* standard deviation

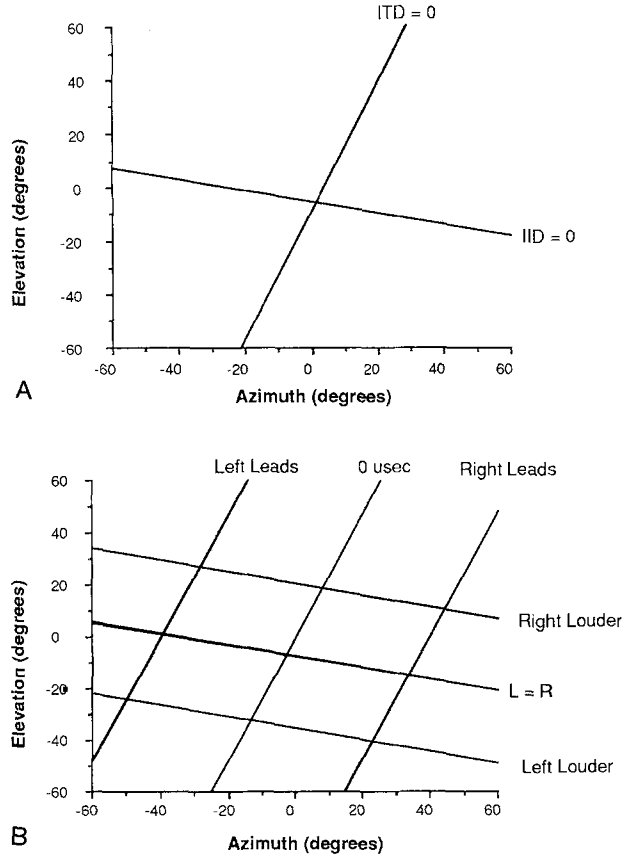

Fig. 5A, B. Non-orthogonal mapping of binaural parameters onto spatial coordinates. **A** Mapping of ITD (while IID = 0 dB) and IID (while ITD = 0 μs) onto spatial coordinates. This is a different way of viewing the data shown in Figs. 2 and 3. **B** Generalization of the bi-coordinate mapping based on the results of the pooled data. Each line traces the spatial locations associated with varying one interaural difference while keeping the other constant. Each line is labelled with the value of the parameter which is being kept constant. The equations describing the relationships between interaural parameters and spatial locations were calculated from the pooled data set and are described in the text. ITD < 0: ITD was kept constant at −150 μs. ITD > 0: ITD was kept constant at +150 μs. Negative values of ITD indicate that the left ear leads the right ear. Left Louder: left ear was kept 20 dB louder than right ear. Right Louder: right ear was 20 dB louder than left ear

non-orthogonal, relationship between spatial coordinates and binaural parameters.

Discussion

The head-turn response to sound delivered by earphones was similar to that elicited by sound from a loudspeaker in free-field. A brief noise elicited a single saccade-like response in both free field and dichotic paradigms. The similarities between free-field and dichotic responses indicated that dichotic signals can be made to mimic the free-field stimulus situations essential for sound localization. Because the earphones constitute two sound sources, fusion of binaural information must underlie the directional turning of the head to the perceived location of a phantom target (Sayers and Cherry 1957; Durlach and Colburn 1978).

Many animals, including man, rely on interaural time differences and interaural intensity differences as important cues for binaural sound localization (Moushegian and Jeffress 1959; Stern and Colburn 1978; Hafter et al. 1979; Houben and Gourevitch 1979). Psychophysical experiments show that interaural time and intensity differences are used for localization of low and high frequencies, respectively. This forms the basis of the duplex theory that states that interaural time differences are used for localizing low frequency tones, whereas interaural intensity differences are favored for localizing high frequency tones (Moushegian and Jeffress 1959; Stern and Colburn 1978; Hafter et al. 1979; Houben and Gourevitch 1979). Most of these studies were limited to the analysis of lateralization in the horizontal plane. Studies concerning the basis of vertical localization concluded that interaural spectral difference is an important cue for vertical location (Brown et al. 1982; Knudsen 1980). In the barn owl, the use of interaural time and intensity cues are not confined to different regions of the auditory spectrum, rather both cues are used simultaneously, over identical regions of the spectrum (Moiseff and Konishi 1981; Takahashi et al. 1984).

The owl uses a bicoordinate system to translate an acoustic signal to a spatial location. Although the nature of the bicoordinate system was nonorthogonal, each spatial location was, nevertheless, associated with a unique combination of ITD and IID (Fig. 5A). The separation between time and intensity cues is consistent with the previously described notion that interaural time and intensity differences are processed by anatomically separate pathways (Takahashi et al. 1984; Takahashi and Konishi 1985; Sullivan and Konishi 1984). The bicoordinate system can be generalized to form a non-orthogonal grid by a family of parallel iso-ITD lines crossing a family of parallel iso-IID lines (Fig. 5B). Each point in the grid is uniquely defined by a pair of ITD and IID. This generalization is suggested by the results of the pooled data analysis. Confirmation of this requires extension of these results to include a large number of trials at off-axis locations. The trends observed in this graph compare favorably with the relationship seen between stimulus position and binaural cues (Moiseff 1989). There too, spatial locations can be transformed into a unique ITD and IID combination. The actual ITD and IID measurements also confirmed that ITD and IID do not encode orthogonal spatial axes.

The quantitative relationships between binaural cues and spatial coordinates were based on simple linear regression analysis of the data. Since the correlations based on the linear model were, in general, highly significant, no attempt was made to fit the data with nonlinear models. Although nonlinear equations might have resulted in a quantitative improvement in the descriptive equations, the linear equations allow a more intuitive understanding of the general trends that were observed. The relationship between stimulus azimuth and ITD differed somewhat from that reported in an earlier study (Moiseff and Konishi 1981). In the earlier study the slope of the regression between azimuth and ITD was $0.52° \mu s^{-1}$ as compared to the $0.38° \mu s^{-1}$ slope measured in equivalent portion in this study (i.e., presentation of ITD while keeping IID equal to 0 dB). The statistical significance of this difference, if any, is difficult to assess because of the lack of confidence limits for the slope of the earlier data.

The linear equations relating azimuth and elevation to ITD and IID were consistent with those that might be predicted on the basis of directional characteristics of the owl's ears (Moiseff 1989). The nonorthogonal relationship between ITD and IID, with respect to the manner in which these cues encode sound location, is evident in both the behavioral experiments and in measurements of the sound field. Quantitative comparison between the behavioral role of IID and the variations in IID measured as a function of frequency and stimulus location (Moiseff 1989) are not possible at this time. Such comparisons should be restricted to those frequency bands that are actually functioning in extracting information for elevational localization. The wide band stimuli used in this behavior study did not shed light on the frequency bands that should be compared. As a result, we are limited to qualitative comparison. Qualitatively, similar trends were observed relating IID and stimulus location in physical measurements (Moiseff 1989) and the behavior data reported here. Because actual ITD measurements did not vary as greatly as a function of frequency (Moiseff 1989) they were more amenable to comparison with the behavior data. The measured variations in ITD as a function of stimulus azimuth (Moiseff 1989) was:

$$\mathrm{ITD} = 2.3\ \mu\mathrm{s/deg} \cdot \mathrm{Azimuth} + 3.36\ \mu\mathrm{s}.$$

By rearranging the equation it is seen that the direct ITD measurements predict that:

$$\mathrm{Azimuth} = 0.44\ \mathrm{deg}/\mu\mathrm{s} \cdot \mathrm{ITD} - 1.46\ \mathrm{deg}.$$

This differs somewhat from the results of this behavior study, but again, the significance of the difference is difficult to ascertain. The difference, if significant, might be attributed to the liberties taken in synthesizing the binaural stimuli utilized in this behavioral study. For example, throughout these behavior experiments our stimulus generation system varied IID and ITD uniformly, over the entire frequency range.

The actual binaural signals that an owl would hear in response to free-field stimuli are undoubtably more complex than those used in this study. In particular, the actual binaural signals would differ from the simple signals used here in that the IID and ITD would vary different amounts for each spectral component of the wide-band, noise stimulus (Esterly and Knudsen 1987; Moiseff 1989).

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