# Effects of Interaural Decorrelation on Neural and Behavioral Detection of Spatial Cues

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#### Summary

The detection of interaural time differences (ITDs) for sound localization critically depends on the similarity between the left and right ear signals (interaural correlation). We show that, like humans, owls can localize phantom sound sources well until the correlation declines to a very low value, below which their performance rapidly deteriorates. Decreasing interaural correlation also causes the response of the owl's tectal auditory neurons to decline nonlinearly, with a rapid drop followed by a more gradual reduction. A detection-theoretic analysis of the statistical properties of neuronal responses could account for the variance of behavioral responses as interaural correlation is decreased. Finally, cross-correlation analysis suggests that low interaural correlations cause misalignment of cross-correlation peaks across different frequencies, contributing heavily to the nonlinear decline in neural and ultimately behavioral performance.

#### Introduction

Many models of human auditory perception use not only human psychoacoustical data but also neurophysiological data from animals. The validity of such models may be judged by their ability to explain the characteristics of the perceptual phenomenon for which the model was made. This approach makes two assumptions: one states that the human and animal auditory systems share the computational properties used in the model, and the other states that human beings and the animal perceive test stimuli in the same or a similar manner. The evidence for the second assumption is particularly difficult to obtain, because one cannot easily judge what animals perceive. The present paper uses an example in which both assumptions are met to discuss the neural bases for a perceptual phenomenon that human beings and the experimental animal share.

The experimental animal is the barn owl, and the perceptual phenomenon is the localization of phantom sound sources. Human beings perceive a single auditory image when they hear identical noise bursts in the two ears. The distinctiveness of the image varies with the degree of similarity between the left and right ear signals, i.e., their interaural correlation (Jeffress et al., 1962; Blauert, 1996). The lower the correlation, the more blurred is the image, and the greater is the variance and bias of assigning a location to the image (Jeffress et al., 1962; Grantham and Wightman, 1979; Blauert and Lindemann, 1986). As with humans, barn owls use interaural time differences (ITDs) to determine the direction of a sound source in the horizontal plane (Moiseff and Konishi, 1981). A broadband stimulus containing an ITD delivered through earphones elicits a head-orienting response, as if the owl perceives a single distinct image in the direction of head turning (Moiseff and Konishi, 1981; Moiseff, 1989).

The neural bases for sound localization are well understood in barn owls (Konishi et al., 1988; Takahashi, 1989a, 1989b). The owl's neural network for derivation of ITDs is based on principles of hierarchical organization. As in the human auditory system, the owl's binaural system carries out cross-correlation of signals from left and right ears to detect ITDs, initially in separate frequency bands, which then converge at higher stations. The owl's optic tectum lies several stations above the site for neural cross-correlation, i.e., the nucleus laminaris (Knudsen, 1984; Carr and Konishi, 1990). The tectum, therefore, provides the additional advantage of investigating ITD encoding after initial cross-correlation. The binaural processing of ITDs after the initial stages of cross-correlation has been a topic of some controversy in the human psychophysics literature (Shackleton et al., 1992; Trahiotis and Stern, 1994). The tectum is also the last stage in the processing of auditory spatial information prior to the motor map for control of head turning (Knudsen, 1982; du Lac and Knudsen, 1990).

We will first show that the consistency with which phantom sound sources are localized varies similarly in humans (Jeffress et al., 1962) and owls as a nonlinear function of interaural correlation. We then examine how the response to ITDs of neurons in the owl's optic tectum also declines nonlinearly as interaural correlation decreases. In the Discussion, we describe the similarities between human and owl behavioral performances in response to stimuli with negative and positive values of interaural correlation, as well as how some subjective reports by humans are congruent with what one may predict from the owls' behaviors. Finally, we compare these neuronal response properties to, first, the response of a cross-correlation model of ITD detection (Sayers and Cherry, 1957; Colburn, 1973) and, second, the variance of the owl's localization responses, with the goal of evaluating the extent to which the owl's consistency in localization is limited and determined by noise at the level of the tectum.

#### Results

# **Behavioral Responses**

Mean head-turning angles and their standard deviations were measured to quantitate the owls' sound-localizing behavior. The results for three owls are shown in Figure 1, where the negative and positive signs denote the left and right angles, respectively. A similar trend in the responses of all owls is evident, although there are small

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Figure 1. Head-Orienting Responses as a Function of Interaural Correlation

The top panels show head-turning responses (i.e., terminal head angle) of three owls as a function of interaural correlation. Initial head position was at 0° (directly in front). Each column of panels shows results from one owl. The four values of ITD were -150 (inverted triangles), -100 (triangles), 100 (squares), and 150 (circles)  $\mu$ s. Error bars indicate one standard deviation. The bottom panels show the standard deviations from the top panels, plotted separately as a function of interaural correlation. The solid curve fits in the right panels are based on analysis of neuronal data (see text).

differences in localization bias and the values of interaural correlation at which performance begins to deteriorate. All owls translated ITDs of 100 and 150  $\mu$ s into different azimuthal angles, 35°-40° and 50°-55° ranges, respectively (top panels). These ranges remained separate and relatively constant for correlation values from 1 to 0.4 or 0.3. However, as interaural correlation declined further, the mean angles became smaller, ultimately converging to 0. The standard deviations of the mean head angles (bottom panels) remained about a few degrees for correlation values from 1 to 0.4 and rose as correlation declined from 0.4 to 0.1. Owls generally performed better on the right side than on the left when interaural correlation became small. The convergence of mean angles to 0° for very small values of interaural correlation is due to the fact that the owls responded randomly to either left or right directions. This produced the 0 mean and large standard deviations observed. An ANOVA test on the combined data from the three owls showed that the mean head-turning angles are significantly affected by ITD (F[3,40] = 379.50, p < 0.01), interaural correlation (F[4,40] = 2.64, p < 0.05), and an interaction between correlation and ITD (F[12,40] = 17.35, p < 0.01). A significant effect of interaural correlation on standard deviations of responses (bottom panels) was also observed (F[4,55) = 36.80, p < 0.01).

The left panels of Figure 2 show behavioral responses to stimuli with negative values of correlation, as well as 0 correlation and catch trials at a correlation of 1. The right panels are neuronal responses and will be discussed in the next section. Each left panel contains data from one owl, and each symbol in these panels indicates one head-turning response. Circles and asterisks represent responses to stimuli with ITDs of +150 and -150  $\mu$ s, respectively. The owls appeared to respond at random with angles ranging from about +60° to -60°, excluding regions near the midline (0°). The index of detectability, d' (Green and Swets, 1966; see Experimental







# Figure 3. ITD Tuning Curves for Two Tectal Neurons

The left six panels are from one neuron (labeled A) and the right six from a second neuron (labeled B). Each panel shows an ITD curve for a different value of interaural correlation, noted at the top left of each panel. Neuron A had a best ITD of 0  $\mu$ s, and neuron B's best ITD was 30  $\mu$ s. Note the reduction in the main peak of the ITD curves as interaural correlation is decreased (different panels). Negative and positive values of ITD correspond to the left ear and the right ear receiving the leading sound, respectively.

Procedures), for detecting the correct direction associated with the stimulus ITD, calculated for the combined data at all negative correlations, was -0.19 (SD = 0.78); d' was infinity for the 1.0 correlation since no errors were made. At the correlation of -1, d' from two owls was 0.46 and 0.88, respectively. Note that no-response cases were excluded from analysis (i.e., owls must respond to a nonzero angle; see also Experimental Procedures). There was a small effect of negative interaural correlation on head-turning responses for the first owl (top panel) but not the second (F[3,165] = 2.89, p < 0.05 and F[2,67] = 2.57, n.s. for first and second owls, respectively). The F tests included only the negative values of correlation. Although it is not readily apparent from the figure, an inspection of the mean responses indicated that the significant effect of correlation for one owl was due to an increase in a right bias as correlation was increased from -1 to 0. The place represented by these stimuli (i.e., ITD), however, is undetectable (F[1,165] = 3.57, n.s., and F[1,67] = 0.25, n.s. for the two owls). The interaction between ITD and negative interaural correlation was also not significant (F[3,165] = 2.02, n.s., and F[2,67] = 1.91, n.s.).

# **Neuronal Responses**

We recorded from a sample of 33 optic tectum neurons and determined, first, their response characteristics, including responses to visual stimuli, sound frequency, and selectivity for interaural time and level differences (ILD). Their response to variation in interaural correlation was then obtained using their most favorable ITD and ILD. The ITD curve (i.e., a plot of discharge rate against ITD) of an optic tectum neuron has a single large peak (main peak) and no other or much smaller peaks (side peaks). Because of the stereotaxic coordinates from which data were collected, most neurons preferred ITDs ranging from -30 to  $+60 \ \mu$ s, where the negative and positive signs denote the stimulus leading in the ipsiand contralateral ears, respectively.

Figure 3 shows ITD tuning curves for two neurons as a function of interaural correlation (different panels). The left six panels are from one neuron (labeled A) and the right six panels from a second neuron (B). The data shown are characteristic of the ITD tuning curves of all other neurons observed. The value of interaural correlation is shown in the top left of each panel. There is a decline in both the main peak of the ITD curve and side peaks with decreasing correlation. Most importantly, the data show that the main peak disappears between correlations of 0.4 and 0.2. Another notable feature is that at a correlation of 0.8, the two neurons show a large difference in firing rate at the main peak. One may also get some sense of the magnitude of this variability from the data of Figure 4 at that correlation.

Figure 4 shows changes in the height of the main peak of the ITD tuning curve from the 33 neurons as a function of interaural correlation. The spontaneous rate (symbols at far left) of each neuron was subtracted from the stimulus-driven discharges at all correlations. The top panel shows responses from units recorded in the superficial layers of the optic tectum, and the bottom panel shows responses of neurons in the deep layers (see Experimental Procedures for description). The most important feature of the data of Figure 4 is the pattern of changes in discharge rate with interaural correlation. All neurons showed a nonlinear (quasi-monotonic) increase in discharge rate from correlation of 0 to 1 and a weak or no response to negative values of interaural correlation. The heavy solid line shows the average of all responses within each panel. An ANOVA test showed no significant difference between responses of deep and superficial layers (after correction for spontaneous rates) as a function of interaural correlation (F[1,341] = 0.97, n.s.), but a significant effect of interaural correlation on response rates was found (F[10,341] = 47.53, p < 0.01). Also,



Figure 4. Mean and Standard Deviations of Discharge Rates Recorded from Optic Tectum Neurons as a Function of Interaural Correlation at the Best ITD and ILD

The ordinate shows the driven discharge rates, i.e., rates with the spontaneous activity subtracted off. The top and bottom panels show data from neurons in the superficial and deep layers of the optic tectum, respectively. Each trace is the response from one neuron. The heavy solid line is the average response from all neurons within that panel. Symbols at the far left are spontaneous rates.

no significant interaction between interaural correlation and neuron type (deep versus superficial layers) was obtained (F[10,341] = 0.51, n.s.). The mean number of neural discharges from -1 to 0 was not significantly different from the spontaneous rates (far left; t[108] = 1.15, n.s. for superficial layers, and t[251] = -0.621, n.s. for deep layers). There was also a small increase in the variance of neuronal responses as interaural correlation increased from 0 to 1 (F[10,352] = 17.73, p < 0.01).

The right panels of Figure 2 show ITD tuning curves for one neuron for two correlations of 1 (top right panel) and -1 (bottom right panel). The curve for the +1 correlation has a main peak at  $+30 \mu s$ . The curve for -1correlation (i.e., antiphasic condition) shows two peaks at ITDs of approximately -30 and  $+90 \,\mu s$  (cf. Albeck and Konishi, 1995). Also note that the peaks in the antiphasic case occur at ITDs that are at the half-point between the main and side peaks of the +1 correlation condition (i.e., homophasic). The ITD difference between main and side peaks in the top panel is  $120 \ \mu s$  (within the 30 µs resolution of our measurements), approximately the period of the best frequency of this neuron (7.5 kHz). The ITD difference between the two main peaks in the antiphasic condition is also  $\sim$ 120  $\mu$ s. The discharge rates at the two main peaks in the antiphasic condition are not statistically different (t[18] = 0.138, n.s.).

# Discussion

Comparison to Findings from Human Psychophysics We will first discuss similarities and differences between humans' and owls' responses to variation in interaural correlation. Humans perceive a discrete image in the center of the head when they listen to broadband noise bursts containing an ITD of 0 and an interaural correlation of 1. The image appears to expand and becomes blurred as interaural correlation decreases. With further reduction in interaural correlation, the image begins to polarize and two primary images at opposite sides of the head (one near each ear) emerge (Licklider, 1948; Jeffress et al., 1962; Blauert, 1996).

Jeffress et al. (1962) examined changes in the variance of localization of intracranial images by human subjects as a function of interaural correlation. The subjects' task was to bring a phantom image from an arbitrary initial locus (i.e., randomized initial ITD) to the center of their heads by adjusting the stimulus ITD. The mean and standard deviation of the selected time delays were calculated after repeated trials. The subjects showed surprisingly small standard deviations as interaural correlation was decreased from 1 to 0.2 ( $\sigma = 45-75 \ \mu s$ ). From a correlation of 0.2 to 0.1, however, the standard deviation increased sharply, i.e., from 75 to 150  $\mu$ s. The form of the function that related standard deviation to interaural correlation is very similar to our data on owls, i.e., a nonlinear function with an apparent transition near a correlation of 0.2. It is important to stress this similarity in performance for essentially identical behavioral tasks.

Broadband stimuli with negative values of interaural correlation are perceived somewhat differently from those with positive or 0 values (Pollack and Trittipose, 1959; Robinson and Jeffress, 1963). A stimulus with a correlation of -1 produces a more compact image than a stimulus with a 0 interaural correlation. As the correlation is increased from -1 to 0, the percept becomes more diffused, as is the case when correlation is decreased from +1 to 0 (Blauert, 1996). If owls perceive these stimuli in a similar manner to humans, then the owls' dichotomous responses at 0 and negative values of interaural correlation can be understood. At a correlation of 0, a two-image percept would result in random responses to left and right positions. At a correlation of -1, a single partially blurred image near the midline may also produce large and random head-turning angles, given that the absence of responses was not reinforced. Of course, it is impossible to determine what the owls perceive, and it may be that even for negative interaural correlations the owl does perceive two images at large angles. Still, the owl's behavioral responses are consistent with what one predicts from how humans perceive sounds with various degrees of correlation.

#### **Cross-Correlation Analysis**

Cross-correlation models have considerable support from human psychophysical experiments (Sayers and Cherry, 1957; Colburn, 1973; Blauert and Cobben, 1978; Colburn and Latimer, 1978; Stern and Colburn, 1978; Stern et al., 1988; Saberi, 1995, 1996, 1998) as well as animal neurophysiology (Yin et al., 1987; Carr and Konishi, 1990; Yin and Chan, 1990; Keller and Takahashi, 1996a; Batra et al., 1997). Although cross-correlation predicts that a lack of interaural correlation will result in a failure of ITD detection, one cannot conclude that the form of the function relating ITD detection to interaural correlation will follow rules strictly predicted from crosscorrelation. Furthermore, there is a lack of information



Figure 5. Response of a Cross-Correlation Model of Binaural Interaction as a Function of Stimulus Interaural Correlation The left six panels show the output of the cross-correlation model, prior to frequency integration, in response to noise bursts of varying degrees of interaural correlation. The stimulus had an ITD of  $+200 \ \mu$ s, reflected in the straight trajectory of cross-correlation maxima at that delay for stimuli with a high value of interaural correlation. At low values of interaural correlation, the trajectories are distorted and identification of the stimulus ITD is difficult. The right six panels show the model output after integration across frequency channels. The straightness of the trajectory at 200  $\mu$ s (left panels) results in a large peak at that delay after frequency integration for stimuli with a high degree of interaural correlation.

and some controversy as to processes that occur after the initial computation of cross-correlation. It is not clear, for example, how binaural information is combined across frequency channels and refined at higher auditory centers (Shackleton et al., 1992; Trahiotis and Stern, 1994; Stern and Trahiotis, 1997; McAlpine et al., 1998). Because the optic tectum lies several synapses above the nucleus laminaris, the site of neural crosscorrelation in owls (Carr and Konishi, 1990), comparison of empirical findings with theoretical predictions provides an opportunity to improve our understanding of structures and computations that occur after cross-correlation.

The model used here consists of an initial bank of bandpass filters, simulating the inner ear mechanisms. The filter bank consisted of 50 logarithmically spaced fourth order GammaTone filters (Holdsworth et al., 1988) with resonant frequencies from  $\sim 0.5$  to 13 kHz (see Experimental Procedures). The output of this filter bank was then followed by vth law half-wave rectification (v = 3; Stern et al., 1988) reflecting the occurrence of phase-locked impulses during the positive phase of the stimulus waveform. Running cross-correlation of the left and right signals was then carried out in each frequency band followed by integration across different bands.

The output of this model in response to a single presentation of a 100 ms broadband Gaussian noise burst, identical to those used in our neurophysiological and behavioral studies, is shown in Figure 5 for six values of interaural correlation. The signal ITD selected here was 200 µs; other ITD values produce similar results. The left panels show the model output prior to frequency integration, and the right panels after frequency integration ( $F_1 = 500 \text{ Hz}$ ,  $F_u = 13 \text{ kHz}$ ). We first describe the top left panel of Figure 5, for which the stimulus had an interaural correlation of 1. The peak values of crosscorrelation in different frequency bands align at 200  $\mu$ s and do not at other delays, indicating that the peak cross-correlation values in narrow frequency bands do not match at any delay other than the true ITD of the stimulus. The corresponding panel to the right, i.e., after frequency integration, shows that summing of crosscorrelation values across all frequency bands gives rise to a maximal value at the true time difference of 200 µs. The remaining panels of Figure 5 show cross-correlation functions for various degrees of interaural correlation. Note that the alignment of cross-correlation peaks across frequency (i.e., straight trajectory at 200 µs) is still recognizable for a correlation of 0.4 but not for 0.2.

The right panels of Figure 5 show the model output after frequency integration for various interaural correlations. These results are similar to the responses of optic tectum neurons (Figure 3). Most importantly, both the neural data and model responses show that between interaural correlations of 0.4 and 0.2, a transition to uncertainty in encoding ITDs is observed. The larger side peaks of the model response compared to the neuron's response are also informative. Smaller model side peaks may be obtained either if cross-correlation values near 0 are more heavily weighted (Stern et al., 1988; Shackleton et al., 1992; Saberi, 1995, 1998) or if one incorporates nonlinear processes in frequency integration, such as inhibition as reported for neurons of the external nucleus of the inferior colliculus (Takahashi and Konishi, 1986; Fujita and Konishi, 1991; Mori, 1997). The main model prediction, without any parameter adjustments, is a failure to code ITDs (a decline of the main peak) when interaural correlation is reduced from 0.4 to 0.2, which is in good agreement with both neuronal and behavioral data. It is possible, however, that some residual cues may still be available at a correlation of 0.2, if considerable averaging is achieved by the binaural system, either across time or across neurons. Interestingly, statistical analysis on the neural data of Figure 4 showed that main peak responses at a correlation of 0.2 (but not 0.1) are significantly higher than those at 0 correlation (t[32] = 3.75, p < 0.01). This significance, however, does not necessarily mean that the owl is capable of effectively utilizing the information, as is evident from the severe decline in behavioral performance.

It is also interesting to note that as interaural correlation decreases, the auditory image becomes more diffused, whereas the main ITD peak becomes smaller without losing its sharpness (Figure 3). One interpretation is that the source of the perceived diffusion lies in higher order processes, above the level of the optic tectum. A second possibility is that the distinctness of the image is related to the relative heights of the main and side peaks in ITD tuning curves. While there are no specific provisions in the model for predicting diffused images, Figure 5 shows that for low correlations the relative height of the main to side peaks declines. A similar argument may be made for the neural ITD tuning curves shown in Figure 3. A final possibility may be that decreasing the interaural correlation would increase the likelihood that a neuron responds to an ITD that is not its best ITD, producing a more blurred image across a population of neurons (see Figure 2).

# Detection-Theoretic Inferences from Neural Statistics

In this section, we seek to find quantitative relationships between the owl's behavioral and neural data. The goal of this analysis is to distinguish the limitations imposed by the statistics of tectal neurons on the behavioral performance from other limitations (e.g., decision processes, variability in motor responses, posttectum neural noise, etc.). The approach we adopt is similar to that used by Siebert (1968) and Colburn (1973, 1977) in relating auditory signal detection by humans to statistics of cat auditory nerve data. From the discharge mean and variance of a sample population of tectal neurons, we derive an index of neural detectability (Green and Swets, 1966; van Trees, 1968) that allows inferences on the variance of behavioral responses. The extent to which the changes in accuracy of behavioral responses



Figure 6. Function  $\delta^{-1}$  Calculated from Statistics of Neuronal Responses (Equation 1)

Each symbol shows the calculated value at that correlation. The solid line is a modified exponential function least-squares fitted to the data (circles); the modified exponential had a constant offset, y = c + exp(ax) where c and a were the fitting parameters. See text for details.

relate to neural noise at the level of the tectum imposes constraints on sites that give rise to the noise that limits performance. If changes in the variability of the owl's behavioral responses correlate well with changes in tectal noise, one may infer that performance is dominated by limitations up to the optic tectum; i.e., posttectum structures may be replaced by an optimum processor with negligible change in performance (see Colburn, 1973). For simplicity, we limit our analysis to positive values of interaural correlation.

The ability of the auditory system to code for a location using ITDs depends on the "strength" of responses by ITD-tuned neurons. Decision theory suggests that both the mean response rates and the variability of these responses be considered in characterizing the "strength" of the neural code. We will assume that neurons encoding a given ITD have a statistical distribution similar to those of Figure 4.

Let  $\overline{Y}_{i,\rho}$  be the mean number of impulses for neuron i and interaural correlation  $\rho$ . For each  $\rho$ , we calculate the mean and variance of the summed distribution over all i,  $\Sigma \overline{Y}_{i,\rho}$  and  $\Sigma VAR(Y_{i,\rho})$ . For  $\rho = 0$ , there is by definition no signal (i.e., ITD) to be detected. Since the no-signal condition is a 0 correlation, we determine the degree to which the distribution of impulses for each correlation differs from the 0 correlation distribution. The mean-tostandard deviation, a d'-like estimate (Green and Swets, 1966) of this difference distribution, a measure of the effective neural information about the signal ITD, is

$$\delta_{\rho} = \frac{\sum_{i} \overline{\mathbf{Y}}_{i,\rho} - \sum_{i} \overline{\mathbf{Y}}_{i,0}}{\sqrt{\sum_{i} \mathbf{VAR}(\mathbf{Y}_{i,\rho}) + \sum_{i} \mathbf{VAR}(\mathbf{Y}_{i,0})}}$$
(1)

We used the inverse of  $\delta$  as a measure of the neural noise that limits signal detection. Since the plot of  $\delta^{-1}$  as a function of interaural correlation appears to vary exponentially (Figure 6), we least-squares fitted this function with a modified exponential curve for smoothing. We then used a free scaling parameter to fit the curve to the distribution of the standard deviations of head-turning responses, with the reasoning that changes in the neurally derived function  $\delta^{-1}$ , a measure of the

neural resolution with which ITDs are detected, will correlate with changes in the variance of the owl's performance. As Figure 1 (bottom panels) shows,  $\delta^{-1}$  and the standard deviations change in a similar way as interaural correlation is increased. The standard deviations of behavioral responses, however, reach a lower asymptote at a correlation of ~0.5–0.7, whereas  $\delta^{-1}$  decreases monotonically until interaural correlation reaches 1.

Our interpretation of this comparison is that when the stimulus is highly correlated at the two ears, the variability in behavioral performance is primarily determined by noise in posttectum neural processes, including motor responses and decision variance. That is, even though the improvement in neural signal-to-noise ratio continues when interaural correlation is increased from 0.7 to 1, the variance of responses does not continue to decrease, indicating the presence of a source of noise, above the optic tectum, that continues to limit performance in spite of the low noise at the tectum for highly correlated sounds. Note that the measurement accuracy of our system, approximately ±4°, would produce a standard deviation of only 2.3°, assuming a rectangular distribution. This is, of course, considerably smaller than the 8° asymptote in standard deviations observed in behavioral data (for 2 of 3 owls), and although it may contribute to the higher standard deviations, it is not the primary source of the observed variance at high correlations. Also note that even at a correlation of 1  $\delta^{-1}$  does not reach 0, since even for perfect correlation the variance of neuronal responses is greater than 0.

Our analysis utilizes a sample of the population of neurons that encode a given ITD (Fitzpatrick et al., 1998). The predictions of changes in detectability of an ITD by that neural sample is therefore not a prediction of variances of behavioral responses in an absolute sense, but rather a prediction of the form of the function that relates this variance to interaural correlation. We have accordingly limited our analysis to this form. Does the form of  $\delta^{-1}$  change with neuron sample size? It is easy to show that with a few simple assumptions, the form of this function is independent of the size of the sample, except for a scaling parameter ( $\beta$ ) that is related to the size of neural samples (N) of the relevant population by  $\sqrt{N}$ . If one assumes that the mean of the mean firing rates at a given correlation is  $\mu_{\bar{Y}_0}$  and the average variance at that correlation is VAR( $Y_{\rho}$ ), then  $\delta^{-1}$  generalizes to  $(N \mu_{\overline{Y}_0} - N \mu_{\overline{Y}_0})/[N VAR(Y_{\rho}) + N VAR(Y_0)]^{0.5}$  or  $\sqrt{N} (\mu_{\overline{Y}_0} - \mu_{\overline{Y}_0})/(N \mu_{\overline{Y}_0} - \mu_{\overline{Y}_0})/(N \mu_{\overline{Y}_0$  $[VAR(Y_0) + VAR(Y_0)]^{0.5}$ . Nonetheless, it is clear that more samples improve the precision with which this function may be derived.

# **Concluding Remarks**

This paper, as well as other recent work (Keller and Takahashi, 1996b; Litovsky et al., 1997), show that the selection of an appropriate animal and perceptual phenomenon allows an evaluation of the neural mechanisms proposed to explain the same perceptual phenomenon in humans. A cross-correlation model of ITD processing, adopted from human psychoacoustics, responds to interaural decorrelation in a manner similar to the way neurons of the barn owl's optic tectum respond. The paper also shows that the statistical characteristics of neural responses to interaural decorrelation may account for the owl's behavioral performance, which resembles that of humans. Approaches that integrate human and animal behavioral analysis, neurophysiology, and modeling can be powerful tools in discovering general principles of auditory perception in humans as well as animals.

#### **Experimental Procedures**

#### Surgery and Animal Care

We describe here the surgical procedures used for both behavioral and neurophysiological experiments. The owls used in behavioral experiments were not the same as the physiology owls. All owls were also used in other parallel behavioral and neurophysiological studies. All surgical instruments were sterilized. Owls were anesthetized with intramuscular injections of Ketamine (10-20 mg/kg/hr, Phoenix Pharmaceutical) and Diazepam (0.25-0.5 mg/kg/hr, Steris Laboratories). A scalp area about 10 mm  $\times$  10 mm was incised after subcutaneous injection of a local anesthetic, Xylocaine (0.2 ml 2% Lidocaine HCL, Astra Pharmaceutical). The first layer of the skull was removed within this area with a pair of rongeurs and an inverted T-shaped post was fixed to the underlying trabeculae with dental cement (Hygenic, Perm Reline and Repair Resin Type II Class I). The whole operation lasted a few minutes. After the surgery, owls were encased in a snugly fitting cylinder to prevent struggling and kicking as they recovered from anesthesia. Owls were observed in small cages in a separate recovery room until they came out of the cylinder. When owls recovered well enough to fly, they were returned to their living cages, where the owls for neurophysiological experiments were fed two mice a day. The weights of the owls for behavioral experiments had to be maintained at ~90% of their free-feeding values to ensure well-motivated behavioral performance. These owls were weighed daily, and the amount of food was adjusted accordingly

The surgery for neurophysiological experiments involved the removal of a scalp area and the underlying skull area about 7 mm  $\times$  7 mm in size to expose the brain surface, under anesthesia as described previously. After each experimental session, which lasted several hours, the craniotomy was cleaned with an antibacterial agent, Chlorhexiderm (0.05% chlorhexidine gluconate, DVM Pharmaceuticals), and resealed with a small plastic sheet and dental cement, and the scalp wounds were sutured shut. The suture and plastic sheet were removed before each experiment and replaced afterward. The owls for behavioral experiments were not subjected to any additional surgery, except for suturing the ear rings in one owl under anesthesia.

#### **Behavioral Methods**

We used three tame adult owls for behavioral experiments. The head-turning response did not need any training, but it had to be reinforced by food for repeated trials. We trained the owls to feed from an apparatus, which dispensed a small amount of mouse meat at a time, allowing 20-30 trials in 1 hr. Test sessions seldom continued more than 2 hr. We initially used a small freefield speaker ("hoop speaker") mounted on a semicircular track to encourage the owls to localize it at various azimuthal angles. The owls had to initially orient to another source ("zero speaker") placed straight ahead and wait for the signal from the hoop speaker. When the owls became consistent in localizing both speakers, they were trained with earphones. We used earphone assemblies similar to the ones used for neurophysiological experiments. For one owl (left panels of Figure 1), the outside-threaded earphone cylinder was screwed into an inside-threaded stainless steel cylinder that was fitted in the ear canal. For the other owls, the ear ring method was replaced by using a metal bar, which was bolted on the head post and held both left and right earphones in place.

The localization tests in this work examined the owls' ability to localize sound ballistically, i.e., without hearing the sound during head turning. The acoustic signal was a single burst of broadband noise (100 ms in duration and 5 ms rise-and-decay times) in which the values of ITD and interaural correlation were varied on each

presentation. These stimuli were generated on an IBM-compatible personal computer, which was also used to run the experiment. The sound-pressure level (SPL) for all stimuli used in the behavioral experiments was 20 dB above the owl's threshold, which is about 0 dB SPL between 3 and 8 kHz at the eardrum (Dyson et al., 1998). ILDs were always kept at 0 so that the owls turned their heads only in the horizontal plane in response to an ITD (Moiseff, 1989).

We trained the owls with interaural correlation of 1 until they reliably responded by head turning to the spatial angles predicted from the stimulus ITD (Moiseff and Konishi, 1981; Moiseff, 1989). We chose four values of ITD, 100 µs right (+) and left (-) side leading and 150 µs right and left side leading, and seven values of interaural correlation (1.0, 0.7, 0.5, 0.4, 0.3, 0.2, and 0.1). These values were chosen as a compromise between the need to collect a statistically meaningful number of data points for each pair of interaural correlation and ITD and the need to prevent the owls from developing the habit of orienting toward fixed angles. For the first owl, we collected  $\sim$ 20 data points for each combination of interaural correlation and ITD, and for the second and third owls, we collected  $\sim$ 10 data points. The reduced points for owls 2 and 3 were due to our desire to know if the general trends in owl 1's results would hold for other owls. For stimuli with negative correlations, the data of one owl were collected by interleaving positive and negative correlations; i.e., the data of the far-right panels of Figure 1 were collected simultaneously with the data of the bottom left panel of Figure 2. This was done in order to prevent the owl from learning to turn its head to the same fixed angle (i.e., a simple right-left response), instead of actually attempting to locate a signal. The owls performed in complete darkness in an IAC soundproof anechoic chamber (5  $\times$  3  $\times$ 3 m) and were monitored with an infrared video camera

For the first owl, we captured both the initial and terminal head angles with a frame-grabber board in the personal computer. The recording speed was 30 frames/s. We measured head angles by aligning a cursor with the image of a sewing needle held in the midsagittal plane of the head by the metal post. The initial angle, which was always at or near the zero-speaker direction, was automatically subtracted from the terminal angle, which was the angle at which the owl stopped. The resolution of this method was  ${\sim}4^\circ$ because of the small area of the computer monitor screen in which head angles were measured. For the other two owls, we measured head angles with a protractor marked on a monitor. The angular resolution of this method was also  ${\sim}4^\circ$ . When the owls were not motivated to localize the sound, response latencies were long and head-turning responses were slow. This occurred only on a small proportion of trials near the end of an experimental run. Since these responses were always correlated with inaccurate localization, all trials in which time to head fixation exceeded 1.5 s were excluded from further analysis. The owls were always required to make a head-turning response to an angle other than 0 (i.e., a forced-choice nonzero response). This was necessary to eliminate no-response trials due to inattention. Clearly, if the owl did indeed perceive a sound at 0° and maintained its head position at 0°, it was not rewarded. While this design eliminates valid cases at 0°, it was necessary to determine the owls' capability to detect one of the four nonzero angles specified by the appropriate ITD.

In some cases (see Results), we calculated an index of detectability, d' (Green and Swets, 1966), from hit and false alarm rates associated with the owls' head-turning responses. Hit rates were defined as the number of head-turning responses to the right when the stimulus ITD was positive divided by total number of trials with positive ITDs. False-alarm rates were defined as the number of head-turning responses to the right when the stimulus ITD was negative divided by the total number of trials with negative ITDs. The Tables of Elliot (Swets, 1964) were used to obtain d's from these hit and false-alarm rates.

#### **Neurophysiological Methods**

We used seven owls for neurophysiological experiments. Owls were kept under anesthesia throughout the experiment, and the edges of the skin wounds were doused with liquid Lidocaine once per hour. Since Ketamine caused a temporary reduction in neuronal discharge, we did not collect data for ~15 min after each booster injection of Ketamine (10–20 mg/kg/hr). Single units were isolated



Figure 7. Frequency Weighting Function

Frequency weighting function estimated from the data of Knudsen and Konishi (1979) and used in the cross-correlation model. The function has been normalized to a maximum of unity.

in the optic tectum with parylene-insulated tungsten microelectrodes (A-M systems, 250  $\mu$ m thick shaft, 5 M $\Omega$  impedance at 1 kHz). The tectum contains two primary types of ITD-sensitive auditory neurons, superficial and deep layer neurons (Knudsen, 1984). This categorization is made on the basis of both the stereotaxic coordinates of the electrode and the response properties of the neurons. Neurons of the superficial layers are bursty type, firing in multiple short bursts separated by variable intervals for the duration of the stimulus. Deep layer neurons are characterized by either phasic or phasic-tonic responses. Phasic (transient) units respond only at the stimulus onset, Phasic-tonic (sustained) units respond with several spikes near the beginning of the stimulus, often followed by a 10–30 ms silent period, and a sustained discharge. Units in the superficial layers generally have a higher spontaneous rate than those in the deep layers (see Results; t[31] = 4.25, p < 0.01).

Neural waveforms were amplified and filtered from 1 to 10 kHz (Beckman Electronics, Microamp 200) and simultaneously monitored with an oscilloscope (Tektronix, 5110) and an audio amplifier (Grass, AM8). A level detector (Beckman Electronics, Microamp 200) or a spike discriminator (Tucker-Davis Technologies, SD1) converted neural spikes to computer-compatible TTL pulses, the times of occurrence of which were stored in a computer file. The identity of tectal neurons was also confirmed by their histological locations, some of which were marked with electrolytic lesions as visualized in cresyl violet-stained sections.

The auditory stimuli were independent bursts of broadband Gaussian noise (0.5-12 kHz, 100 ms in duration with 5 ms rise-anddecay times) containing different values of interaural correlation and different combinations of ITDs and ILDs to which tectal neurons are tuned. To obtain different values of interaural correlation, we used the following methods. Three random noises (N1, N2, and N3) were generated on the computer. N1 was delivered to one ear, and its copy with a time shift was delivered to the other ear. N2 was added to N1 in one ear and N3 was added to N1 in the other ear. These additions reduced the correlation between the signals in the two ears, depending on the relative amplitudes of the uncorrelated and correlated noises. Interaural correlation was calculated from  $\rho$  =  $1/(1 + k^2)$ , where k is the ratio between the root-mean-square amplitudes of the uncorrelated and correlated noises (Jeffress and Robinson, 1962). We multiplied the waveform going to one ear by -1 to obtain negative correlations.

All sound stimuli were digitally synthesized with a Sun Microsystems Sparc/IPX workstation or a Dell Dimension XPS Pro200n computer and delivered by a digital signal processor equipped with a 16 bit, 48 kHz digital-to-analog converter (S56X+ProPort-656, Berkeley Camera Engineering) or by a stereo analog interface (DD1, Tucker-Davis Technologies). ITDs were computed online, whereas ILDs were set by two digital attenuators (PA4, Tucker Davis Technologies), which were controlled by the computer. ITDs could be varied in 30 µs steps in either direction, i.e., leading or lagging to each ear. ILDs were varied in 5 dB steps from -40 to 40 dB.

Sound stimuli were delivered by an earphone assembly consisting of a Knowles ED-1914 receiver or a Sony MDR-E535 as a sound source, a Knowles BF-1743 damped coupling assembly for

smoothing the frequency response of the receiver, and a Knowles 1939 microphone for monitoring sound pressure levels in the ear canal. A short length of an aluminum pipe led sound from the Sony speaker to the ear canal in which sound levels were monitored with the Knowles microphone. The Knowles components were encased in an aluminum cylinder 7 mm in diameter and 8.1 mm in length. The cylinder was inserted into the ear canal and the gaps between the cylinder and the canal were filled with a silicon compound (Earmold and Research Laboratories, Wichita, Kansas). The microphone was initially calibrated against a 12 mm Bruel & Kjaer microphone with a probe tube whose tip was placed close to the center of the eardrum. This procedure allowed translation of the voltage output of the Knowles microphone into dB SPL. A standard value of 20 dB above a neuron's threshold was chosen as the stimulus sound level in all cases.

To confirm that acoustic signals show the same value of correlation that was assigned to the electronic signals, we measured the correlation between the two (left and right) acoustic waveforms monitored by two probe-tube microphones surgically inserted through the squamosal bones (Pena et al., 1996) behind the ear canals to within 2 mm of the eardrum of one owl (this owl was not used in the experiments). The measured Pearson product-moment correlation coefficients at the eardrums were quite similar to the various values of correlation coefficients calculated from the digital waveforms ( $r^2 = 0.997$ ) but with a slope of slightly less than unity (0.92), suggesting a slight decorrelation by the time the stimulus reaches the eardrums.

#### **Cross-Correlation Model**

The model consisted of preprocessing by a Gammatone filterbank (Holdsworth et al., 1988), whose frequency responses were

$$H(f) \propto \left[1 + \frac{j(f - f_0)}{b}\right]^{-4} + \left[1 + \frac{j(f + f_0)}{b}\right]^{-4}$$
(2)

where  $f_0$  is the filter's center frequency in Hz, b controls the width of the filter and is a function of  $f_0$ , and j is the complex number  $\sqrt{-1}$ . The data of Dyson et al. (1998) were used to determine critical bandwidths for the barn owl's auditory filters, which in turn were used to determine the parameter for filter width, b. The output of each filter was followed by half-wave rectification and cross-correlation,

$$R(T,\tau) = \int_{FI}^{Fu} \int_{-\infty}^{T} q(f) X_{r}(f,t) X_{l}(f,t-\tau) e^{-(T-t)/0.01} dt df$$
(3)

where X<sub>r</sub> and X<sub>I</sub> represent the right and left waveforms, respectively,  $\int_{T}$  running cross-correlation and  $\int_{F}$  integration of frequency bands from F<sub>I</sub> = 0.5 to F<sub>u</sub>= 13 kHz. The exponentiation has a time constant of 10 ms and heavily weighs the more recent activity (Sayers and Cherry, 1957; Blauert and Cobben, 1978), and q(f) is a frequency-dependent weighting function that reflects psychophysical findings on the dominant frequency region for localization by the barn owl (Knudsen and Konishi, 1979). Comparable frequency-weighting functions have been used in modeling findings from human psychophysics (Stern et al., 1988). The function used here was a fourth order polynomial fit to the data from Figure 3 of Knudsen and Konishi and has a peak near 7 kHz: q(f) =  $1/\Sigma(a_1f^{1-1})$  with  $a_1 = 47.54$ ,  $a_2 = -17.60$ ,  $a_3 = 3.96$ ,  $a_4 = -0.475$ , and  $a_5 = 0.0237$  where f is in kHz. Figure 7 shows this function, normalized to a maximum of unity.

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