EFFECT OF DECORRELATION OF BINAURAL SOUND ON BARN OWL'S ABILITY TO DETECT CHANGE IN INTERAURAL TIME DIFFERENCE UNDER A BAYESIAN PROCESSING MODEL

by

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Approved: Terry Takahashi

Terry Takahashi

Barn Owls (Tyto alba) have an exceptional ability to spatially localize sounds in their environment. Barn owls are able to localize prey using hearing alone (Konishi, 1973). By processing the interaural time and level differences of incoming sound stimuli, owls are able to place sounds in a neural space map. The neural pathway for processing interaural time difference (ITD) is well documented in the literature (Carr & Konishi, 1988; Carr & Konishi, 1990; Wagner, Takahashi, & Konishi, 1987). Recent literature has suggested that the classical place coded model for barn owl sound localization is ineffective in predicting behavior, and a Bayesian model for localization is a more accurate representation neural and behavioral results. (Fischer & Peña, 2011). Our research aims to show how owls' ability to detect an ITD is altered by varying levels of binaural correlation of incoming sounds. I hypothesized that decorrelation of binaural sound stimuli would lead to owls' decreased accuracy of detecting an interaural time difference. Results have shown owls' ability to accurately detect a change in ITD of 8μs at 100 percent binaural correlation. Our data also shows that owls are able to detect 8 microsecond changes in ITD at binaural correlation values as low as 60%, leading us to believe that the birds can maintain high behavioral accuracy with low levels of binaural correlation. Future research will require more experiments to build a data set with less variance and to develop a complete model of owls' ITD detection capabilities given a broader range of binaural decorrelation values.

Acknowledgements

I would like to thank my advisors Terry Takahashi, PhD, Avinash Singh Bala, PhD, and Kip Keller, PhD, all of whom have been my mentors since day one, giving me the opportunity to be involved in the lab; they guided me through the research and writing process and spent countless hours with me helping me understand such a complex and difficult subject. Without their help I would not be where I am today. To my honors college representative and advisor, Mark Carey, PhD, who has been a tremendous role model and guide for me both in classes and in an advisory role; he helped me to understand what was so special about the opportunity I have to complete a project like this, and the growth I've seen in myself through the process. To my parents, who have stuck with me and supported me throughout my (more than anticipated) years here. To my friends, who have given me support, offered me guidance, and kept my head up through the past two years. Thank you Brittany for the constant encouragement, artwork, carbs, and caffeine. I love all of you that I have mentioned, and many more. My words cannot express the depth and degree of my gratitude.

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Nomenclature

HRTF	Head Related Transfer Function
ITD	Interaural Time Difference
ILD	Interaural Level Difference
ICc	Central/Core Nucleus of Inferior Colliculus
ICx	External Nucleus of the Inferior Colliculus
MAA	Minimum Audible Angle
MLD	Mesencephalicus Lateralis Dorsalis
NM	Nucleus Magnocellularis
NA	Nucleus Angularis
PDR	Pupillary Dilation Response0
SD	Standard Deviation
SPL	Sound Pressure Level
ROC	Receiver Operating Characteristic

Background

Barn owls are nocturnal hunters that rely on an exceptionally finely tuned sense of hearing in order to localize prey. Owls are able to localize sounds in the dark, even when lacking all visual input (Konishi, 1973). An owl’s ability to place sounds in space relies on separate nervous processing pathways dedicated to spatial axes: azimuth (horizontal axis) and elevation (vertical axis) (Knudsen and Konishi, 1979). Orientation of sounds on these spatial axes is determined by computation of interaural time difference (ITD) and interaural level difference (ILD) in several nuclei of the brainstem (Knudsen and Konishi, 1979); for the purposes of this study we have focused on owls’ capacity for localization along azimuth using ITD.

Sensory encoding and localization in the auditory system

The auditory system of the barn owl is unique in the way it localizes sound relative to other vertebrates, and even relative to many other owls. As in other owls, the bird’s ruff (the rigid outer layer of feathers in the bird’s face) acts like the pinna (auricle) in a human, directing the sound towards the ear as an amplifier and directional filter (Hausmann, 2010). Barn owls are unique in their ability to localize sound as their ears are vertically offset (one ear is directed slightly upwards while the other is slightly directed downwards), giving the owl the ability to utilize interaural sound level difference cues to compute the elevation of the sound source.

Sound waves are transduced from airborne waves, through the tympanic membrane and bones of the middle ear as a mechanical signal, through the oval window and into the cochlea as a signal in liquid. Finally, via the vibration of the basilar membrane and activation of hair cells, the sound signal is transduced to the cochlear nerve. Once the sound wave has been converted to an electrical nervous signal, processing the sound may begin. Axons of the eighth cranial nerve carry the auditory signal to nucleus magnocellularis (NM) and nucleus angularis (NA). Eighth nerve afferents carry information regarding both sound pressure level (SPL) and timing of the sound wave. NM processes the stimulus for time (sound wave phase) and NA processes the stimulus for level (sound wave amplitude) (Sullivan & Konishi, 1984). NM process monaural inputs from the ipsilateral ear for phase, and shows phase locked firing; this information is delivered bilaterally via phase-locked afferents to Nucleus Laminaris (NL) neurons for processing binaural information. NM neurons carry information about sound timing within frequency channels in NL (Sullivan and Konishi, 1986; Carr and Konishi, 1990)

Nucleus laminaris contains tonotopically arranged coincidence detection arrays that encode interaural time difference using bilateral inputs from NM neurons. Jeffress' model for coincidence detectors is the currently accepted anatomical model for NL (Jeffress, 1948); see figure 1 for a simplified visual representation of said model. NL receives these contralateral and ipsilateral inputs on ventral and dorsal sides of NL, respectively. The interaural time difference is computed from the time phase of the binaural inputs across frequency bands, and delay lines of NM afferents projecting onto NL soma that producing maximal responses at band-specific ideal ITDs (Carr and

Konishi, 1988). HRP staining of NM afferent projections on NL has strongly suggested the existence of tonotopically organized Jeffress-esque coincidence detectors (Takahashi and Konishi, 1988; Carr and Konishi, 1990).

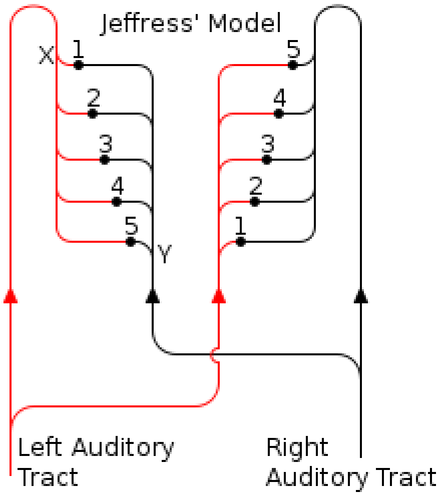

Figure 1: Visual representation of Jeffress’ model for coincidence detection, as is present in NL neurons.

Auditory tracts are nucleus magnocellularis afferents projecting onto nucleus laminaris soma. Reprinted from Jeffress' Model. Digital image. Coincidence Detection in Neurobiology. Wikipedia, n.d. Web. 02 Feb. 2016.

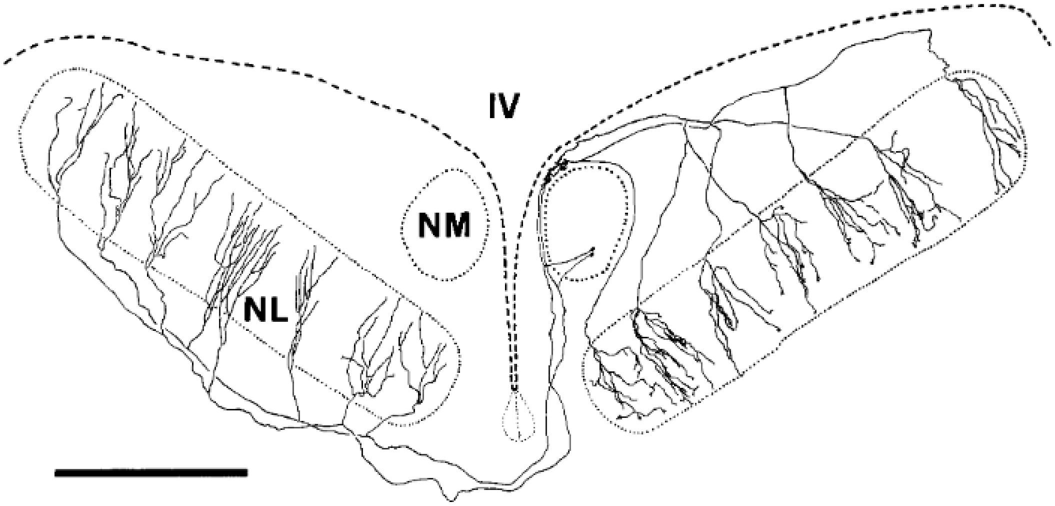

Figure 2: Representation of the projection of NM axons onto NL.

Afferents from R-NM project ipsilaterally to the dorsal side of NL and contralaterally to the ventral side of NL. This bilateral projection pattern forms the Jeffress' coincidence detection array, organized dorso-ventrally in NL. Scale bar represents 1mm. Reprinted from "A circuit for detection of interaural time differences in the brain stem of the barn owl." by Carr, C. E., and M. Konishi. The Journal of Neuroscience10.10 (1990): 3227-3246.

Localization of acoustic stimuli is an integrated process that uses place-coded ITD and ILD cues. Laminaris neurons project onto the central nucleus of the inferior colliculus (ICc), which is organized by frequency, and interaural time difference. This organization can be seen in a three-dimensional model depicted in Figure 3 (Carr and Konishi, 1990; Wagner, Takahashi, & Konishi, 1987). Neurons in ICc are tuned to ITD; individual cells respond to ITDs maximally with a particular best delay (Hancock and Delgutte, 2004).

The classical model for the localization of sounds in cognitive space is a place code model. This model relies upon the presence of a neural representation of space in the external nucleus of the inferior colliculus (ICx), with the highest concentrated rate of firing indicating the sound orientation (Knudsen and Konishi, 1978; Takahashi et al, 2003). One could visualize this model as a topographic map of auditory space, with the direction of the sound being the highest peak on the map. The classical view has only recently been contested by the implementation of a new statistical model, which presents a different model of decoding ITD cues that more closely aligns with owl behavior (Fischer & Peña, 2011).

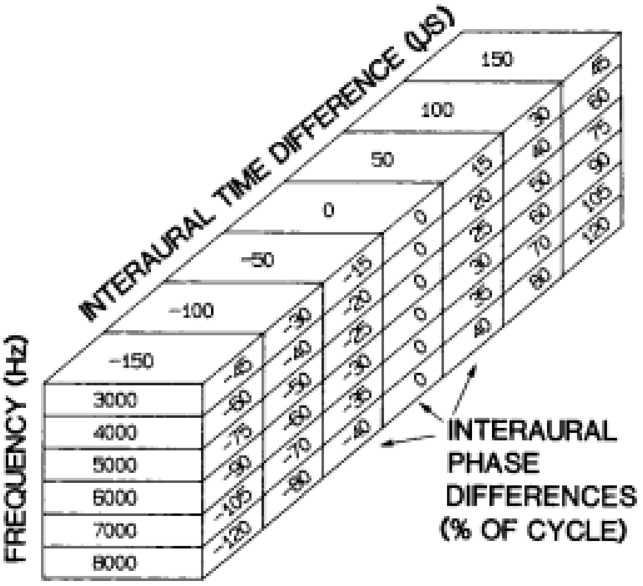

Figure 3: Schematic model of ICc organization.

In the figure, right to left represents mediolateral axis and top to bottom represents the dorsoventral axis. Reprinted from "Representation of interaural time difference in the central nucleus of the barn owl's inferior colliculus." Wagner, Hermann, Terry Takahashi, and Masakazu Konishi. The Journal of Neuroscience 7.10 (1987): 3105-3116.

Bayesian Inference

Bayesian inference is a statistical model used to predict and explain outcomes of certain behaviors. The theorem can be used to explain phenomena from a broad spectrum of applications: from courtroom case outcomes to disease predispositions in clinical patients. Fischer and Peña (2011), published their new model proposing a Bayesian model for sound localization in barn owls. The model uses Bayes' theorem to explain the systematic underestimation of peripheral sound sources; owls' behavior showed excellent accuracy in central sound localization tasks, but consistently predicted more distant sounds to be closer to the point of the birds' central focus.

$$P(A|B) = \frac{P(B|A)P(A)}{P(B)}$$

Bayes' Theorem represents probability of a particular outcome given potential conditions relative to that outcome. P(A|B), the posterior probability, is the probability of A given B and in the case of sound localization is the probability of a computed sound direction given the ITD. P(B|A), the prior probability, is the probability of observing B given event A, for sound localization this is the probability of the ITD given the sound direction. P(A) is the prior probability, which, for our purposes, is the probability of a sound direction. P(B) is the marginal likelihood, or model evidence, and is a constant value for all hypotheses in consideration. In sound localization, this is the probability of an ITD.

The model proposed by Fischer and Peña explains the systematic underestimation the birds displayed in behavioral tasks, with the behaviors posterior probability being statistically dependent on the prior probability. The prior probability is represented by more neurons being tuned to sounds near the center of visual attention in ICx and the optic tectum and the central-dominant prior distribution of target directions (Knudsen, 1985; Fischer & Peña, 2011). Previous place code models do not predict owls' behavior with the same accuracy as a Bayesian inference model (Fischer and Peña, 2011). For the purposes of our study, we manipulated the likelihood variable of Bayes' theorem via changes in binaural decorrelation.

$$P(\theta|ITD) = \frac{P(ITD|\theta)P(\theta)}{P(ITD)}$$

This is the Bayesian model for ITD discrimination. The likelihood statistic is the manipulation in experiments; by changing the accuracy of owls' ITD detection, the probability of the $P(ITD)$ value is less certain. Increasing the magnitude of the denominator in the theorem leads to a smaller certainty of the correct behavior (ITD discrimination of a specific location along azimuth).

Binaural correlation and the present study

Binaural correlation of sound refers to the neural representation of the similarity of the sound wave heard in each ear. The similarity of the sounds is not simply the correlation of the sound waves between each ear, but rather, is the neural representation of peak-to-peak similarity in the waveform. Each point in the binaural sound wave is cross-correlated between each ear, and the breadth of that tuning curve (variance) for space map neurons represents the binaural correlation, and under the Bayesian model, is also indicative of ITD detection accuracy.

Fully binaurally correlated sounds represent the ideal efficiency of the ITD circuit, or the maximal probability for correct ITD detection. Previous studies have shown that binaural decorrelation has no effect on ILD discrimination (Egnor, 2001); however, models for binaural decorrelation and its effect on ITD detectability are not well defined. Saberi et al tested owl ITD capabilities using head saccade experiments with various levels of binaural decorrelation and determined there to be an initially slow drop in behavioral performance followed by a steep decline after approximately 40% decorrelation (Saberi et al, 1998). A higher degree of binaural decorrelation led to an increase in variance of responses, which led to mean saccade angle drifting towards zero (Figure 4). Physiology data also indicates a correlation between neural response and interaural correlation (Albeck & Konishi, 1995). Manipulating binaural correlation and investigating the effects on owls' ability to detect a change in ITD is something that has yet to be explored. By increasing the variance of the prior probability of perceived ITD direction, there should be an increase in variance in the behavior of the bird.

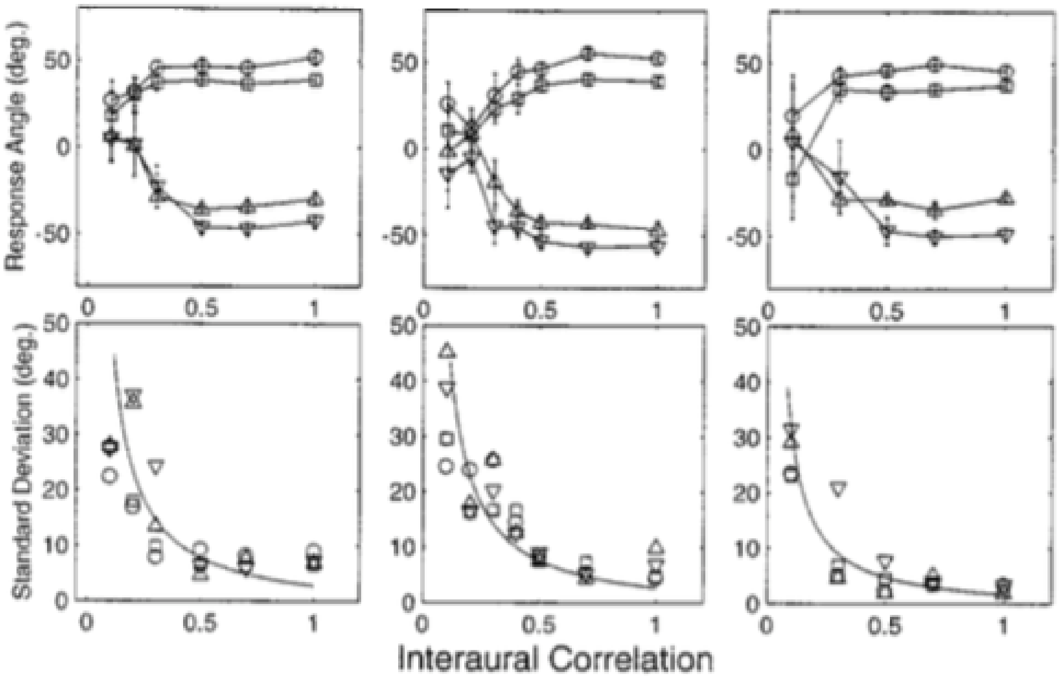

Figure 4: Head turn response angle of owls given interaural correlation levels ranging from 0 to 1.0.

Birds were trained to turn to either 50 or -50 degrees from center; decrease in interaural correlation led to a higher rate of behavioral error, increasing the variance and leading the birds to an average head turn of zero degrees. Note the negligible drop in behavioral performance from 1.0 to 0.5 interaural correlation. Reprinted from "Effects of interaural decorrelation on neural and behavioral detection of spatial cues." Saberi, Kourosh, et al. Neuron 21.4 (1998): 789-798.

In the present thesis, I investigated the effects of binaural decorrelation of sound stimuli on owls' ability to accurately detect a change in ITD using pupillary dilation response (PDR) as a measure of owls' detection under a Bayesian inference model for owls' behavior.

Research Questions and Hypothesis

What are the effects of binaural decorrelation of sound stimuli on a barn owl's ability to detect a change in interaural time difference?

1. I hypothesize that decreasing the correlation of binaural sound will degrade owls' ability to accurately detect a change in ITD.
2. I hypothesize that owls will show little degradation in ITD detection performance at high levels of binaural correlation, but will show a steep drop off at a certain level of binaural decorrelation.

Methods

Owl subjects

All our experiments were performed on adult barn owls (*Tyto alba*) from a captive breeding colony on the University of Oregon premises. The birds were held in our colony under a permit from the US Fish and Wildlife Service (SCCL-723257). Our procedure required the owl subject's head to be constantly fixed relative to the experimental apparatus; in order to prevent their movement during the experiment, birds were fitted with a headplate attached by dental cement to their cranium. Description of the process for headplating surgery can be found elsewhere (Takahashi and Keller 1994). For post surgery recuperation, birds were given a recovery period, the duration of which lasted a minimum of 2 weeks. Birds were not returned to the colony until the incision was fully healed and feathers grew over the surgery location (Bala and Takahashi, 2000). Owls were acclimated to experimental procedures as per protocol in order to ensure birds' safety and minimize stress on the animals; protocol on acclimatizing birds to PDR procedures can be found elsewhere (Bala and Takahashi, 2000).

Behavioral stimuli

Our stimuli were binaural synthetic sound stimuli played through etymotic earphones inserted into the owl's external auditory canal. The stimuli consisted of pairs of randomly noise-modulated noises (40-ms duration; 2.5-ms linear ramps) presented from different locations in frontal space, generated by use of a custom MATLAB 6.3 script (MathWorks). The carriers comprised reproducible, broadband noise bursts filtered between 2 and 10 kHz, the range relevant to the barn owl for sound localization. To synthesize the envelopes, we generated noises with random phase and energy below 150 Hz, near the upper cutoff of the owl's modulation transfer function (Dent et al., 2002; Keller and Takahashi 2000). These noises were transformed into the time domain by an inverse Fourier transform. Sound stimuli were decorrelated by diluting the sound in one ear with a contaminating stimulus. For 100% correlated stimuli, an identical stimulus was played in both ears. For sounds of less than 100% correlation, a second dissimilar sound was played as a contaminant in order to decrease the similarity between both ears to the desired degree of correlation. Product of contaminant sound and binaural sound is compared to the binaural sound to test correlation, and various combinations were tried until the desired correlation value was obtained.

$$100\%\ correlation\colon (Left\ ear) Sound\ A — (Right\ ear) Sound\ A$$

$$< 100\%\ correlation (Left\ ear) Sound\ A — (Right\ ear) Sound\ C$$

$$Sound\ C = Sound\ A + contaminant\ Sound\ B$$

Experimental apparatus

All experiments were conducted in a double-walled anechoic chamber located on the University of Oregon campus (Industrial Acoustics Co. IAC; 4.5 m × 3.9 m × 2.7 m). In order to record a pupillary dilation response to a sound stimulus, the experimental apparatus required the presence of both a light emitter (ideally outside the owl’s visual spectrum) as well as a detector for the emitter’s spectrum of light. For these purposes, procedures utilized an infrared light emitting diode (LED; F5D1QT; emission peak at 880 nm; QT Optoelectronics, Sunnyvale, Calif.) and an infrared detector diode

(QSC114; absorption maximum at 880 nm; QT Optoelectronics, Sunnyvale, Calif.). The small size (emitter: 6.4 mm high x 4.7 mm diameter; detector: 4.9 mm high x 3 mm diameter) and light spectrum had little effect on the owl subject's pupillary constriction (Bala and Takahashi, 2000). We sampled the pupillary light reflection at a sampling frequency of 1875Hz. Data was stored and analyzed after each session. Experiments were monitored at all times for the owl's safety by a researcher with an infrared camera streaming onto a television monitor in the anteroom to the anechoic chamber. If a bird struggled, the session was stopped immediately, lights turned on, and the experimentor comforted the bird for the duration of the experiment, so as not to condition birds to associate struggling with immediate removal from the experimental apparatus.

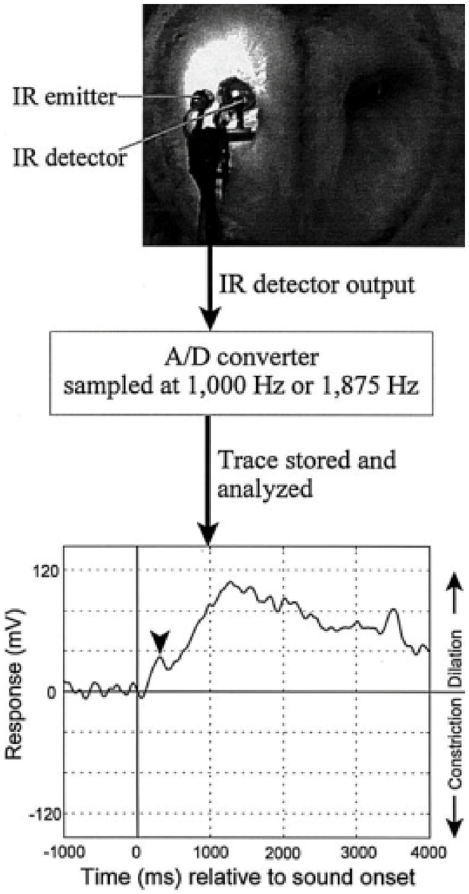

Figure 5: Anterior view of IR emitter and detector apparatus in place with a bird fixed in via headplate to the headplate mount.

IR detector sampling for our experiment used only a sampling frequency of 1875Hz, different from the two sampling frequencies shown in the figure. PDR trace was zeroed at every stimulus onset, giving the magnitude of the response as an integration of the post-stimulus trace and depicting post-stimulus response as either constriction or dilation relative to pre-stimulus pupil status. Reprinted from Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology Vol. 186; A. D. S. Bala and T. T. Takahashi, “Pupillary Dilation Response as an Indicator of Auditory Discrimination in the Barn Owl," p.427, Copyright (2000), with permission from Springer-Verlag.

Behavioral paradigm and measures

For each session, The bird was presented with identical 40 ms burst of sound at ITD = 0, every 11 +/- 2 seconds, for a total of 310 trials. After either 99 or 149 of these "habituating" trials (changed to 149 after seeing better results), however, Test stimuli were substituted for every 50th trial. This provided ample time for the bird to habituate to the noise bursts at the start of the experiment and to re-habituate between test stimuli. Habituating stimuli and test stimuli carried the same binaural correlation over a session, the difference being that a non-zero ITD was presented for the test trials. Acoustically evoked PDR was measured by the aforementioned IR detector/emitter apparatus. Data significance was determined by comparing the pupil size of habituation trials to test trials after stimulus presentation Response accuracy to ITD was determined using receiver operating characteristic (ROC) curves of ITD detection for various values of ITD and binaural correlation values presented to birds. ROC analysis shows behavioral error by plotting the number of hits versus the number of false alarms, with the area under the curve representing the percent of responses that are correct. Seventy-five percent correct or greater is usually considered to be a threshold of significance, in this case indicating the animal's ability to accurately detect a change in the ITD test stimulus. The last steps in analysis were plotting the accuracy of responses (p(C)) against the binaural correlation (Figure 11) and the ΔITD threshold versus binaural correlation of the binaural sound stimuli, portraying the effects of binaural correlation on behavior accuracy.

Post-stimulus pupil size was recorded and measured for 1 second pre-stimulus presentation, and 4 seconds post-stimulus presentation, for a total of a 5 second measurement. Experiments were performed with overhead lights on for bird 1043 and off for bird 1053, contrary to previous PDR procedures which were performed in darkness alone (Bala & Takahashi, 2000). Response character under lit conditions was much faster and sharper than in complete darkness. Baseline oscillation of pupil diameter continued after the bird habituated to habituating stimuli (after approximately 100 trials) similarly to in darkness. Responses to test trials under lit conditions were shorter and required less habituation between stimuli than in darker environments, where the trace would not return to the baseline for 15 seconds given particularly strong responses (Bala & Takahashi, 2000). When variables in the experimental apparatus failed (for example, eyelid tape coming loose), the session was stopped, the variable corrected, and the session restarted after a brief recovery time allowing for the bird to return to a baseline pupil size.

Results

Owls show ITD detection performance levels above 75% correct with 8µs ITDs given binaural sound correlation levels at least as low as 60% (Figure 6; Figure 11). Owls' ITD threshold at 100% binaural correlation was approximately 8µs. Behavioral performance fell below behavioral criterion for ITD of 6µs (Figure 7). Further research is required to complete the dataset for the entire range of binaural correlation values. Normalized data on single neuron activity in the auditory pathway to partially correlated binaural signals indicated a correlation between neuronal activity and binaural correlation (Albeck & Konishi, 1995), while our results initially show no perceivable drop in percent correct at low levels of binaural decorrelation. Data presented include 100% binaural correlation at 6 µs, 8 µs, or 10 µs ITD (figures 7 and 9); additionally, birds were tested for 8 µs ITD at different values of binaural correlation (figures 8 and 10). ROC curves are of all sessions of a particular data category (e.g. 100% correlation or 8µs ΔITD) for one bird. Our results show some trends but lack large enough sample range to show much significance. Most data contain between 1-3 sessions for each stimulus parameter set (binaural correlation and ITD for each bird). In terms of hypothesis support, rough trends support the notion that behavioral performance does not rapidly degrade with a decrease in binaural correlation, as was discussed earlier in regards to head saccade experiments (Saberi et al., 1998). Our application of Fischer and Peña's Bayesian model for ITD detection accuracy under the assumption that Bayes' theorem accurately predicts the behavior relies on data showing the decrease in behavioral performance of ITD detection for support. Our results currently don't hold conclusive evidence for this drop in detection performance, however progress has been made in understanding the surprising capacity for owls to detect ITDs as low as 8μs with binaural correlation values as low as 60%. Continued testing will fill in the gaps in our model (future plot we wish to fill with results is shown in the discussion section: Figure 11). All results are organized by the bird tested; results from bird 1043 are shown first, followed by bird number 1053. Figure 11 incorporates all the data collected up to this point for both birds, depicting percent correct (mean p(C) of each bird’s ROC results) versus sound similarity index. Figure 11, and all tests of binaural decorrelation shown in these results, are with a test trial stimulus of ITD=8μs.

Bird No. 1043

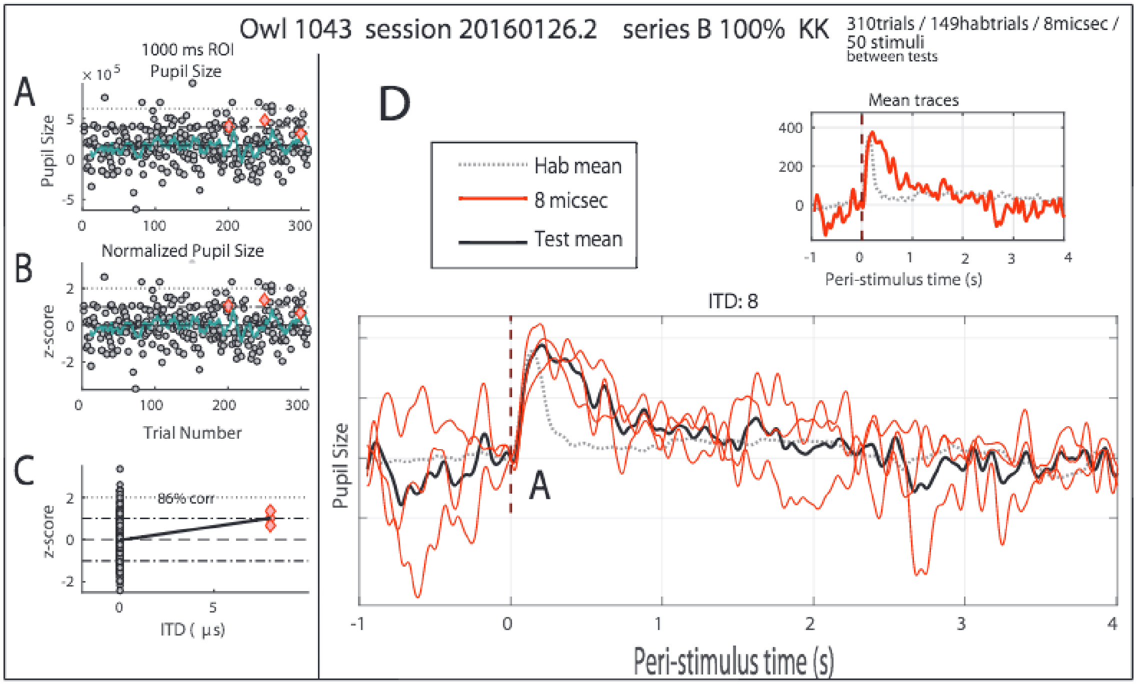

Figure 6: 100% Binaural correlation for 1 session of bird no.1043 with a test trial of ITD=8µs.

This is a sample of the data collected from one experiment session. Part A depicts the pupil size of the owl after presentation of the stimulus. Part B depicts the normalized pupil size, showing the statistical significance as a z-score relative to the mean of the distribution of all trials. Part C depicts the percent correct of responses, and shows the distribution of z-scores for the values of ITD that were presented during the experiment (0µs and 8µs). Part D shows the owl's pupil size as a function of time. Test trials are depicted as red lines, habituation trial mean is depicted as a dashed black line, and the test trial mean is depicted as a solid black line. Note the significant gap between the mean test trace and mean habituation trace which is indicative of a correct response post-stimulus dilation.

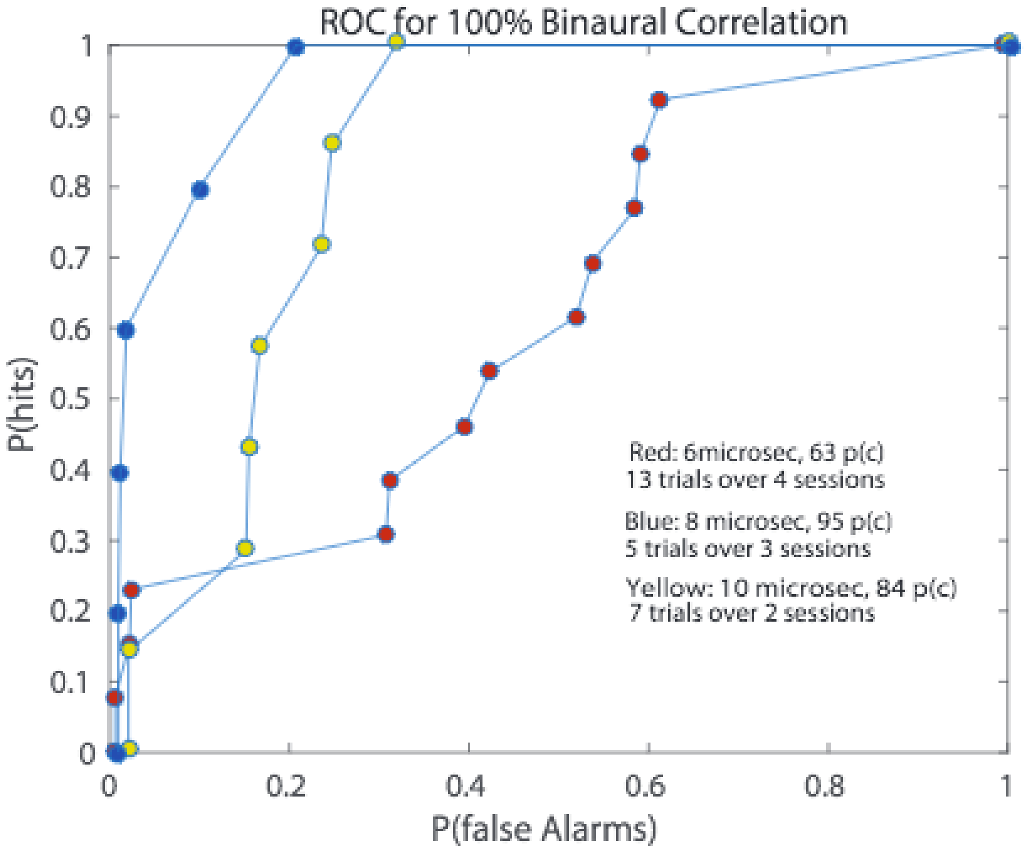

Figure 7: ROC curve for 100% Binaural correlation for all presented ΔITDs for bird 1043.

Three curves indicate the ΔITD used for the test trial; red representing 6μs, blue representing 8μs, and yellow representing 10μs. Both 8 and 10 μs ΔITD were above criterion with 95 and 84 percent correct, respectively, while 6 μs ΔITD fell below criterion at 63 percent correct.

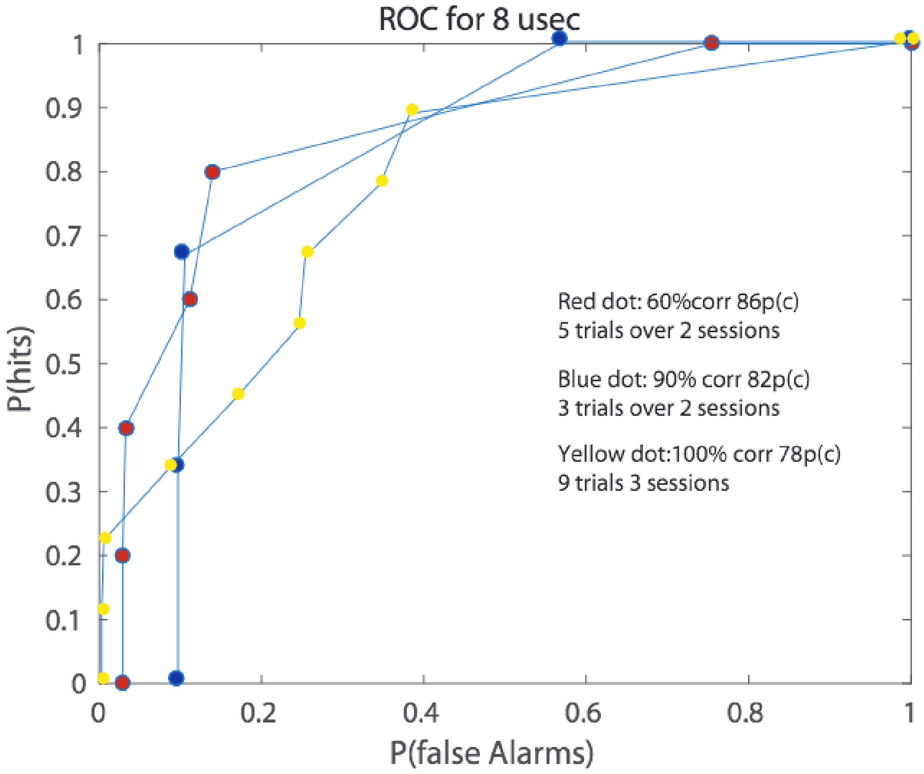

Figure 8: ROC curves for 60%, 90%, and 100% interaural correlation values using an ITD of 8 μs for test trials.

Three curves indicate the different interaural correlation: Red dots are for 60% correlation, blue dots are for 90% correlation, and yellow dots are for 100% correlation. All three tests of binaural correlation resulted in above-criterion performance.

Bird No. 1053

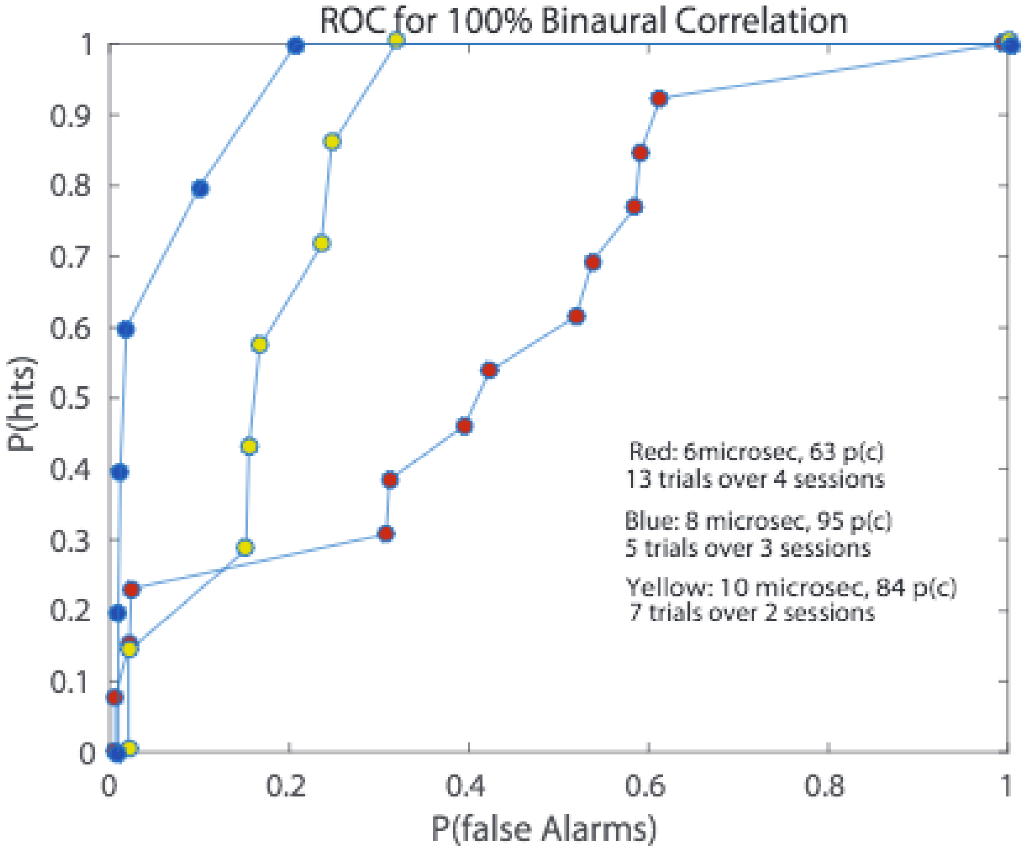

Figure 9: ROC curve for 100% Binaural correlation all recorded ΔITD test trials.

Three curves indicate the ΔITD used for the test trial; red representing 6μs, blue representing 8μs, and yellow representing 10μs. 63% correct falls below criterion for behavior, leading us to believe 6μs is a sub-threshold ITD for this bird. Testing more ITDs between 6 and 8 μs could lead to more precise understanding of the owl's ΔITD detection threshold.

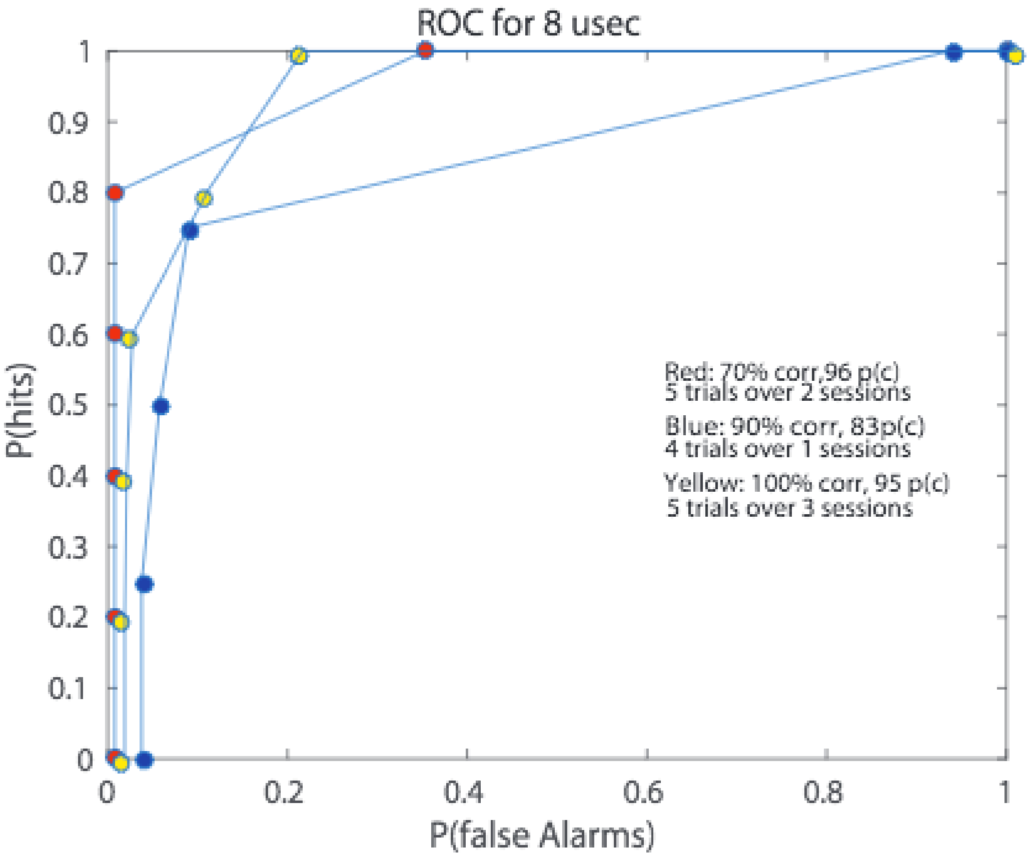

Figure 10: ROC curve for 70%, 90%, and 100% interaural correlation values using an ITD of 8 μs for test trials

Three curves indicate the different interaural correlation: Red dots are for 60% correlation, blue dots are for 90% correlation, and yellow dots are for 100% correlation. Bird maintained accurate ΔITD detection for all tested binaural correlation values; no tests fell below criterion for an 8μs ΔITD detection test.

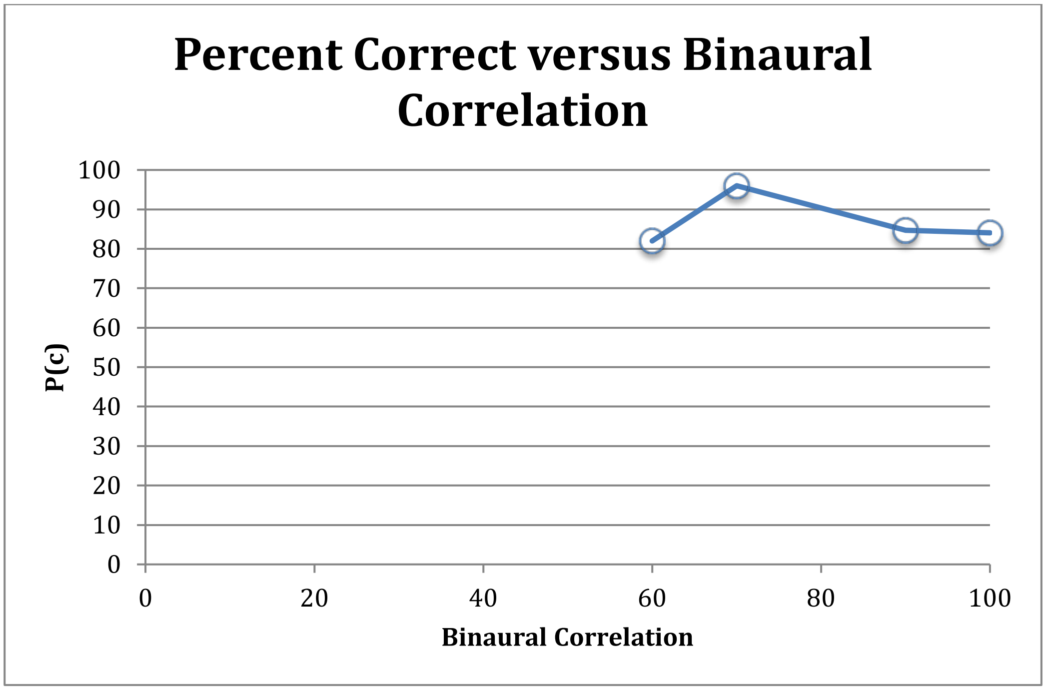

Figure 11: Percent Correct as a function of Binaural Correlation.

Results were taken from two birds and compiled together. Results show very little drop in percent correct for all binaural correlation values tested thus far, similar to trends shown in physiological data published in Saberi et al. (1998).

Discussion

The goal of experimentation was to investigate the effects of binaural decorrelation on owls' ability to detect a change in interaural time difference. I hypothesized that decorrelation of sound would decrease owls' ability to detect a change in ITD and that owls would show little drop in percent correct of responses at low levels of binaural decorrelation but a steep drop in percent correct at a certain binaural correlation level. Our results show that birds are able to detect 8 µs ITDs (approximately the ITD threshold for 100% correlated sounds) with binaural correlation values as low as 60%. No evidence was shown for a profound drop in ITD change detection due to birds maintaining behavioral accuracy through all of the tested values of binaural correlation. Results did not refute either hypothesis, but were not sufficient to support them conclusively. Data show some support for hypothesis two, due to the maintained behavioral performance of ITD change detection from 60-100% interaural correlation. Considering the negligible drop in percent, one can infer a greater potential for hypothesis support.

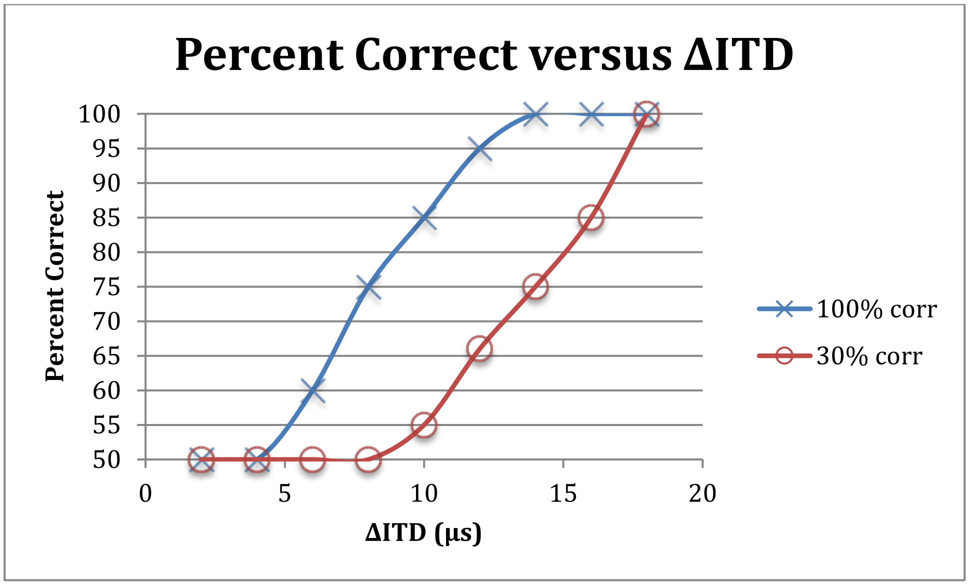

Figure 12: Predicted trends for change in percent correct as a function of ΔITD (μs) for two values of interaural correlation

This is a prediction for projected change in percent correct given a change in interaural time difference. Y-axis represents the predicted change in percent correct, while the x-axis represents the change in ITD in microseconds. Note the increase in ΔITD required for the bird to detect 75% correct ΔITD for 30% interaural correlation (red).

Figure 12 represents the predicted change in the accuracy of owls' ITD change detection. Based on data from other experiments testing the effects of interaural correlation on sound localization and detection tasks, decorrelating the sounds should lead to a drop in detection accuracy (Jeffress et al., 1962). Jeffress et al. investigated the effects of interaural decorrelation on the precision of a noise-centering task; results of their tests showed little initial increase in variance with a decrease in binaural correlation (σ=40-75μs), until 20% correlation, at which point performance standard deviation increased from approximately 75 to 150 μs. Results from our tests agree with Jeffress' and other previous experiments regarding partial interaural correlation in owls

(Albeck & Konishi, 1995). Normalized response of neurons in NL, ICc, and the ventral lateral leminiscal nucleus all showed a roughly linear type response while ICx showed a ramp type response. Both groups showed a positive correlation of neuronal response with interaural correlation. Saberi et al. (1998) showed an increase in response variance with a decrease in interaural correlation. Owls' less accurate neural and behavioral performance with partially interaurally correlated sounds from these experiments were what led to formulating our hypotheses.

While human's mechanism for ITD detection led to a slightly different perception of decorrelated sounds, some parallels can be drawn between owl and human behavior. Human processing of an ITD of zero leads to a perception of an image in the center of auditory space, and decreasing interaural correlation blurs and broadens the image until two independent images are perceived on separate sides of auditory space (Jeffress et al., 1962). Owl behavior followed trends consistent with how humans perceive ITDs under different levels of interaural correlation (Saberi et al., 1998).

Experimental limitations include the limitations of using animal subjects, the limits of PDR, especially in this case due to small sample size and only having two owl subjects. Introducing more owls to the pool of PDR subjects and furthering data collection will provide some remediation to the noise. PDR is useful, as it requires no training for the bird aside from acclimatization to the restraints in the procedure. However, limits of PDR include a lack of definition regarding the bird's attentiveness (lacking the same motivation as might be present in an operatively conditioned task) and the inability to present multiple test stimuli too close together in time, which increases the amount of experiment time required to accrue data. Using animal subjects limits feedback from experiments.

Our results will be a different test of the validity of the Bayesian model than the results in Saberi et al. (1998); that experiment tested the increase in variability of head turn localization caused by reduction in interaural correlation, resulting in a drift of the mean response towards a zero degree head turn (bird tested with either +50/-50 degree stimuli). The results of Saberi et al. could be due to the formation of one neural image from two low correlation sounds, similar to the results seen in human tests (Jeffress et al., 1962). Our experiment tests accuracy of detecting a change in ITD, and uses signal detection theory to determine accuracy over a range of binaural correlation values. Fischer and Peña produced their model under the assumption that Saberi et al.'s data was depicting drift in behavior towards a zero degree head turn, that is to say, the binaural image was becoming blurred and birds were turning to zero degrees at very low binaural correlation. This is incorrect; the data portrayed in the first figure of Saberi et al. (1998) shows a drift of the mean response towards zero, not an increase of zero degree head turns. Our experiment, on the other hand, has the ability to show the percent correct behavioral accuracy for detecting a change in the ITD when compared to varying levels of binaural correlation, which will show, at a finer resolution, what kinds of effects binaural correlation has on owls' behavior. Showing response accuracy over a full range of binaural correlation allows us to connect the variance of ITD (likelihood statistic) with behavioral accuracy (posterior probability), thus testing the validity of a Bayesian model in a different fashion. Aside from the range of our results, our methods have the benefit of portraying owls' behavior at a finer resolution than head turn experiments.

Our findings do not support the hypothesis that interaural correlation decreases owls' accuracy of detecting a change in ITD, but neither do they refute it. Data show some support for the second hypothesis. Should future research under the same experiment support these hypotheses, it will lend further backing to Fischer and Peña's proposed model of a Bayesian model for ITD decoding. Showing that a decrease in correlation of binaural inputs (the likelihood statistic) correlates with a decrease in behavioral accuracy (posterior probability) would be consistent with a Bayesian model.

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Figure 1: *Jeffress' Model*. Digital image. *Coincidence Detection in Neurobiology*. Wikipedia, n.d. Web. 02 Feb. 2016.

Figure 2: Representation of the projection of NM axons onto NL. Reprinted from "A circuit for detection of interaural time differences in the brain stem of the barn owl." by Carr, C. E., and M. Konishi. *The Journal of Neuroscience*10.10 (1990): 3227-3246.

Figure 4: Reprinted *from Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* Vol. 186.5; A. D. S. Bala and T. T. Takahashi, "Pupillary Dilation Response as an Indicator of Auditory Discrimination in the Barn Owl," p.427, Copyright (2000), with permission from Springer-Verlag.

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