

EVALUATING THE BENGALESE FINCH AS A MODEL FOR
LATERALIZED AUDITORY PROCESSING VIA
A MODIFIED DICHOTIC LISTENING TASK

by
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ABSTRACT

The dichotic listening (DL) task is a method for studying auditory attentional processes and investigating lateralization of auditory processing in humans. For the majority of people with left hemispheric dominance (LHD), there is a right ear advantage (REA) in auditory processing. Bengalese finches have similar brain regions specialized for learned vocalizations that are analogous to human language centers and are often used as a model for vocal and auditory processes in humans. There is a significant history of research supporting lateralization and LHD in Bengalese finches, and we therefore predicted that birds tested in a modified DL task would also display REA and vary in the latency, number, and amplitude of calls generated in response to stimuli to either the left or right ear. In order to create a paradigm for such a task in finches, we tested individual birds in a series of experiments, examining the effects of different stimuli and environmental conditions on the calling behaviors of 7 female Bengalese finches. We modified an existing blueprint for creating miniature headphones to play stimuli specifically to either the left or the right ear while the other ear received white noise or silence.

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First and foremost I would like to thank my academic advisor, teacher, supervising professor, and tireless supporter Dr. Brenton G. Cooper. Thank you for letting wreak havoc in your lab and believing I was worth the time and effort, even when I thought the opposite. I will always be grateful to you for taking me in when I was a little orphan looking for a lab and allowing me the opportunity to learn all that I have from you.

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INTRODUCTION

The dichotic listening (DL) task has been in use as a tool since the 1950's, when Donald Broadbent implemented it as a method for studying auditory attentional processes. (Broadbent, 1992, p. 126) Later, in 1961, Doreen Kimura modified the task to investigate lateralization of auditory processing in subjects with a history of epilepsy and lobectomies (Kimura, 1961a) as well as in non-epileptic subjects (Kimura, 1961b). Her findings suggested that stimuli presented to the ear contralateral to the dominant hemisphere for auditory processing were recognized more efficiently than those to the ipsilateral ear. (Kimura, 1961b, p. 169) For the majority of people, in whom the left hemisphere is dominant in auditory processing, this means stimuli arriving to the right ear is processed more efficiently, a trait that has since been referred to as right ear advantage or REA.

Researchers have used DL tasks in many contexts since these original experiments, with various modifications. The typical dichotic listening task involves presentation of two separate auditory stimuli simultaneously to bilateral ears of the subject; headphones are used to ensure that each ear receives a different stimulus. This is followed by testing the participant on their ability to comprehend,

recall, and respond to the given stimulus (Broadbent, 1992, p. 125) or repeat what was heard (Kimura, 1961a, p. 158). While researchers initially used digits as the stimuli, a variety of stimuli have been used since that time including simple words, paired consonant-vowel syllables, and simple tones, among other examples (Bruder, 1983). Results obtained can be dependent on the stimuli used (Findlen & Roup, 2011, p. 14), making DL a task amenable to testing lateralization of different factors ranging from language comprehension to emotional voice cues and pitch differentiation (Bruder, 1983).¹

This diversity in DL tasks has facilitated a variety of clinical uses, and dichotic listening is implemented diagnostically in a number of neurological and psychological disorders. Due to its ability to evaluate lateralization and hemispheric dominance, DL has been used frequently in cases of callosal dysfunction (Musiek & Weihing, 2011). Subjects who have had their corpus callosum split due to seizure disorders, those with traumatic brain injuries or multiple sclerosis that affect the callosum, or

¹ Many studies have investigated whether there are differences between the sexes on DL task performance, a meta-analysis of such studies performed by Daniel Voyer (2011) demonstrated a "significant and homogeneous" effect in favor of greater laterality in males, though the effect was "particularly small, representing a mean difference of 0.054 standard deviation unit" between the sexes (p. 248).

those with various other dysfunctions such as agenesis of the callosum generally have abnormal functioning and greater left ear deficits on dichotic listening tasks (Musiek & Weihing, 2011, p. 230). Subjects with seizure disorders have been evaluated with DL tasks on their performance in attention tasks, demonstrating extended auditory processing deficits post-ictally (Carlsson, Wiegand, & Stephani, 2011, p. 315). Dichotic listening is also used frequently in language and learning disorders, where it can help evaluate basic language comprehension levels (Asbjørnsen & Helland, 2006) and conditions like dyslexia (Helland, Asbjørnsen, Hushovd, & Hugdahl, 2007), and even help differentiate between different sub-types of learning disorders (Obrzut & Mahoney, 2011, p. 327) and their most effective therapies (Helland, et al., p. 50). In addition, subjects with disorders such as bipolar depression, schizophrenia (Bruder, 1983), and post-traumatic stress disorder (Asbjørnsen, 2011) are evaluated with DL and differences in DL performance may correlate with the severity of hallucinations, intrusion and other symptoms characteristic of the various disorders.

While primarily a diagnostic tool, dichotic listening also has therapeutic use in certain disorders. Subjects with central auditory processing disorder may be evaluated

diagnostically with DL, and modified DL tasks are also subsequently used as a tool to modify and improve their ability to differentiate and process speech (Putter-Katz, Adi-Bensaid, Feldman, & Hildesheimer, 2008). In subjects with depression, differences in performance on DL tasks can help determine the utility and effectiveness of certain drug therapies over others (Bruder, Stewart, McGrath, Deliyannides, & Quitkin, 2004). Given the wide-ranging use of DL tasks in human psychology, it would be useful to have an animal model to help illuminate how and why such differences in processing and DL performance exist.

The possibility of using Bengalese finches as a human model derives from their analogous patterns of language acquisition as well as lateralization in the vocalization-producing centers in their brains. Songbirds, like humans, develop their song through hearing and imitating conspecific tutors, going through phases of sensitivity and subsong that are analogous to childhood and the babbling of infants (Bolhuis, Okanoya, & Scharff, 2010, p. 749). Research into the foundation for such similarities in language acquisition "suggests that analogous mechanisms underlie auditory-vocal learning in humans and birds at the behavioural, neural, genetic and cognitive levels" (Bolhuis et al, 2010 , p. 755).

On the neural level, songbirds have auditory processing pathways and regions with roles analogous to those in humans; for example, the premotor nucleus HVC appears to be analogous to Broca's area and the caudomedial nidopallium (NCM) serves a similar association function as Wernicke's region (Moorman et al, 2012 p. 12782). Further, Bengalese finches demonstrate left hemispheric dominance analogous to that of humans in terms of activation of brain regions in response to stimuli (Moorman et al, 2012, p. 12784). This dominance is also demonstrated in the difference in performance of birds in operant auditory discrimination tasks following lesions of either the left or right neural vocal centers (Okanoya, Ikebuchi, Uno, & Watanabe, 2001, p.243), where left-lesioned birds performed more poorly than those with lesions to the right. In certain species, the lateralization of these auditory processes may demonstrate sexual dimorphism, but maintain similar underlying mechanisms and regions (Hauber, Cassey, Woolley, Theunissen, 2007, p. 771).

Given the strong history supporting lateralization and left hemispheric dominance in Bengalese finches, it follows that birds tested in a DL task would also display a REA analogous to that found in human subjects. In order to evaluate and create a paradigm for a DL task in finches, we

tested individual birds in a series of experiments, examining the effects of amplitude, background noise, isolation, stimulus variety, stimulus frequency, and habituation on the calling behaviors of female Bengalese finches. If a right ear advantage does exist in these birds, we hypothesize that stimuli presented to the right ear will generate a higher number of returned calls with a shorter latency period and greater amplitude than those presented to the left ear.

GENERAL METHODS

Housing and Diet

The subjects of this study were 7 adult female Bengalese finches. Prior to testing, the birds were housed in a communal aviary on 14:10 light:dark cycle with seed and water available *ad libitum*. Additionally the birds' diet was supplemented with vegetables, vitamins, and eggs. During testing, birds were moved to individual housing (approximately 12 x 10 x 10 inches) and kept on their regular feeding, supplement, and lighting schedule. Birds were allowed several days to accommodate to their individual surroundings in a sound attenuating chamber (approximately 31 x 13 x 13 inches) that was lined with 1 inch thick acoustic foam (source: Auralex Acoustics, Indianapolis, IN). A microphone was suspended from the top

of the cage. Headphone wires were tethered to a pulley system that entered the cage via a 1 inch hole in the top center of the chamber. See individual methods for any experimental variations in housing.

Materials and Surgical Procedures

Headphones were built based on an existing model developed by Hoffman, Kelly, Nicholson, and Sober (2012) for Bengalese finches and surgically implanted based on the procedures recommended by Hoffman et al (2012). Birds were anesthetized, then feathers were removed from the crown of the head and surrounding the subjects' ear canals. The subjects were transferred to a modified stereotaxic frame with adjustable ear bars to hold the subject steady during the procedure. An incision was made the scalp along the anterior-posterior axis; we then parted the skin and exposed the subjects' skull. We secured the crossbar of the headphones to the skull surface using epoxy; the ear posts were likewise secured to the crossbar with soft foam earbuds pressed snugly against the subjects' head to ensure an effective acoustic seal. The birds were given 24 hours for the epoxy to cure. All surgical procedures were carried out under isoflurane anesthesia (1-2%), and birds were allowed time between initial implantation, wiring, and testing to acclimate to the headphones.

Initially, the headphones were fabricated by hand using lightweight wood, foam, and plastic; in later experiments, headphone frames were made with a lightweight plastic using a 3D printer. The volume output of the speakers was measured to ensure stimuli from both ears were played at equal amplitudes. The speakers were then placed in the headphone frame when the subject was ready to be tested. The subjects were given time to habituate to the weight of the headphones prior to testing, with backpack tethering used in some experiments to offset headphone weight.

Data Acquisition and Parameters

Stereo wav files were played on a randomly timed schedule and responses recorded using Recorder (Avisoft Bioacoustics, Berlin, Germany). Using wav files enabled the Recorder program to play stimuli occurring on the two separate left and right channels simultaneously. Stimuli were played with variable intervals and recordings were triggered by the stimulus onset, followed by 15 seconds of data collection. The stimuli, inter-trial interval, and testing schedule varied between studies. Male Bengalese finch calls and songs sourced from a previously recorded library of data were used as stimuli. The stimulus played was recorded and correlated to the response recording track

in order to differentiate between left or right ear presentation, stimulus source, and the type of stimulus.

SASLabPro (Avisoft Bioacoustics, Berlin, Germany) was used to analyze the latency, number and average amplitude of response calls. Latency was calculated by subtracting the time of the initial response from the time the stimulus was played. Calls were disregarded if latency to respond was greater than 5 seconds, as it was unclear whether the call was a response to the intended stimulus or a spontaneous vocalization. Calls were also disregarded if interference from outside sound sources was visible on the spectrogram prior to a response. Examples of such interference include lab noise, human speech, and calls and songs from other birds in the lab to which the subject might respond.

Lastly, calls were categorized as either contact calls or tet calls. Calls were required to consist of 3 or more pulses to be considered contact calls; this is the call type with the greatest significance for our experiment, as they serve a social communicative function for Bengalese finches and are used to facilitate flocking behavior. In addition to such contact calls, finches produce tet calls, which may consist of 1 or 2 audible pulses and are generally less robust and lower in amplitude than contact

calls. Though the social significance of this type of vocalization is currently unknown, tet calls were also measured as responses.

We selected individual response calls and measured their average amplitude using the Fast Fourier Transform function in SASLab Pro. These were recorded and the amplitude of all the calls on a single stimulus-response track were averaged together; if any calls occurred after interference in the track, these calls were not counted as responses and thus were also excluded from the calculations for average amplitude.

The number of calls, average response amplitude and latency to respond were compared between left and right ear presentation and song and call stimuli. Further, the numbers of calls recorded in response to stimuli presented at different amplitudes were compared.

INDIVIDUAL METHODS

Study 1

This study involved two subjects housed in the sound-attenuating chambers described earlier. The first was tested for 6 days consecutively and the second was tested for 6 days, then allowed a rest period of 12 days due to suspected habituation to stimuli before being tested for another 3 days. Both birds were equipped with the first

generation model of headphones built using wood crossbars, and their frame weight was offset using tethered backpacks which were connected via a pulley system. Testing ran for 6 hours with random playback to left and right ears and variable ITI between 15-30 minutes.

Study 2

Study 2 also involved two subjects, with their testing run simultaneously in different environmental conditions. Birds used first generation headphone frames with tethered backpacks to offset frame weight.

Auditory Isolation Condition

Initially, testing of the subject in auditory isolation was a replication of the first study, with the same testing schedule and variable ITI of 15-30 minutes. The subject appeared to show the same pattern of habituation as birds in the previous study, so after 3 days of consecutive testing she was given an 11-day rest period. After this rest, she was tested on alternating days with an increased ITI variable between 1-1.5 hours and lengthened testing day that lasted 10 hours. After 2 days in this condition, simultaneous white noise was removed from the non-call-receiving ear and replaced with silence. This change was due to the persistent lack of robust contact

calls in subjects. Throughout testing, adjustments of the amplitude of stimulus playback were made.

Auditory Proximity Condition

The second bird in the study began to be tested after the extension of ITI and lengthening of the test day was made. Additionally, this bird was not housed in a sound attenuating chamber; rather, her enclosure was placed in the antechamber to the communal aviary that houses the rest of the colony, putting her in auditory proximity to conspecifics as well as miscellaneous environmental sounds. The subject was tested for 3 days on an alternating schedule with the original white noise/call stimuli, and subsequently tested for 5 more days with silence/call stimuli. Throughout testing, adjustments of the amplitude of stimulus playback were made.

Study 3

This study was a retest of the white noise to silence stimulus change and included the use of stimuli taken from multiple male sources. Due to the lack of response from the bird previously tested in the auditory proximity condition, this bird was chosen to be retested. The bird was moved to a sound attenuating chamber and tested for 3 days with white noise and call stimuli; the sources for the call stimuli were 3 different male Bengalese finches. After 3

days, the bird was given a 12 day rest period and then retested using the different source stimuli and white noise replaced with silence. Testing was run for 10 hours with 1-1.5 hour variable ITI. Throughout testing, adjustments of the amplitude of stimulus playback were made.

Study 4

This study replicated the design of Study 1, but used stimuli from different sources and without noise on the non-call receiving ear. Birds were placed in sound attenuating chambers and used the second generation 3D printed headphone frame. Testing ran for 9 hours with a 15-30 minute variable ITI. There were two subjects in this study; the first was tested every other day for 9 test days with pseudo-randomization of the source for the stimulus by day, followed by a rest period of 8 days. The bird was then given a second testing trial of 10 days with alternating stimulus sources each day. Throughout testing, adjustments of the amplitude of stimulus playback were made. The second bird was tested for 9 days with alternating stimulus sources by day, but was unable to be given a second trial after having dislodged the headphone apparatus.

Study 5

In the final study, the subjects were housed in a separate testing room without a sound attenuating chamber

but out of auditory proximity with/of other conspecifics. Testing ran for 3 consecutive days in 2 1-hour blocks separated by a 1 hour test interval. The ITI was shortened to a variable delay between 3-5 minutes and the stimuli included randomized calls and songs from different male sources.

RESULTS

Study 1

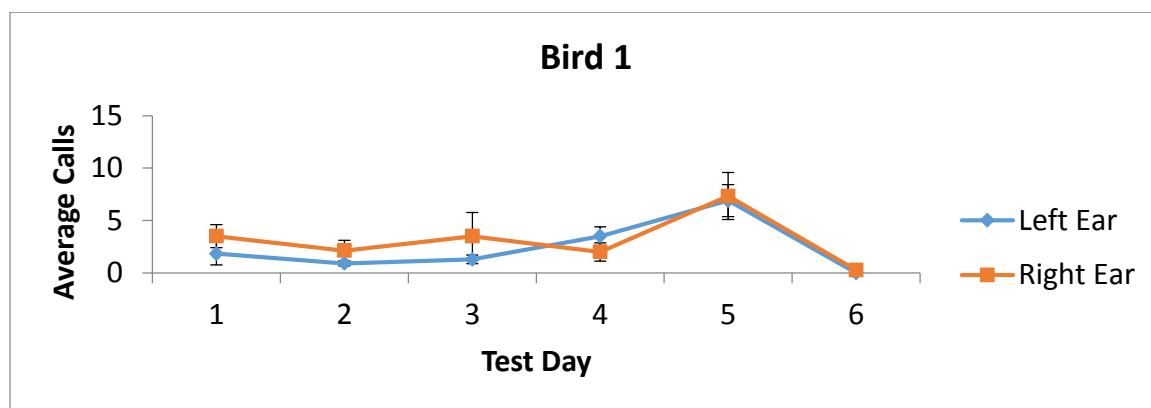


Figure 1. Average calls by day for Study 1, Bird 1. This subject showed fairly reliable calling over the course of 5 days with habituation by day 6.

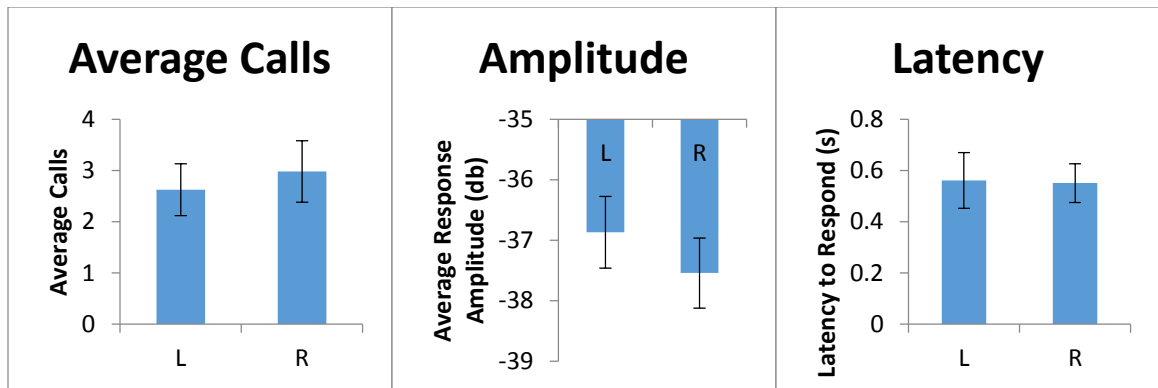


Figure 2. Average calls, average response amplitude and average latency to respond by ear for Study 1, Bird 1. No clear advantage is noted for either ear in any of these measures. L signifies responses to stimuli presented to the left ear; R signifies responses to stimuli presented to the right ear.

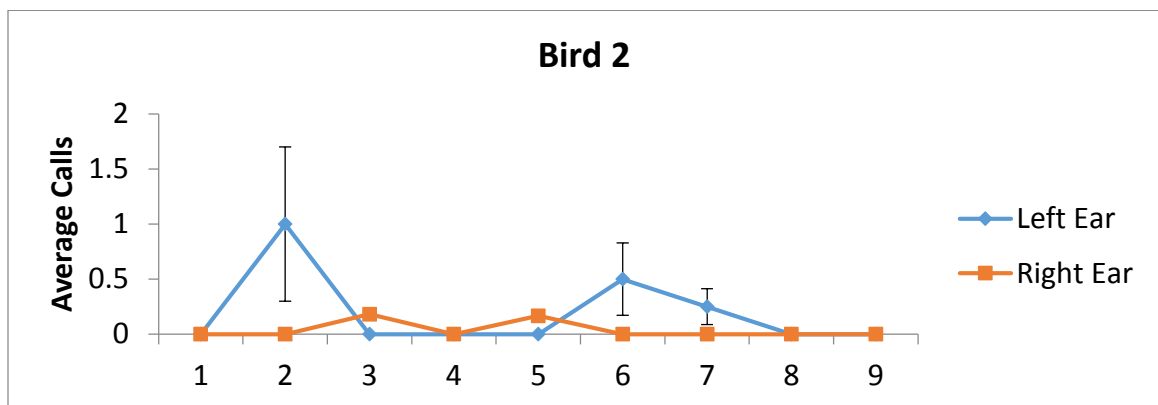


Figure 3. Average calls by day for Study 1, Bird 2. This subject showed unreliable calling behavior. Even after a rest period, the bird appeared to habituate to stimuli.

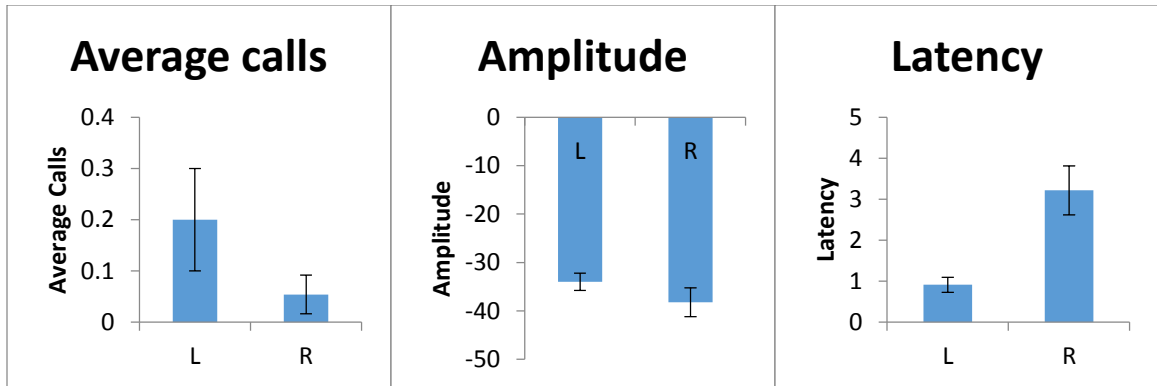


Figure 4. Average calls, average response amplitude and average latency to respond by ear for Study 1, Bird 2. This subject responds more often, more loudly and more quickly on average to responses presented to the left ear. This trend suggests a possible left ear advantage for this bird.

Study 2

The bird in study 2 that was placed in auditory proximity to the colony failed to produce any responses to call stimuli. Data for the other subject is shown.

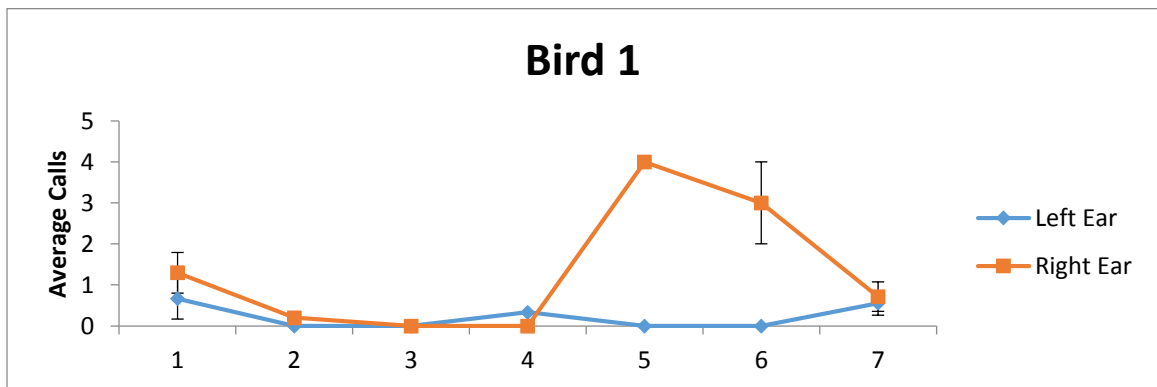


Figure 5. Average calls by day for Study 2 bird 1. This subject demonstrated fairly unreliable calling.

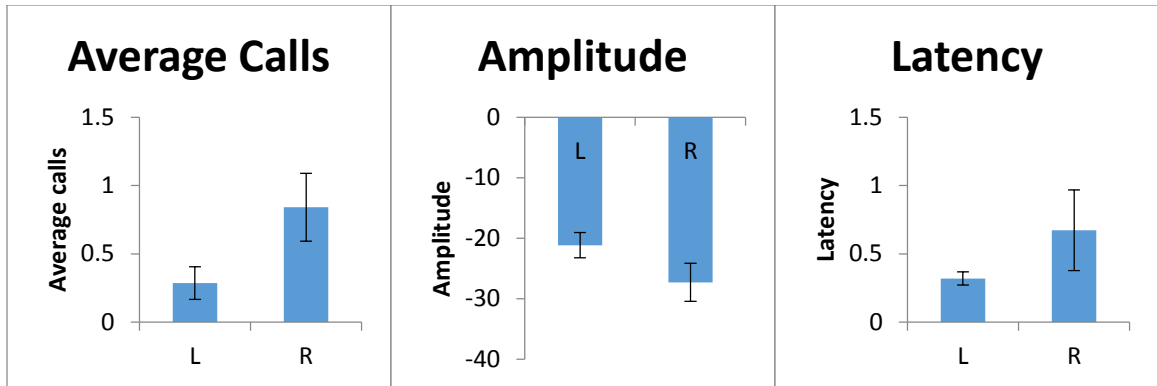


Figure 6. Average calls, average response amplitude and average latency to respond by ear for Study 2, Bird 1. This bird called more frequently to right ear presented stimuli, but with slightly lower latency and greater amplitude to left ear stimuli. There is no clear left or right ear advantage for this bird.

Study 3

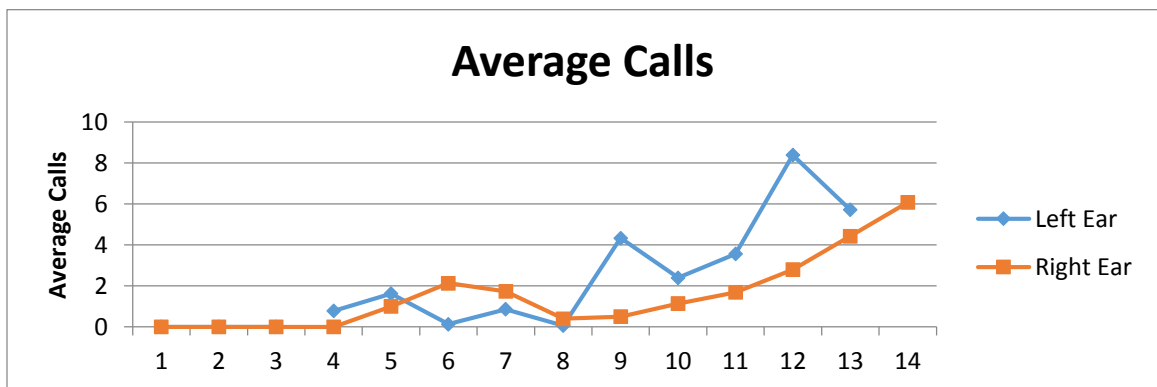


Figure 7. Average calls by day for Study 3. The separation between day 3 and day 4 data points represents the removal of white noise from stimuli. After white noise removal, the subject demonstrated increased number of calls and more robust responding with greater numbers of contact calls.

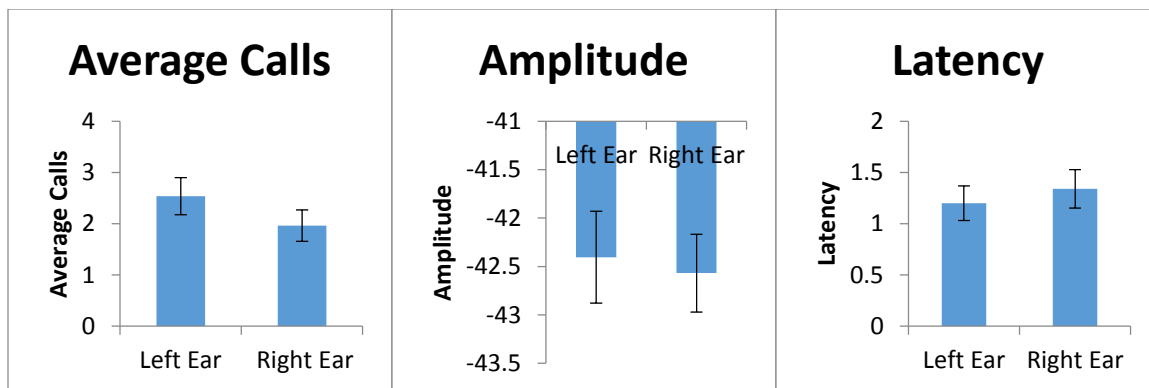


Figure 8. Average calls, average response amplitude and average latency to respond by ear for Study 3. Slightly more calls, with greater amplitude and lower latency to respond were produced in response to left ear stimuli.

Study 4

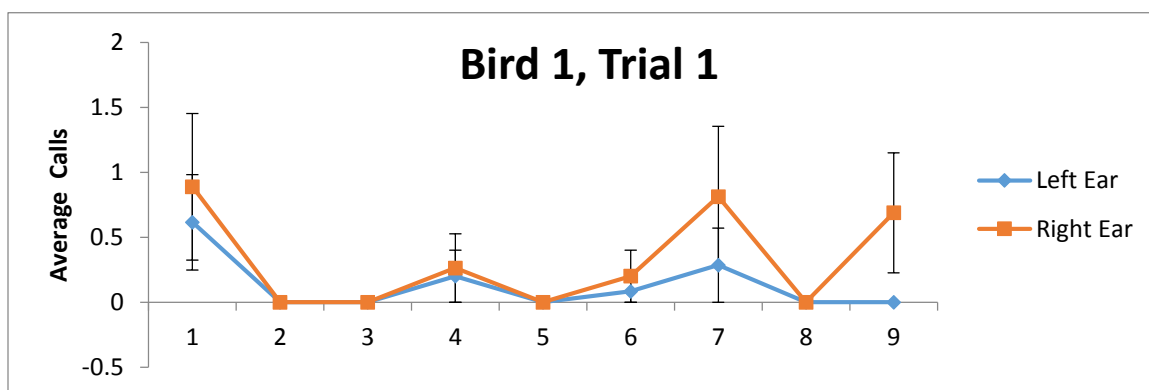


Figure 9. Average calls by day for Study 4, Bird 1, Trial 1. This bird demonstrated erratic calling behavior, but continued to call to the last day of her first trial.

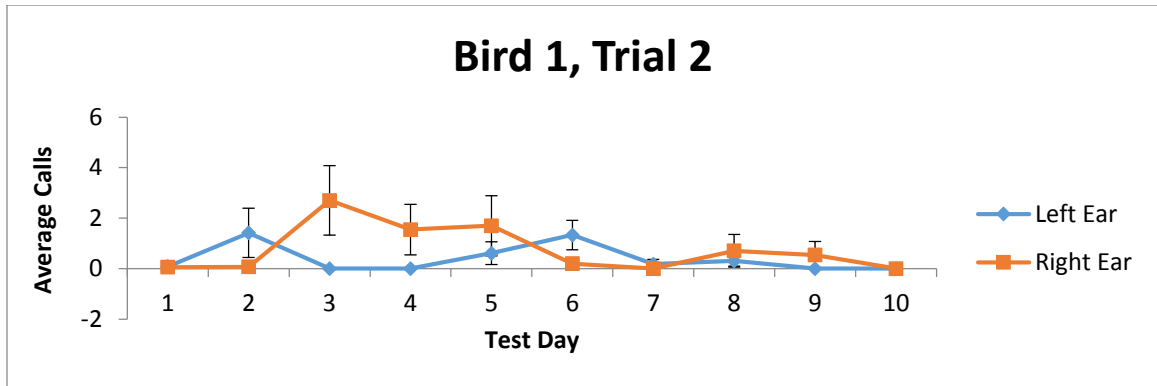


Figure 10. Average calls by day for Study 4, Bird 1, Trial 2. In her second trial, calling behavior was slightly more reliable, but the subject appeared to habituate to stimuli by the end of the trial.

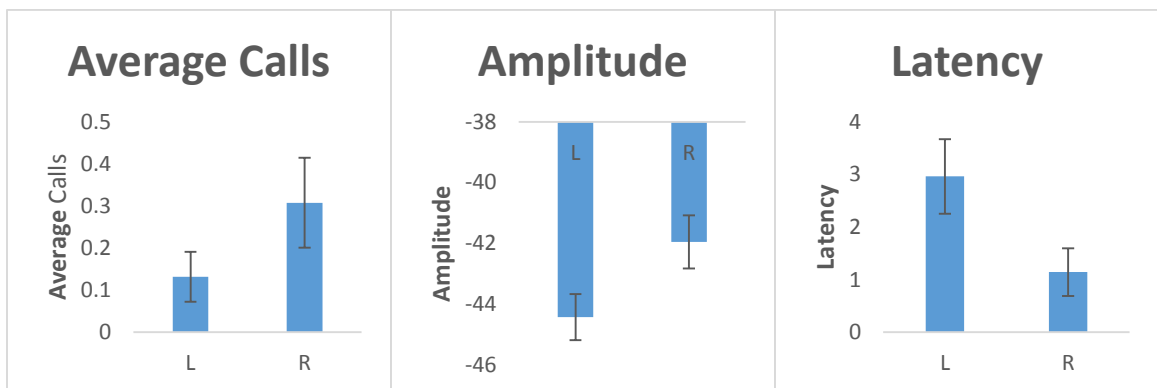


Figure 11. Average calls, average response amplitude and average latency to respond by ear for Study 4, Bird 1, averaged with data from both trials. This subject demonstrated greater number of calls to stimuli presented to the right ear that were louder with a shorter latency period compared to responses generated from left ear stimuli, suggesting a right ear advantage for this subject.

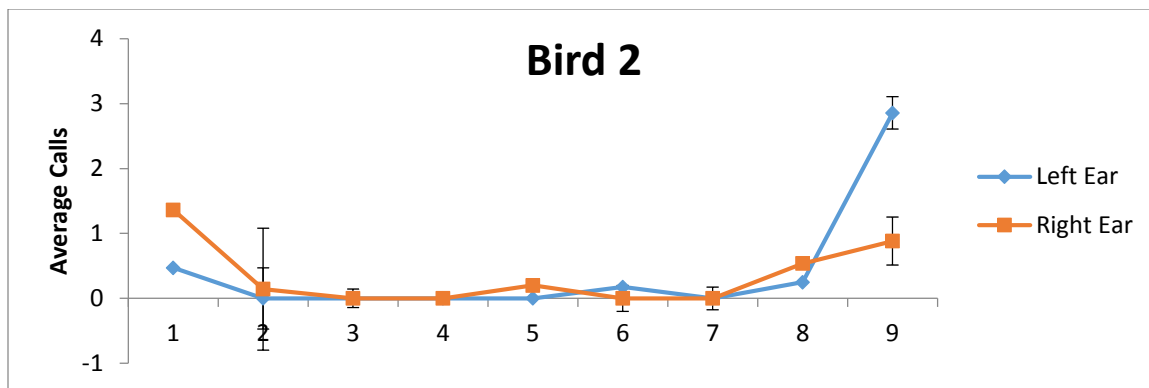


Figure 12. Average calls by day for Study 4, Bird 2. This bird responded very little, though responses increased near the end of her testing period with no change of conditions. This was not able to be tested because the bird was withdrawn from the study due to dislodgement of headphones.

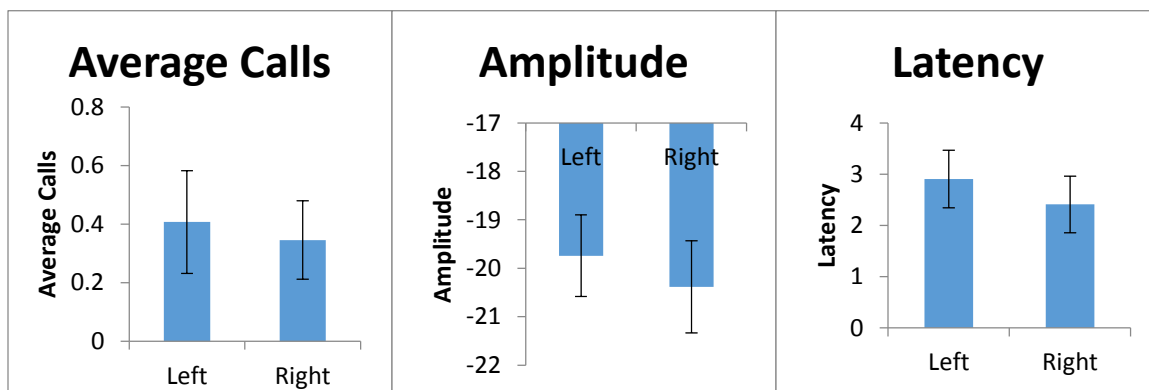


Figure 13. Average calls, average response amplitude and average latency to respond by ear for Study 4, Bird 2. This bird demonstrates slightly more numerous and slightly louder calls to stimuli presented to the left ear, though latency does not show a significant trend.

Stimulus Amplitude Changes

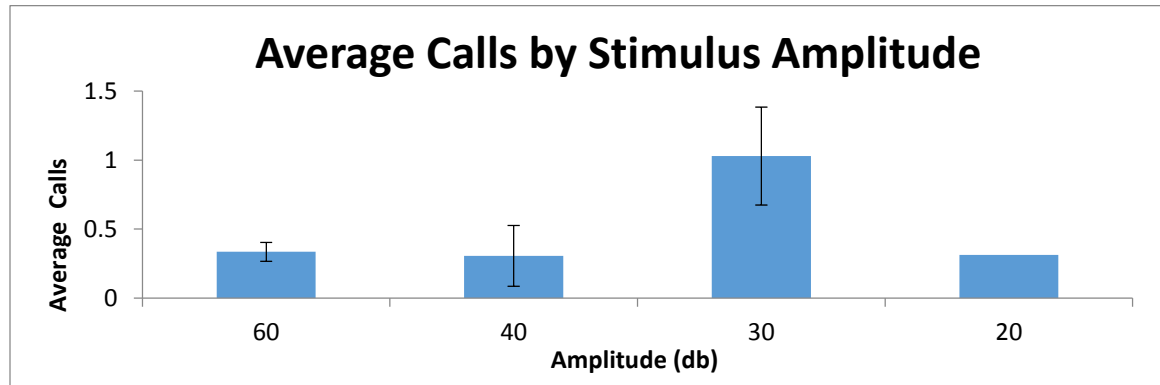


Figure 14. Combined results for changing stimulus amplitude in Studies 2, 3, and 4. Stimuli presented at approximately 30 dB generated the highest response rate overall with no significant differences between calls generated in response to 60 dB, 40 dB, or 20 dB calls. This appears to be an effect of perceived distance of the auditory stimulus.

Study 5

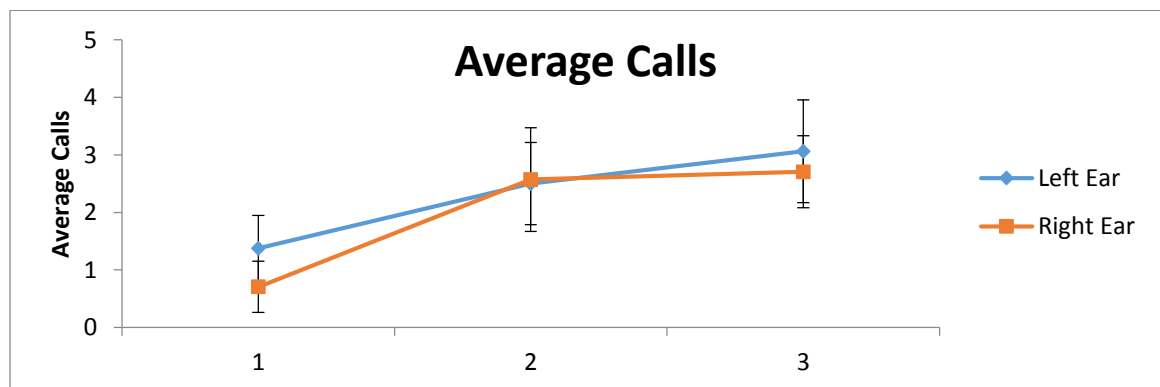


Figure 15. Average Calls by day for Study 5, Bird 1. This subject called reliably throughout. Response rates to left and right ear stimuli remained fairly similar, with slightly more responses produced to left sided stimuli.

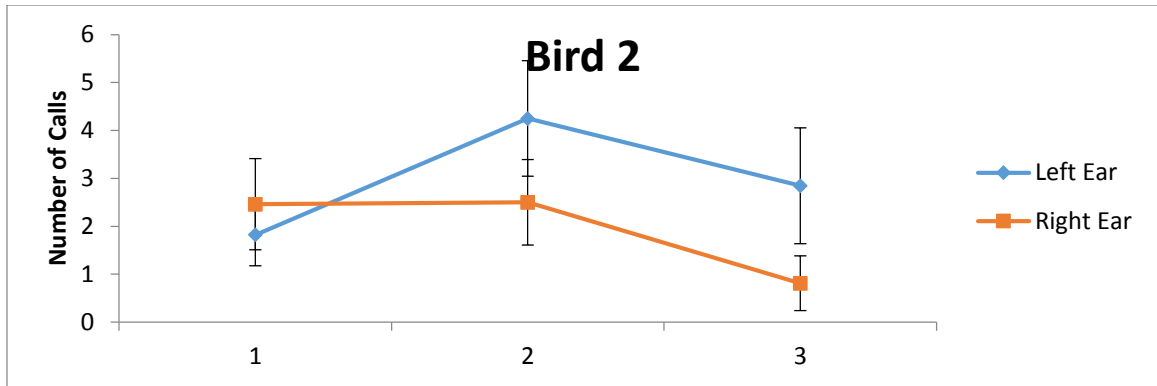


Figure 16. Average Calls by day for Study 5, Bird 2. This subject called reliably across the three days of her participation with slightly higher response rate than her counterpart. Slightly more calls were initially generated in response to right ear stimuli, but over time the left ear generated a greater number of calls.

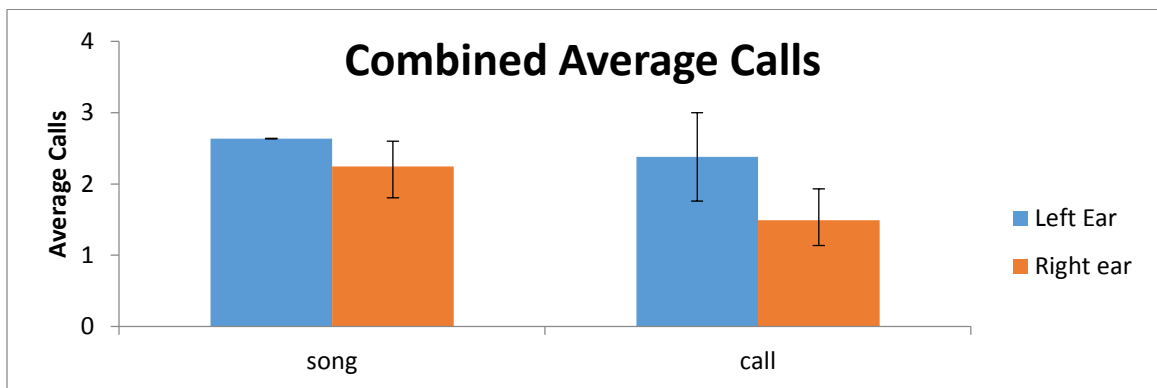


Figure 17. Combined average Calls generated in response to song versus call stimuli for Study 5, Birds 1 & 2. There was greater variability in the number of calls produced in response to call stimuli. Song stimuli generally produced slightly greater number of responses than call stimuli.

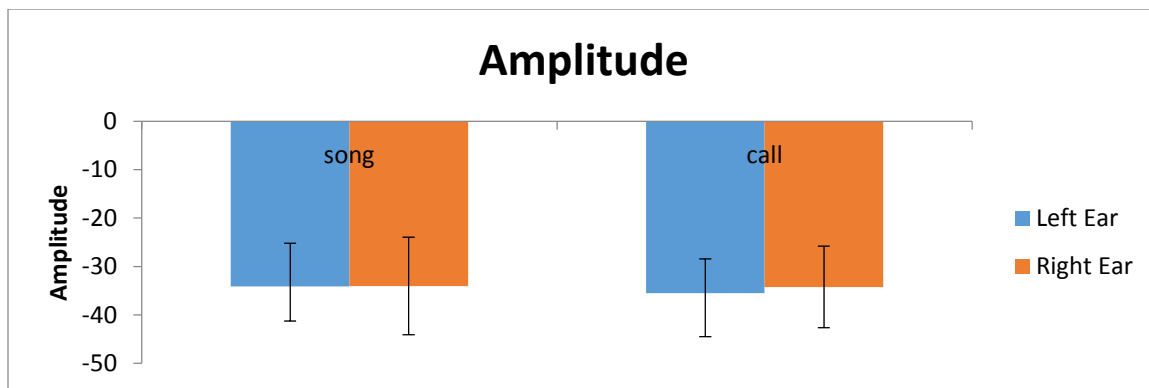


Figure 18. Combined average amplitude of calls generated in response to song and call stimuli for Study 5, Birds 1 & 2. No significant differences were observed between left or right or songs and calls. Controlling stimulus amplitude may have negated the need to modulate response amplitude; alternatively, poor acoustic quality due to the lack of a sound attenuating chamber may have masked any differences.

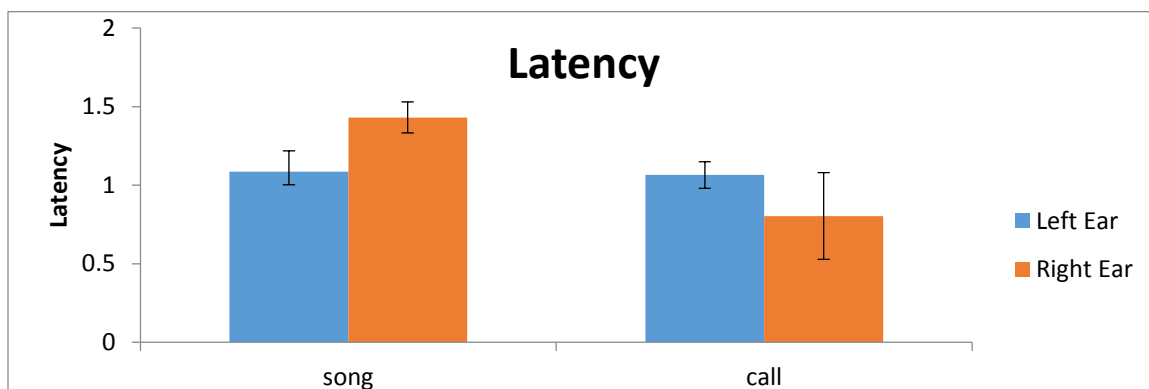


Figure 19. Combined average latency of calls generated in response to song and call stimuli for Study 5, Birds 1 & 2. Both birds responded more quickly on average to song presented to their left ear than song presented to their right ear. There was slightly greater variability in

latency to respond to calls versus stimuli, and an opposite trend was noted, with slightly quicker response times to right ear than left ear stimuli. This suggests that there may be a difference in auditory processing or response motivation that is dependent on the variety of stimuli presented.

DISCUSSION

A strong left or right ear advantage is not easily demonstrated by call stimuli. There was considerable individual variability in the amplitude, latency, and rate of responses to single calls. Individual birds had a trend towards one ear or the other; however, these were not consistent between birds or within studies. Given the small sample size of these preliminary experiments in dichotic listening, there may not be enough subjects to demonstrate an overall effect or a population level trend towards either one ear or the other. The primary goal was to develop a paradigm for dichotic listening task, so the current studies may represent idiographic approach rather than a nomothetic one. This, however, is necessary given the goals and circumstances of the undertaking.

Additionally, the quality of the call stimuli may not be similar enough to actual interactions between birds. In the colony, calls are more likely to take on a

conversational character, with the two participants calling multiple times in succession, usually alternating between the two callers. Our call stimuli consisted of a single, isolated male contact call; it is possible that the lack or subsequent calls in the "conversation" discouraged the subjects' further responses or did not provide enough reward or social stimulation to continue to generate responses over time.

Isolation housing increases calling behavior and is the preferred environment for recording contact calls in response to conspecific stimuli. Isolation housing produced more reliable results than the proximity condition, and any interference was clearly seen and able to be disregarded. Isolation housing also mimics an environment where a bird may be encouraged to make contact with other members of the flock, as Bengalese finches are social animals.

In contrast, proximity to the colony produced considerable background noise that was evident on the recorded files; this background noise reduced experimental control. Given the constant level of background interference, it unclear if the individual was able to hear and differentiate between the stimuli and the background. Had there been a greater level of calling, it would also be unclear whether this was in response to the intended

stimulus or background colony noise. It is also possible the presence of constant colony noise in the background limited the need for contact calls or the inability to make contact with the colony discouraged the subject in this condition from responding.

As shown most clearly in the third and fifth studies, variability in male stimuli enhances calling behavior, leading to the generation of more robust contact calls and delaying habituation to stimuli. The use of different male sources for call stimuli increased the rate of calling for the bird tested in Study 3, and she continued to call at increased rates several days into her trial. Compared to the previous studies that produced unreliable calling behavior that tapered quickly after the initial test day, Study 3 seemed to demonstrate delayed habituation to stimuli.

Inclusion of song stimuli in Study 5 also appeared to enhance contact versus tet calls, and the highest rates of response were elicited with a mixture of calls and song with lower inter-trial intervals. Subjects in previous studies with single source call-only stimulus presentation demonstrated a rapid habituation to stimuli, requiring the inter-trial interval to be extended. However in the final study, subjects continued to respond to stimuli after

multiple stimulus presentations in relatively quick succession and over the course of multiple test days. This condition perhaps most closely mimics the natural acoustic environment of the colony while maintaining experimental control. Hearing songs and calls from multiple male sources appears to delay inter-trial habituation and habituation over the course of testing, along with generating the most robust ratio of multiple pulse contact calls to stimuli presented.

Song stimuli may have a slight left ear advantage compared to calls, though this finding would require more individuals to be tested in order to be confirmed. Such a selective advantage may be ethologically relevant due to the social function and complexity of songs, which can uniquely identify individuals. Calls are acoustically similar across individuals, and thus may provide less information socially, therefore requiring or enabling a lesser level of individual recognition. Additionally, the level of stimulation provided by songs—which generally last several seconds—is likely greater than that provided by calls—which last approximately 0.2 seconds. This increased stimulation may result in the increase in calling behavior, or the advantage for one ear over the other may derive from

attentional processes, which are known to modulate REA in human subjects (Hiscock & Kinsbourne, 2011, p. 271).

While stimuli variability seems to enhance calling behavior, white noise appears to be aversive to birds and inhibits calling behavior. The lack of a significant number of multiple-pulse contact calls in the first two studies was worrisome, necessitating the removal of white noise from the stimuli and changing the study design from a dichotic to a monotic task. Study 3 is the most demonstrative of a difference in white noise versus silence condition. Variable stimuli paired with white noise did not generate responses, while removal of white noise from stimuli resulted in an immediate increase in responses, suggesting the effect is due to the lack of noise rather than the inclusion of multiple sources. If white noise discourages calling as it appears to do within these studies, further studies are necessary to find suitable pairs of auditory stimuli for dichotic versus monotic listening.

Future Directions

The primary concern to be addressed in the future is finding a suitable stimulus to replace the white noise component in our initial studies. Although the final condition closely simulated the colony environment, it

lacked the simultaneous stimulus presentation necessary to qualify as a DL task. Additionally, more natural conversational call-response stimuli with multiple calls presented in sequence may have a greater effect on subjects' responses; including female calls as the stimuli may also have an effect on calling behavior. Although it is not necessarily an issue with dichotic listening, the aversive nature of white noise should be explored further. It would be helpful to investigate how white noise affects calling and singing behavior in Bengalese finches or other songbirds.

Having only used female subjects in the current studies, a possible difference in DL performance should be investigated in male Bengalese finches. Given the history of slight sex differences in auditory processing and lateralization, males may exhibit more robust ear advantage due to sexual dimorphism in the vocal processing centers of songbird brains. Additionally, other species of songbirds may be candidates for such experiments, and across species comparisons in left/right ear advantage might be possible.

While the small sample of subjects used in these studies limits the conclusions that can be drawn, the equipment and testing paradigm developed over the course of the investigation are applicable to a much wider range of

studies and subjects. Further modifications of the headphone schematic—such as the inclusion of Bluetooth receivers—may prove helpful in streamlining the headphones and eliminating the need for wiring and tethering. The relative ease of production of miniature custom headphones may also facilitate ease of experimenting using other animal models and improve technology and methodology available for studying auditory feedback models of behavior in other types of experiments.

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