STRATEGIES FOR IMPROVED BIOSONAR PERFORMANCE IN BAT SOCIAL NETWORKS

An Undergraduate Research Scholars Thesis

by

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TABLE OF CONTENTS

Page

ABSTRACT……………………………………………………………………………1

DEDICATION…………………………………………………………………………2

ACKNOWLEDGMENTS…………………………………………………………...3

CHAPTER

I INTRODUCTION……………………………………………………...4

II METHODS…………………………………………………………....10

Animal and Facilities………………………………….…………...…….10
Stimulus…………………………………………………………………..11
Experiment 1: Measuring changes in echolocation emission…………….11
Experiment 2: Measuring changes in sonar navigation performance…….12
Experiment 3: Measuring sonar changes when flying multiple bats……..14

III RESULTS……………………………………………………………...16

Experiment 1……………………………………………………………...16
Experiment 2…………………………………………………………...…18
Experiment 3……………………………………………………………...19

IV DISCUSSION…………………………………….…………………....22

REFERENCES………………………………………………………………….…...28

ABSTRACT

Strategies for Improved Biosonar Performance in Bat Social Networks. (May 2014)

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For decades researchers have wondered how echolocating bats avoid interfering with one other's sonar while flying in dense swarms or in crowded roosts (2). This thesis explores how groups of bats manage this by applying lessons learned from communications theories. Wireless communications networks optimize signaling efficiency by slowing transmission rates during periods of high traffic to minimize interferences among users attempting to transmit simultaneously over a single shared channel (12). It's hypothesized that bats may improve sonar performance by adapting emission rates proportional to population density using similar algorithms. The hypothesis will be tested using playback stimuli mimicking the presence of other bats presented to flying bats performing challenging sonar-guided navigational tasks in solitary versus social contexts. These experiments will characterize those behavioral algorithms, revealing an important adaptation for echolocating in social contexts.

DEDICATION

I dedicate this research to my family, especially my mother and fater, for their unconditional love and support.

ACKNOWLEDGEMENTS

First, I would like to acknowledge Dr. Michael Smotherman for helping me with the thesis, including planning and setting up the experiment. Without his knowledge, expertise, and hours of dedication, this project would not have been possible.

I would like to thank Samantha Trent and Alyssa York for helping me fly and train the bats during the experiments. They spent months helping me, and without their help, the experiments could not have been done.

Lastly, I would like to thank Texas A&M University for allowing us access to Kyle Field where we collected the bats used in the experiments.

CHAPTER I

INTRODUCTION

Bats (order Chiroptera) are one of the most diverse and widely distributed animals in the world, living on every continent except Antarctica. Their wide distribution is most likely due to the fact that they can fly, making them the only mammal capable of true flight (1) which accounts for their diverse feeding and roosting habits (2). Some bats roost collectively with many conspecifics (3,4) while others are solitary and live alone or in small groups (1). Bats will roost just about anywhere they can hide, such as caves, hollow trees, and man-made structures. Free-tailed bats, in particular, are on the far end of the spectrum that forms massive congregations in caves, with numbers reaching the millions (3,4). These bats form clumps in their roost when they are not foraging, and then at dusk the majority of the bats leave the roost to go forage. This may mean that thousands of bats are leaving at the same time in close proximity. Bats' diet is extremely diverse, including insects, fruits, flowers, fish, and small vertebrates. Usually, bats are only placed into two categories: insect-eating bats and fruit-eating bats. Fruit-eating bats tend to be larger, and rely heavily on their vision to find fruit during the day. However, most insect-eating bats are smaller and nocturnal which makes seeing prey difficult. To make up for lack of vision at night, bats have evolved system to "see" by echolocating.

Of the approximately 900 species of bats, about half rely on echolocation for finding prey (1). Echolocating bats perceive their surroundings by emitting ultrasonic pulses several times per

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This thesis follows the format of P*NAS* second and gleaning detailed information from the time-course and characteristics of returning echoes (2) (Figure 1). Echolocation sounds are produced through constraint muscles in the larynx which can be further characterized by frequency, pitch, duration, and intensity (1). The majority of echolocation calls are greater than 20 kHz, making them ultrasonic and beyond the range of human hearing. Bats use echoes from the time-frequency patterns of emitted calls to determine the distance to the target. Through echolocation, the bats can collect information about targets by comparing characteristics of the original signal with the echo. (1) Since many species of bats live in large, dense colonies and forage together at prime hunting grounds, this raises the question about how bats recognize their own echoes from the din of many neighboring bats. Free-tailed bats have been shown to exploit both acoustic and temporal changes in pulse emissions in response to interfering noise.

Free-tailed bats (*Tadarida brasiliensis*) are able to forage and navigate by sonar while flying at speeds exceeding 10 m/sec through cluttered habitats. This guarantees that the bat sonar system has sufficient adaptions to optimize efficient information flow. Some acoustic mechanisms bats use are to call louder (5,6) or changing the spectral bandwidth of their echolocation pulses in a behavior known as jamming avoidance response (JAR) (5,7,8). This strategy reduces interference by making spectrotemporal differences more noticeable among competing users' signals and offers some relief from pulse-echo uncertainties that arise when two or more bats are in the same acoustic space. JAR has been described in both field and lab experiments, but only in the context of pairs of bats responding to one another. Free-tailed bats are limited to the extent at which they can change their pulse acoustics because they are constrained by physiological mechanics needed to produces pulses that are species-specific. Though shifting an entire pulse bandwidth above or below neighboring conspecific call is impractical, free-tailed bats do appear to make subtle changes in the spectrotemporal acoustic features of their pulses. This can be done by shifting the peak of the pulses up or down 2-3 kHz, increasing the duration of the pulses by a few milliseconds, or adding a brief constant-frequency "tag" to the beginning of their pulses (5). These mechanisms can help facilitate recognizing one's echoes from conspecifics but does not truly provide an escape for signal overlap. The free-tailed bat's auditory system is finely tuned to a specific range of pulse acoustics (9). Thus, any drastic changes in pulse bandwidth or duration would shift pulse characteristics away from the optimal acoustic values for being able to detect and interpret faint echoes. Bats may also produce louder pulses when there is interfering noise; however, most bats are already emitting very loud pulses during flight (10) to maximize detection range and target resolution. Both JAR and calling louder provide poor solutions for any but pairs or small groups of bats. JAR and other acoustic manipulations reflect at best one part of a larger strategy for improving sonar performance in even modest group size. As evidence of temporal mechanisms, bats echolocating in small groups may take turns emitting pulses to minimize acoustic overlap in time (11), but again this strategy quickly becomes impractical for groups of more than a few bats. Other more comprehensive answers are needed to explain how bats echolocate in large groups.

It was recently discovered that free-tailed bats delayed the timing of pulse emissions upon hearing the emissions of nearby conspecifics (11). It was hypothesized that this behavior might lead to slower pulse emissions in social settings, but how this would benefit the bats was unclear. Here it's proposed that lessons learned from modern communications networks may explain how slowing pulse emissions can improve a bat's sonar performance when echolocating within a group. Modern communications networks rely upon regulatory protocols constraining when and how often users transmitted their signals over a shared channel (12). One of these, known as the “carrier sense multiple access” protocol (CSMA) is relevant to bats because CSMA incorporated a “listen-before-send” algorithm, in which transmitters first checked to see if the channel is free before transmitting, and if not briefly postpone transmissions, thereby greatly reducing channel traffic load and increasing network utilization and information flow for all users. When bats hear the pulse emissions of conspecifics, they briefly postpone their own emissions. Hence, it’s hypothesized that this behavior serves a function similar to CSMA in wireless communication networks (12), theoretically improving sonar performance in social settings (Figure 1) (16).

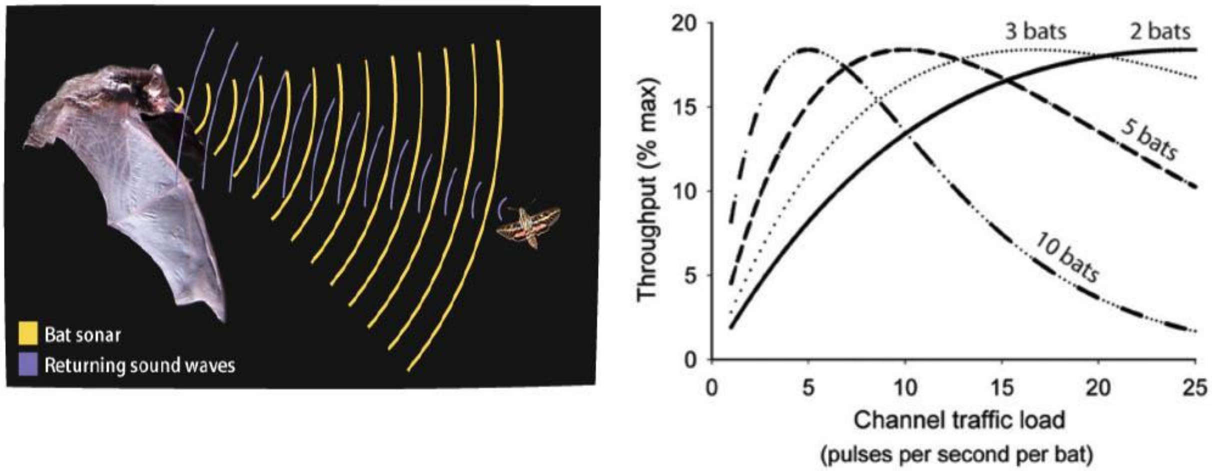

Figure 1. Applying communication network theories to predict how bats will change pulse emission with group size. Echolocation (left) requires that bats are able to recognize their own echoes to navigate. Pulses emitted by other bats create ambiguities by jamming the sonar signal. In wireless communication networks, it is known that the optimum user transmission rates are reduced to accommodate any increases in users sharing a channel. Applying this principle to bats (right) indicates that bats might significantly improve information flow (throughput) by slowing pulse emissions in the presence of other bats.

This experiment tests the hypothesis that echolocating bats optimize sonar performance by slowing their pulse emission rates proportional to population density. We have already shown that crawling bats slow pulse emissions in proportional to increasing population density, which leads us to think that by reducing emission rates bats can cooperatively improve the sonar at the group level. Theoretically, flying bats have as much if not more to gain from this proposed mechanism. I hypothesize that bats performing a sonar-guided navigational task will emit fewer pulses per second flying in groups than when alone, and the change in pulse emission rate will be proportional to group size. In addition, reduced pulse emission rates used in social settings improve sonar-based navigational performance, but only if the mean pulse emission rates of all bats are reduced.

To test our hypothesis, we must first demonstrate that flying bats reduce emission rates in the presence of other bats and that this behavior improves sonar guided navigation performance. To answer the proposed question, we will first measure context-dependent changes in pulse emission rates using real and simulated groups. In the real groups, bats will be flown back and forth in a 6-meter long tunnel while mean pulse emission rates are recorded. This will be done under two conditions: an open condition (no obstacles) and a maze condition in which bats must navigate through a 6x4 matrix of loosely hanging ropes. In the simulated groups, solitary bats will be flown through the tunnel (in open and maze conditions) while hearing playback simulating the emissions of one or two additional bats flying through the maze. To measure changes in sonar navigation performance, we will measure how many ropes are hit in the maze by a bat under three conditions: no stimuli, free-running playback, and interactively slowed playback. Using this method allows us to tell if the navigation performance is weakened by interference from other bats and improved by reducing mean pulse emission rates across the group.

I predict that bats will have faster pulse emission rates when flying through the maze than flying under open conditions. In contrast, while flying in groups or when there is playback simulation imitating bats, I predict the bats to slow down their pulse emission rates. Lastly, I predict that when flying through the maze, the navigational performance will be significantly degraded by free-running playback but significantly less degraded when playback is slowed in a naturalistic interactive pattern. These results will either confirm or refute the hypothesis that bats have a strategy to cooperatively improve their sonar performance when flying in groups.

CHAPTER II

METHODS

Animals and Facilities

The Texas A&M campus is home to over 250,000 wild free-tailed bats (*Tadarida brasiliensis*) living in the cracks and crevices of buildings, stadiums and parking garages. The animals used in the study were wild-caught but housed in our custom-built 5x10 meter bat vivarium. Animals were trained to listen for an acoustic cue (an artificial acoustic stimulus mimicking the *Tadarida brasiliensis* directive call (13, 14) that triggers them to fly between two platforms at opposite ends of a 6-meter long flight tunnel in exchange for a food reward. The tunnel was fully equipped with all necessary acoustic hardware and software. Within this flight test zone emission patterns were highly consistent across bats and trials. For analytical purposes, only the pulses emitted within the test zone were included in the analysis. During all experiments two people were in the room at opposite ends of the tunnel to handle the bats, provide food rewards, and coordinate data collection. The neighboring room housed all computer and acoustic hardware for stimulus presentation and data acquisition. A third person managed the stimulus and data acquisition from this room during the experiments. The setup relied on two PCs with two 16-channel A/D data acquisitions and two 2-channel playback systems. Auditory stimuli were constructed on a PC using TDT® OpenEx software and generated using the TDT RX6 real-time processor fed into a commercial amplifier.

Stimulus

The stimulus was an artificially constructed echolocation pulse that had 50-20 kHz range over 5 ms. There were three different conditions the bats were tested under 1) control: no stimulus 2) 14 pulses per second stimulus representing a bat flying through an open field and 3) 40 pulses per second stimulus representing a bat flying through a maze condition. The order in which each subject encountered each stimulus was random. The microphone was calibrated for gain and frequency response by playing the artificial stimulus from a calibrated speaker placed at fixed position relative to the microphone and normalizing signal amplitudes. Signals were amplified by a custom preamplifier circuit, bandpass filtered, and the waveform envelope extracted by analog circuits before being digitized at 48 kHz.

Experiment 1: Measuring changes in echolocation emission

Individual Flight

First, a solitary bat was flown back and forth in the tunnel and mean pulse emission rates were recorded. This was done in two conditions: an open condition (no obstacles) and in a maze (Figure 2) condition, in which the bats must navigate a maze comprised of a 6x5 matrix of loosely hanging light-weight 1/8” nylon ropes serving as obstacles (similar to Petrites et al., 2009) (15). Flying bats normally avoid the ropes but may make sporadic contact via light wing touches that do not cause injury or impede flight. Pulse emissions were recorded using a centrally positioned Avisoft® CM16 ultrasonic condenser microphone in the maze. Mean emission rates and temporal patterns were quantified from 20 flights per condition per bat (n=20 bats). Both mean pulse emission rates and individualized emission rates were obtained from the microphone array data. To optimize the spatial parameters of the maze (numbers of columns and rows) and establish upper and lower limits of pulse emission rates we tested bats in a variety of different maze configurations of varying rope numbers and densities.

Stimulated Groups

Solitary bats were flown through the tunnel (open and maze condition) while hearing playback simulating the emissions of 1-2 additional bats also flying through the maze. Playback output was digitally subtracted from audio recordings to facilitate extraction of the target bat's emission rates and patterns. Any changes in typical flight paths and speed through the maze triggered by hearing the playback stimuli were also assessed.

Experiment 2: Measuring changes in sonar navigation performance

To measure sonar-guided navigational performance the bats' ability to navigate the rope maze in the tunnel was quantified using custom-built vibration sensors attached to the bottoms of the ropes. The sensors weigh 3 grams and are heavy enough to stabilize the ropes but do not add enough weight to impede flight when the bats wings make contact. The rope maze consists of 6x5 evenly spaced rows and columns separated by 20 cm (Figure 2). Each time the bat made contact with a rope, an event was registered and the mean number of contacts per flight was used to quantify sonar navigational performance. The shape and size of the maze is critical to defining the resolution of this behavioral assay. In general, the more ropes the bat must pass through on each flight, the more sensitive the assay will be. A 2x5 array was sufficient to demonstrate an increase in navigational errors (hit rates) in the presence of interfering stimuli, but insufficient to discriminate amongst the relative impact of different stimuli. A 4x5 array was sufficient to distinguish the graded effects of different stimulus types and rates on navigation performance but required sample rates of >40 flights per bat per condition (10 bats). A 6x5 array provided finer resolution of graded stimulus effects and only required 20 flights per bat per condition (10 bats) to reveal a statistically significant effect.

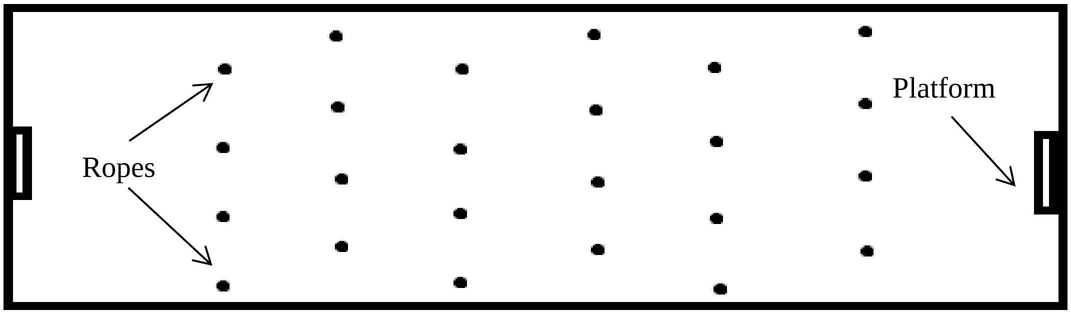

Figure 2. Top view of testing chamber.

In this experiment, the vocal presence of other bats was mimicked using an array of independently controlled ultrasonic speakers positioned in and around the maze. We measured how the sounds of other bats simultaneously traversing the maze impacted how often the target bats made contact with the ropes. Using real groups is impractical because of difficulties tracking which bat hit which rope. In the first series of experiments, flying bats were exposed to playback mimicking pulses repeated at static intervals corresponding to emission rates typical of solitary bats flying through the maze in the silent condition. Each speaker was independently controlled and activating additional speakers simulated increasing numbers of bats. The temporal relationship amongst speakers was varied pseudorandomly so as to mimic as nearly as possible the sounds of multiple independent bats entering the maze from different angles, including transversely, parallel to, and in the opposite direction of the target bat.

Each bat’s navigational performances through the maze were compared across two conditions: 1) no stimuli and 2) free-running playback. It was predicted that navigational performance would be significantly degraded by free-running playback. All results were analyzed for statistically significant differences using appropriate one- and two-way analysis of variance methods and non-parametric t-tests as in Jarvis et al. (2013) (16).

Experiment 3: Measuring sonar changes when flying multiple bats

Training for Group Flight

Three bats that showed a strong preference for being hand-fed were trained to fly from one end of the flight tunnel to the other in response to an acoustic cue. After three months of training, the bats would sit on a platform on one side of the flight tunnel. When they heard the tap of a food bowl, they stopped moving, turned around, and faced the trainers. We would then move to the opposite side of the flight tunnel, where we would play a pre-recorded naturalistic food begging call from a hand-held speaker. This stimulus mimicked the sound baby bats use when begging for food from their mothers. When the call was played, the bats would fly side-by-side across the flight tunnel and land simultaneously on the opposite platform where they would be rewarded with food.

Recording of Group Flight

Groups of two bats (n=3) where flown together in the flight tunnel without the maze. Each group flew side by side for a total of ten times in each trial per pair. Mean pulse emission rates and individualized emission rates were obtained from the centrally positioned Avisoft® CM16 ultrasonic condenser microphone.

Control: Robotic Bat

A robotic bat was built to grossly mimic the flight patterns but not the echolocation behavior of a bat. It was tethered to hang 1 meter from the ceiling in the center of the tunnel, and its motorized wing beats caused it to fly in a circular motion around the room. Thus, it flew in a circular pattern directly in line with the trained bats normal flight path but did not echolocate. We flew two bats (n=2) in the presence of the robotic bat ten times each. Mean pulse emission rates were obtained from microphone array data from the centrally positioned Avisoft® CM16 ultrasonic condenser microphone and analyzed.

CHAPTER III

RESULTS

Experiment 1

It took the average bat less than one second (n=10 bats, 0.93±0.02 seconds) to fly through the test zone in the open condition, and 1.25±0.42 seconds to fly the same distance through the maze. Solitary bats flying unobstructed through the tunnel emit evenly timed pulses (Figure 3A) at an average rate of 14.4±0.4 pulses per second (n=10 bats, 20 flights per bat). The same bats flying through the maze elevated their pulse emission rates by three-fold, up to 42.8±0.8 pulses per second. The increase in pulse emissions is achieved by emitting pulses in bursts or "strobe groups" (17) of 2-4 pulses per grouping (Figure 3C) similar to big brown bats (15). When bats flew through the open tunnel in the presence of an acoustic stimulus mimicking the sounds of one additional bat, they lowered their mean pulse emission rates by roughly 15% to 12.2±0.4 pulses per second (n=10 bats, $P<0.01$). Solitary bats flying through the maze in the presence of the playback stimulus mimicking a single bat also slowed their emission rates by approximately 15% down to 36.8±0.8 pulses per second (n=10 bats, $P<0.01$) (Figure 4A).

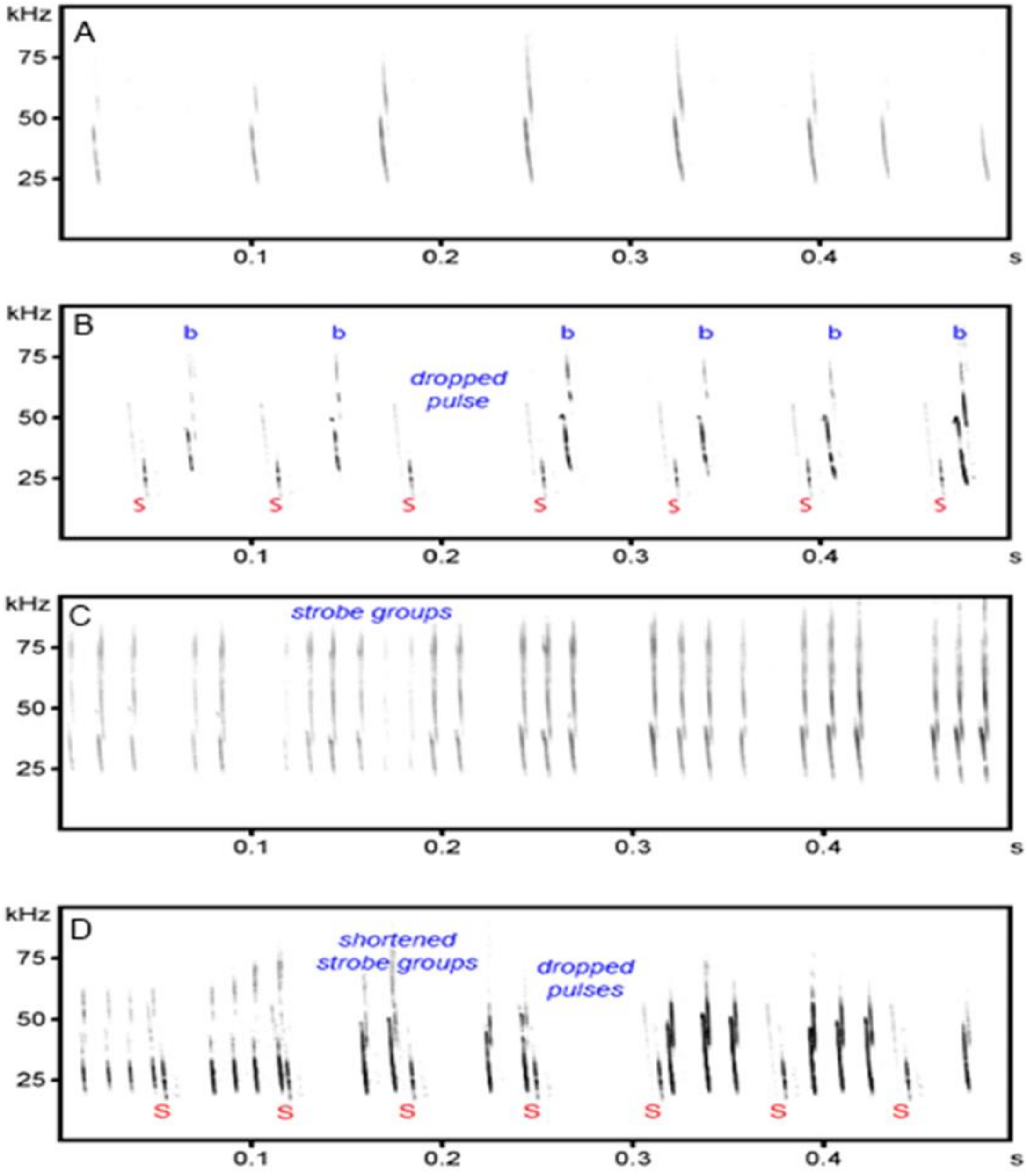

Figure 3. Spectrograms of pulse trains emitted during flight through the open tunnel (A, B) and maze (C,D), in silence (A,C) and while hearing the echo mimic stimulus (B,D). In B and D the stimulus is visible in the spectrogram and demarcated with an S. The bat's own pulses are denoted with a "b". Comparing A and C illustrates how the bats switch from emitting an even series of single pulses to strobe groups when faced with the more challenging task of navigating the maze. B illustrates a typical example of how the bats drop single pulses in a probabilistic fashion when hearing the stimulus and D illustrates how pulse groups may be shortened or dropped in the presence of the acoustic stimulus.

Experiment 2

Trials with 10 bats flying through a 4x5 matrix (20 trials per bat per condition) confirmed that they made contact with the ropes significantly more frequently per trial when exposed to free-running playback (2.3±0.2 hits per flight) than when flying in the silent condition (1.1±0.1 hits per flight; $p<0.01$) (Figure 4B). Increasing stimulus repetition rate from 15 to 40 pulse mimics per second significantly increased the mean hit rate to 2.9±0.2 hits/flight in the 4x5 maze. Expanding the maze to 6x5 gave better resolution of this effect: the hit rate in silence was 1.85± 0.20, in response to the 15 Hz stimuli it was elevated to 4.0±0.25, and at 40 Hz the mean hit rate was 4.8±0.4. All results were significantly different from one another at or below $p\leq0.01$. Power analyses (one-tailed test, 80% power, $\alpha=0.05$) indicated that with a 6x5 maze we can discriminate a mean change of less than 0.3 hits per flight with n=10 bats (20 flights/bat/condition). An increase in stimulus rate from 15 to 40 Hz caused a mean change of 0.8 hits/flight. Thus, with the 6x5 maze we were able to clearly discriminate graded changes in sonar performance and detect whether or not changing playback emission rates in a naturalistic manner produced any significant differences in sonar navigation performance.

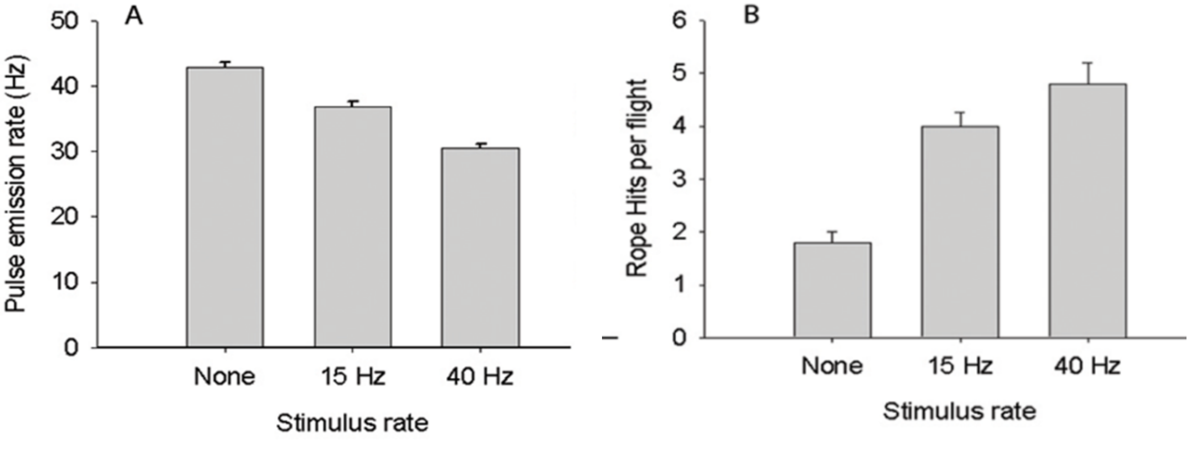

Figure 4. Effect of playback on pulse emission rate (A) and maze performance (B). Playback was a downward FM sweep similar to a normal echolocation pulse. All changes significant ($P<0.01$, n=10 with 10 flights per bat).

Experiment 3

Trials with four groups of pairs showed that bats flying alongside each other produce slightly less pulse emissions than their full potential of 42.8±0.8 pulses per second as shown when single bats fly through the maze. For each trial, the recordings of the pulse emissions were analyzed by selecting the 500 ms time-windows entered on the loudest pulse recorded indicating when the bats were directly above the microphone in the center of the maze. The total number of echolocation pulses was then multiplied by two to convert emission rate to hertz (pulses per second). Over 5 trials with each of the four groups, the average emission rate was 32.9±0.9 Hz (Figure 5). This number is the average number of emissions each bat produces in one second flying side-by-side with a conspecific. To show that the bats' emissions were suppressed relative to what they would do in the absence of hearing another bats emissions, bats were recorded while flying with the robotic bat (n=2, 10 flights under both conditions). When flying with the robotic bat, the bats emitted pulses at their maximum rate of emission (Figure 6). Thus, the bats in real pairs showed increase pulse rates similar to their response when avoiding obstacles. The acoustic recordings revealed that they emitted fewer pulses in an erratic pattern similar to their response to hearing an acoustic stimulus. Together these results show that flying bats appear to be suppressing each other's emissions even when performing challenging navigational tasks.

Upon examination of the spectrograms of two bats flying together, it is observed that the bats either drop groups of pulses or shortened strobe groups (Figure 7), similar to the dropped pulses we observed in the presence of the artificial stimulus in an open tunnel (Figure 3B). This may be the underlying mechanism. Although it was not always possible to segregate each bats unique series of pulses during flights of pairs of bats, the records indicate that both bats were sporadically dropping pulses. Based on this we speculated that mutual interferences occur, causing both bats to drop pulses at the same time, although we cannot yet exclude the possibility that bats differ in their sensitivity to acoustic suppressions (i.e. there may be dominant and submissive bats).

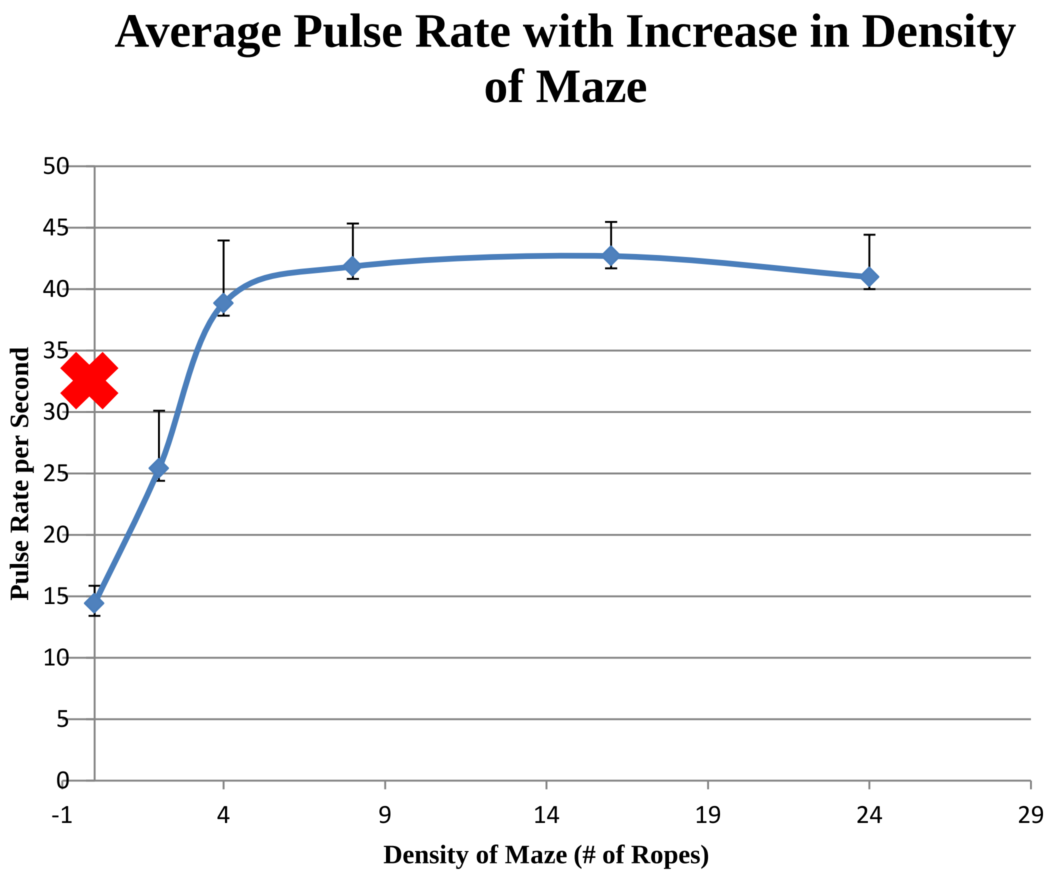

Figure 5. Effect of maze density on pulse emission rates. Increasing the number of ropes in the maze caused bats to increase their pulse emissions up to a stable maximum of about 42 pulses per second. Bats also increase their pulse emission rates in the presence of other bats but not as high as maximum value (represented by the red X).

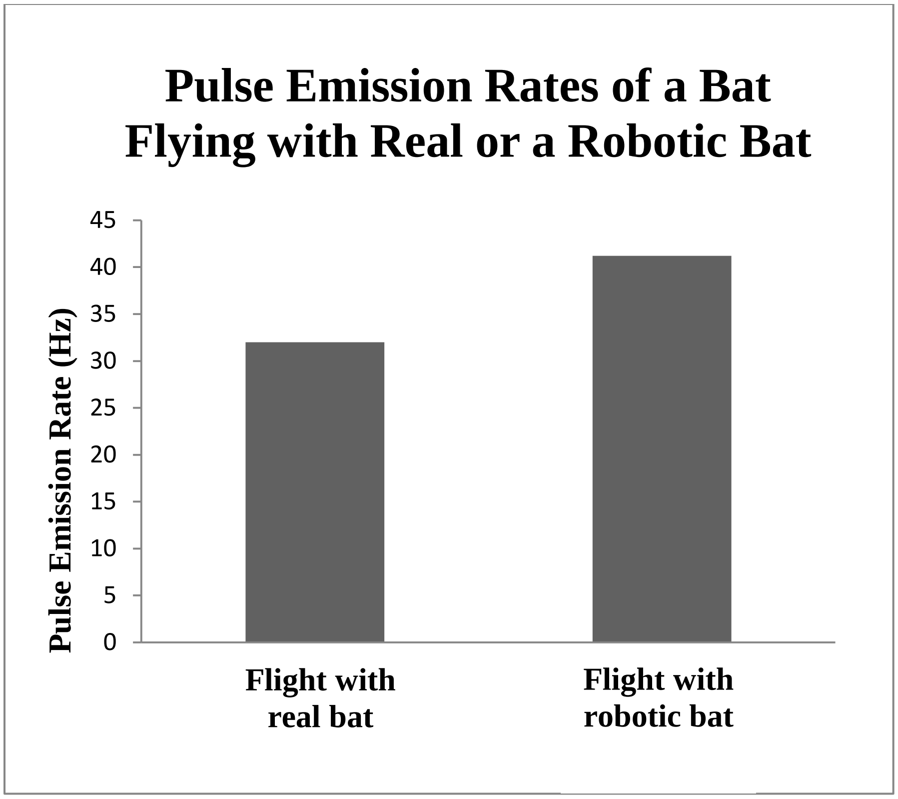

Figure 6. By flying a bat along with a non-echolocating robotic bat, it was found the bat responds to the robotic bat (and other bats) as obstacles, raising their pulse emission to the maximum rate of 42 Hz (n=2 bats flying ten flights under both conditions). However, they raised pulse emissions to a lower maximum when flying with a real bat relative to the robotic bat.

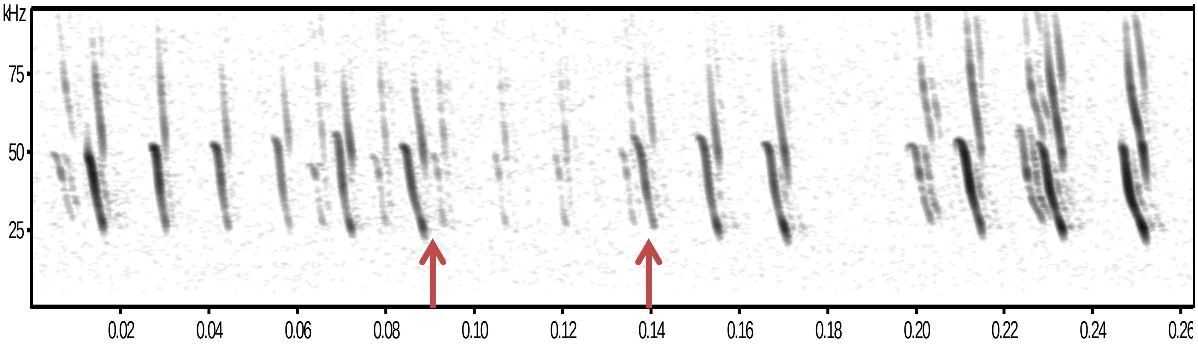

Figure 7. Example of two bats flying together. Here we can see where the sounds of one bat are interrupted by another bat's regular pattern of pulse emissions. It is also reasonable to interpret that at the time 0.18, the other bat was mutually interrupted. Thus, this figure may illustrate "mutual interferences".

CHAPTER IV

DISCUSSION

Echolocating bats forage and navigate by emitting sonar pulses, and the size and distance of obstacles and prey are revealed by the time course and patterns of returning echoes. Since many bats live in large, dense colonies and forage together at prime hunting grounds, a long-standing question has been how can many bats echolocate in the same space without interfering with one another's' sonar? We recently discovered that free-tailed bats delayed the timing of pulse emissions upon hearing the emissions of nearby conspecifics (16) but how this benefited the bats was unclear. Here it is hypothesized that this behavior leads to slower pulse emissions in social settings, which improves the average sonar performance for all bats in the group. Our hypothesis is based upon similar observations in wireless computer networks (Figure 1), where it is known that when many users share the same communication channel, overall information flow can be optimized by restricting when and how often each user transmits their signals.

To test this hypothesis, this project measured the pulse emissions and navigational performance of bats alone versus in pairs or groups while performing a challenging navigational task. We used loudspeakers to mimic the sounds of other bats and were thereby able measure precisely how bats adjusted their own emissions when hearing those of other bats. Echolocation reflects the integration of many competing influences; higher pulse emission rates improve temporal resolution of the sonar system which is important when the bat is performing more demanding navigational tasks such as flying in cluttered spaces, but higher emission rates also increase the problem of mutual interference for bats, which might best be mitigated by emitting fewer pulses. The three experiments outlined in this thesis allowed us to see how bats balanced these competing motivations and successfully revealed that bats modify the timing of their echolocation pulses in the presence of conspecifics. If all bats in a swarm echolocated at their maximum rate, it would be hard to distinguish one's echoes from another's which could cause confusion and decrease in navigational abilities. The experiments not only showed that bats suppress their emission rate in the presence of conspecifics, but also how they suppress their emissions.

In bats it is known that there is a tight mechanical correlation between wing beat rhythm and the respiratory cycle, and pulses are emitted only during the expiratory phase of the wing beat cycle (19). It is not known whether bats alter wing beat rate to change pulse emission rate, or if instead they alter the number of pulses per wing beat. As shown in the first experiment, as the navigational task became more challenging, they increased echolocation rate up to a maximum of about 42 pulses per second (Figure 5) by adding pulses to each wing beat while at the same time flying more slowly through the maze. This confirms that bats use changes in the number pulses per wing beat rather than adjusting the wing and respiratory cycle duration to alter pulse emission rate. For our experiments, we observed a wing beat rate of about 10 per second and an average of roughly four pulses per wing beat. After the bat reaches it maximum emission rate, no matter how many more obstacles are present, they continued to only produce 42 pulses per second in the absence of conspecifics and stimuli. These measurements provide a reliable measure of the overall range of emission rates and clarifies the relationship between emission rate and sonar task. Based on this, we could show that playback of an artificial acoustic stimulus suppressed pulse emissions by forcing bats to emit fewer pulses per wing beat (Figure 4A).

It was also shown that the bat's navigational performance suffered proportional to stimulus repetition rate. More ropes were hit on average as the repetition rate increased (Figure 4B). It is hypothesized that if all the bats in a group reduced their pulse emission rates, then all bats would see a modest improvement in their sonar performance. This was not tested directly, but Figure 4B clearly indicates that the average reductions in pulse emission rates exhibited by bats (Figure 4A) are of sufficient magnitude to generate a measureable improvement in sonar navigation.

By flying two bats side-by-side, we were able to confirm that the bats responded similarly to real and artificial stimuli. Two key observations were made. First, we learned that bats view their conspecifics as major obstacles, which makes it very unlikely that pairs or groups of bats are cooperatively gleaning information from each other's echoes. Bats flying together in an open tunnel emitted many more pulses per second than when alone indicating that the movements of the other bat elicited a behavioral response consistent with a challenging navigational task. Secondly, we observed that conspecifics' pulse emissions cause suppression of a bat's own pulse emissions (Figure 6). Bats flying alongside each other in an open tunnel emitted roughly 25% fewer pulses than their maximum emission rate allows. To show that the suppression of a bat's pulses was due to the conspecific's pulse emissions, we created a robotic bat that flew but did not echolocate. Bats responded to the robotic bat by calling at their maximum rate, providing evidence that the real bats suppressed pulse emissions via the added presence of natural pulse emissions.

Now that we know that bats suppress their emissions in the presence of conspecifics, we can now address physiological mechanism by which emissions were altered by examining the spectrograms of their echolocation under the various conditions. Bats in the open tunnel slowed their mean pulse emissions not by increasing the mean inter-pulse interval but rather by sporadically omitting single pulses that led to an irregular overall emission pattern (Figure 3B). Bats flying through the maze sporadically omitted entire strobe groups and/or reduced the number or pulses per strobe group (Figure 3D). We saw no evidence that the bats were cooperatively calling out of phase with one another or attempting to predict when the other bat would call. Instead, by dropping random pulses in a probabilistic fashion the bats may have been able to reduce overall inference rates in an ongoing fashion rather than acutely, in a moment by moment fashion. In this way, the bats appear to be using strategies similar to computer networking protocols, where users are forced to slow down their transmissions as the number of users sharing the network increases.

Here we showed that, similar to a behavior recently reported in big brown bats (15), free-tailed bats increase pulse emissions in response to navigational challenges. However, they slow their pulse emissions when echolocating in groups and when hearing artificial pulses. The results confirm that increasing playback repetition rate increasingly degraded sonar performance. This constitutes the first demonstration that echolocating bats significantly degrade one another's sonar performance. This led to the hypothesis that free-tailed bats cooperatively adjust emission rates and patterns to optimize their own performance in a network context: by calling less frequently they minimize mutual interference. This behavior differs from other animal models, such as chorusing frogs and birds, in that rather than focus attention on just one or two neighbors, free-tailed bats follow a probabilistic algorithm that is better suited to accommodate the random activities of many nearby animals. If so, this would represent a significant expansion of current models of animal communication networks. Decoding the bats social sonar algorithms provides a biologically-inspired model of a fast, efficient and stable networking protocol that can improve emerging technologies such as autonomous sensor networks.

Whether all echolocating bats exhibit this behavior is unknown. Not all bats are equally social, so it is possible that solitary species of bats may not slow down pulse emission to improve performance since they do not live or forage with conspecifics (18). This behavior may be more important for bats that live in dense groups such as the free-tailed bats who live in colonies with numbers in the millions (3,4). Whether this behavior is beneficial could also depend on type of pulse produced or the type of habitat the bat forages in. Free-tailed bats emit short broadband sweeps typical of many aerial hawking bats, but there are others like horseshoe bats and mustached bats that emit long constant-frequency pulses, and these biosonar systems are thought to be less sensitive to overlapping temporal interferences. It is therefore possible that bats with different pulse types or live in specific habitats may not gain the same advantage for decreasing pulse rates like the free-tailed bats. It may also be true that this behavior exists in different forms in different species, much like how different types of artificial communication networks utilize different user access protocols.

In conclusion, these experiments revealed that bats slow their pulse emissions when echolocating in groups following strategy similar to ones commonly used to coordinate users sharing computer networks. These results provide the first cohesive explanation for how groups of bats adapt their echolocation behavior to accommodate the emissions of their neighbors. Future experiments will explore details about how similar the bat’s behavioral algorithm is to the ones currently used in artificial communication networks.

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