ABSTRACT

Title of Dissertation: ADAPTIVE ECHOLOCATION AND FLIGHT BEHAVIORS IN FREE-FLYING BATS, *EPTESICUS FUSCUS*

Chen Chiu, Doctor of Philosophy, 2008

Dissertation directed by: Professor Cynthia F. Moss
Neuroscience and Cognitive Science Program

Echolocating bats emit ultrasonic sonar pulses and listen to returning echoes, which are reflected from targets or obstacles, to probe their surroundings. Their biological sonar system is well-developed and highly adaptive to the dynamic acoustic environment. Bats are also agile flyers and they can modify their flight behavior in order to capture insects efficiently. Adaptable echolocation and flight behaviors evolved in bats in response to environmental demands. This study employed changes in the external ear of bats and in the acoustic environment to examine how the big brown bat, *Eptesicus fuscus*, modifies its echolocation call design and flight patterns to cope with these new experimental conditions.

Study one investigated the influences of changes in sound localization cues on prey capture behavior. The tragus, which is part of the external ear, is believed to contribute to sound localization in the vertical plane. Deflecting the tragus affected prey capture performance of the bat, but it adapted to this manipulation by adjusting its flight behavior. The tragus-deflected bat tended to attack the prey item from above and show lower tangential velocity and larger bearing from the side, compared with its flight pattern in the tragus intact conditions. The bat did not change its echolocation call design in the tragus-deflected condition.

Study two paired two bats together and allowed them to perform a prey capture task in a large flight room. Echolocating bats showed two adaptive strategies in their echolocation behavior when flying with another conspecific. The bat either stopped vocalizing or increased its difference in call design from the other bat. In addition, one bat tended to follow another bat when flying together and antagonistic behavior was found in male-male and female-male pairs. The pursuit strategy the bat uses to track another bat is different from the strategy it uses to capture flying insects.

This thesis confirms that the big brown bat’s echolocation and flight behaviors are highly adaptable and describes several strategies the bat employs to cope with changes in sound localization cues and conspecific interference.

ADAPTIVE ECHOLOCATION AND FLIGHT BEHAVIORS IN FREE FLYING BATS, *EPTESICUS FUSCUS*

By

Chen Chiu

Dissertation submitted to the Faculty of the Graduate School of the
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Advisory Committee:
Professor Cynthia F. Moss, Chair
Professor Robert J. Dooling
Professor P. S. Krishnaprasad
Professor Jonathan Z. Simon
Professor Gerald S. Wilkinson

DEDICATION

This work is dedicated to my dear husband, Houng Li,

who can always see the best of me.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1: Introduction

Animals exhibit the plasticity in their behaviors to adapt to environmental changes. Adaptive behavior is important for the survival of animals because the environment in changes constantly, and they need to adjust their behaviors to optimize their chances of success in foraging, breeding and avoiding predators. Human subjects adjust their movement when wearing prisms that distort their vision (Shratton 1896; 1897a; 1897b), and learn to track sound sources precisely when wearing ear molds that modify features of incoming sound waves (Van Wanrooij and Van Opstal, 2005). A prey animal changes its flight path to avoid being captured by predator, while a predator also modifies its chasing strategy in order to catch its prey. Adaptive behaviors occur widely in the daily life of almost all human and other animal species. Echolocating bats are chosen in this thesis as subjects to investigate adaptation in their echolocation and flight behaviors because of their well-developed and highly adaptive aerial biosonar system (Haykin, 2006).

Ever since Griffin (1958) discovered that some bats produce high frequency sonar pulses and listen to the returning echoes for orientation, prey localization and obstacle avoidance, scientists have been intrigued by these nocturnal creatures and continue to be amazed by their echolocation performance in darkness. Thanks to advances in modern technology, people can now easily record the high frequency vocalizations generated by echolocating bats and analyze them to investigate how bats track their prey's location in space, discriminate its texture, and avoid signal interference from conspecifics/heterospecifics by producing sonar pulses with various call features and processing returning echoes.

Echolocating bats are excellent animal models for studying hearing because they rely predominantly on their biological sonar for orientation, foraging and acoustic communication. The ability to track and locate sources of returning echoes, which are reflected from objects, makes bats excellent subjects for spatial hearing research. Spatial hearing studies investigate how a subject determines the position of a sound source using different acoustic cues, such as interaural differences in intensity, arrival time or spectral features. In addition, bats are good subjects for auditory scene analysis because they can echolocate efficiently in a complex acoustic environment. Auditory scene analysis research explores how a subject segments, integrates and segregates signals of interest in order to extract information about auditory objects.

Furthermore, echolocating bats are the only flying mammals, and they can serve as excellent subjects for studies of flight behavior. Flight behavior is as adaptable as echolocation behavior in bats. For example, the bat alters its flight path to track and intercept its prey, when chased by a predator, or to avoid colliding with obstacles. Understanding bat flight behavior during predator-prey interaction, insect pursuit and attack strategies and plasticity of flight patterns, as well as echolocation, contributes to our broad knowledge of auditory-guided behavior.

1.1 Echolocation Behavior

Echolocation is a form of active sensing, which bats use to explore their surroundings, track prey, avoid obstacles and interact with conspecifics (Nelson and MacIver, 2006). Animals that rely on active sensing include electric fish, dolphins, whales and echolocating bats. Weakly electric fish generate an electric field with an electric discharge organ, typically located in the tail, to detect prey objects and the presence of conspecifics through modifications in the electric field. Electric fish can be categorized into two types, wave-type and pulse-type, according to their electric organ discharge (EOD). Wave-type electric fish produce signals with long duration and short pauses between each electric discharge, while pulse-type electric fish generate short duration EOD and with long pauses between each pulse (Heiligenberg, 1991). Odontocetes (dolphins, porpoises, sperm whales, killer whales, etc.) produce ultrasonic clicks underwater and use returning echoes to determine the position and material of objects. The sound production mechanism of cetaceans has not been fully understood yet, but it is generally believed that the echolocation signals are generated from the nasal complex above the skull and are projected through the melon (the fatty tissues in the forehead) into the water (Cranford and Amundin, 2004).

Megachiroptera and Microchiroptera are two suborders of bats but only microchiroptera bats use sonar vocalizations for orientation and prey capture. Megachiropteran bats, also known as flying foxes, use vision instead of echolocation for navigation and foraging. One genus of Megachiropteran bats, *Rousettus,* uses tongue clicks for echolocation (Holland et al., 2004). All Microchiroptera bats orient by echolocation and they can be roughly divided into two groups according to their echolocation call structures, either constant- frequency (CF) or frequency-modulated (FM). All data collection and discussion in this thesis will focus on Microchiropteran bats which generate FM vocal signals.

This section will introduce the echolocation behavior of bats and parameters used to describe echolocation call design. The sound localization section summarizes possible cues for the bat to perceive the three-dimensional position of an object. The auditory scene analysis section reviews past studies about how an animal may segregate signals of interest from a complex acoustic environment and avoid signal jamming from conspecifics. The last section will introduce the experimental design briefly and predict experimental results based on previous research about how the bat adjusts its vocalizations to cope with changes in sound localization cues and the presence of conspecifics.

1.1.1 Call design

Inter- and intra-specific variation in call design are common in echolocating bats, and even one individual bat can produce calls with different time-frequency structure which adapt to different behavioral tasks or habitats. Studies of call design variation help us understand how one individual bat adjusts call features to cope with various acoustic environments or how call design of one bat species is adapted to its ecological niche.

Call parameters, which are commonly applied in bat echolocation research, include start/end frequencies, duration, bandwidth, sweep rate and pulse interval. These parameters measure the spectral and temporal features of an echolocation call.

Interspecific variation in echolocation call features can be a consequence of the bat's ecological niche (Jones and Holderied, 2007; Schnitzler et al., 2003; Siemers and Schnitzler, 2004). Low frequency sounds transmit further than high frequency sounds, because of the excess atmospheric attenuation of ultrasonic frequency vocalizations (Lawrence and Simmons, 1982a). A high frequency signal has a shorter wavelength, which reflects well from small insects. Broad bandwidth calls help the bat segregate returning echoes from the cluttered background (Siemers and Schnitzler, 2004). Signals with long duration are well suited for detecting target movement but are more likely to overlap with returning echoes and other individuals' calls. Short pulse intervals are commonly used when the bat prepares for landing or encounters another bat or obstacles. FM bat species that forage in the open space tend to use narrowband shallow sweep calls, while those that fly in dense vegetation produce broadband steep sweep calls (Schaub and Schnitzler, 2007; Schnitzler et al., 2003). Species with broad bandwidth search calls were able to capture prey closer to a clutter screen, which reflected clutter echoes, than those with narrow bandwidth calls (Siemers and Schnitzler, 2004).

Just like each person has his/her unique voice, and people can identify the gender and individual merely from listening to his/her speech, echolocating bats who generate FM signals show intraspecific variation in calls and have the same ability to identify other individuals by their vocalizations (Kazial et al., 2001; Kazial et al., 2008; Masters et al., 1995). Juvenile bats show different call design in their isolation calls, and mother bats are capable of discriminating these differences in vocalizations (Bohn et al., 2007). Not only do pups show individual signatures in their isolation calls but so do some adult bats. Similar intraspecific differences in call design have also been observed in several bat species (Fenton et al., 2004; Kazial et al., 2001; Kössl et al., 1999; Masters et al., 1995; Mora et al., 2005; Pearl and Fenton, 1996), with few exceptions (Siemers et al., 2005; Siemers and Kerth, 2006).

Many external factors, such as obstacles, prey, conspecifics and heterospecifics, can influence variation in call design among individuals. A bat's echolocation behavior can be categorized into three phases, approaching, tracking and terminal, when pursuing and attempting to capture prey, and distinct call design characterist are associate with each phase. Research on three pipistrelle bats (*Pipistrellus pipistrellus*, *P. nathusii* and *P. kuhlii*) showed high frequency, long duration and long pulse-interval in the approach phase; while their calls in the terminal phase were low in frequency, short in duration and had short pulse intervals (Kalko, 1995).

The environment in which a bat flies is another factor that can influence call design. Pipistrelle bats (*P. pipistrellus*, *P. nathusii* and *P. kuhlii*) produce narrowband signals when flying in an uncluttered environment and switch to broadband signals when flying in a cluttered environment (Kalko and Schnitzler, 1993). It has also been reported that the big brown bat (*Eptesicus fuscus*) changes the temporal pattern of its echolocation calls to adapt to the cluttered environment (Moss et al., 2006). The presence of conspecifics can also affect call frequency of an individual bat. Past studies have demonstrated that when flying with conspecifics, several species of bats (*E. fuscus*, *Euderma maculatum*, *Lasiurus borealis*, *L. cinereus*, *Tadarida brasiliensis*, *T. teniotis*) shift their call frequencies either upward or downward to avoid possible call interference and overlap with neighboring individuals (Bates et al., 2008; Gillam et al., 2007; Obrist, 1995, Ratcliffe et al., 2004; Ulanovsky et al., 2004).

1.1.2 Sound localization

An echolocating bat probes the environment with its sonar vocalizations which provide stimulus energy for perception, just as light does for vision. The bat uses echo returns to localize an object's 3-D position in space, *i.e.* the elevation, azimuth and range, in order to capture prey successfully. Horizontal sound localization depends on the binaural comparisons of incoming signals (Obrist et al., 1993), such as interaural level differences, while vertical sound localization relies on the spectral cues generated by the external ear (Firzlaff and Schuller, 2003; Fuzessery, 1996; Lawrence and Simmons, 1982b; Wotton and Simmons, 2000). A bat determines the distance between itself and other objects from the time delay between the pulse it produces and the arrival time of returning echoes. Research has shown that the minimum discriminable angle in the horizontal plane is 1.5° (Simmons et al., 1983), in the vertical plane is 3° (Lawrence and Simmons, 1982b) and range difference discrimination is 6-15 mm (Miller, 1991; Surlykke, 1992) in the big brown bat. Recent research findings also suggest horizontal and vertical cues are not dichotomous, and binaural cues are available for high frequency localization in the vertical plane (Aytekin, 2004).

Sound localization in echolocating bats not only includes active echolocation, which means localizing the source of returning sonar echoes, but also passive listening, which refers to tracking sound sources produced in the environment, e.g. by conspecifics or prey in proximity. The bat's azimuthal localization accuracy via active echolocation is higher than passive listening (Koay et al., 1997, 1998; Simmons, 1973). Although self-generated signals are believed to be the dominant mode for active sensing animals to probe the environment, passive sensing could play an important role in orientation and prey capture as well. Electric fish can detect electric fields which are produced by others and align themselves perpendicular to the outside electric fields (Hopkins, 2005). They often use this passive sensing during the encounter of conspecifics or as a stealth strategy to conceal their presence. A bottlenose dolphin (*Tursiops truncatus*) is capable of recognizing an object by only listening to its companion's echolocation calls at a close distance (Xitco and Roitblat, 1996). Rough-toothed dolphins (*Steno bredanensis*) and Hawaiian spinner dolphins (*Stenella longirostris*) that swim in groups can use other individuals' echolocation for navigation (Gotz et al., 2006; Lammers and Au, 2003). Gleaning bats listen to prey-generated sound rather than use echolocation to localize their prey (Page and Ryan, 2005; Russo, 2007). When studying how active sensing animals use their self-generated energy to detect prey and conspecifics, the role of passive sensing is also worth investigating because past research suggests that it can sometimes substitute for active sensing, conceal an animal's movement or avoid signal interference from conspecifics (Heiligenberg, 1991; Moller et al., 1989; Scheffel and Kramer, 1997; Ulanovsky et al., 2005; Werneyer and Kramer, 2002).

1.1.3 Auditory scene analysis

Most animals live in an environment full of other sounds, and they need to separate signals of interest from background noise and the signals of neighboring animals. Auditory scene analysis refers to the processes by which a complex environment is represented. Female frogs are capable of selecting potential mates from multiple vocalizing males in a chorus (Schwartz, 1993). Male frogs separate their calling time to avoid call overlap and interference with the signals of conspecifics (Greenfield and Rand, 2000), and a model was proposed to explain how a male frog in a chorus controls the timing of its sound production to prevent call overlap with conspecifics (Narins, 1992). Mothers of king penguins and bats recognize and retrieve their offspring by listening to their vocalizations, which contain individual signatures in call structure (Aubin and Jouventin, 1998; Balcombe, 1990; Bohn et al., 2007).

Bregman (1990) suggests several cues, such as spectral and temporal separation in a series of auditory signals, which can be used for segregating auditory streams. A series of alternating high frequency sounds tends to be categorized into separate streams if the interval between sounds is appropriately adjusted. Human subjects use frequency and time differences in a series of auditory signals to segregate auditory streams (Carlyon 2004; Darwins et al., 1997; Moore and Gockel, 2002). Signals with small frequency differences tended to be considered as one auditory stream by human subjects more often than those with large frequency separation. Two signals with a short pulse interval are more likely to be viewed as the same auditory stream than those with a long pulse interval. Other animals, such as fish, can segregate two different pulse trains by their differences in spectral features and frequency (Fay, 1998; 2000). Segregating auditory streams and grouping this information to represent an auditory object could potentially allow the bat to minimize the experience of jamming by signals from conspecifics. When flying with other bats, the bat receives echoes reflected from sonar pulses it generates, together with signals emitted from other bats. The bat must recognize echoes reflected from targets, which it intends to track, and segregate this auditory information from other background noise or vocalizations of other bats. Theoretically, the bat could segregate a complex acoustic environment into different auditory streams by recognizing call features of these streams and grouping several echoes with similar call features into one stream (Figure 1.1).

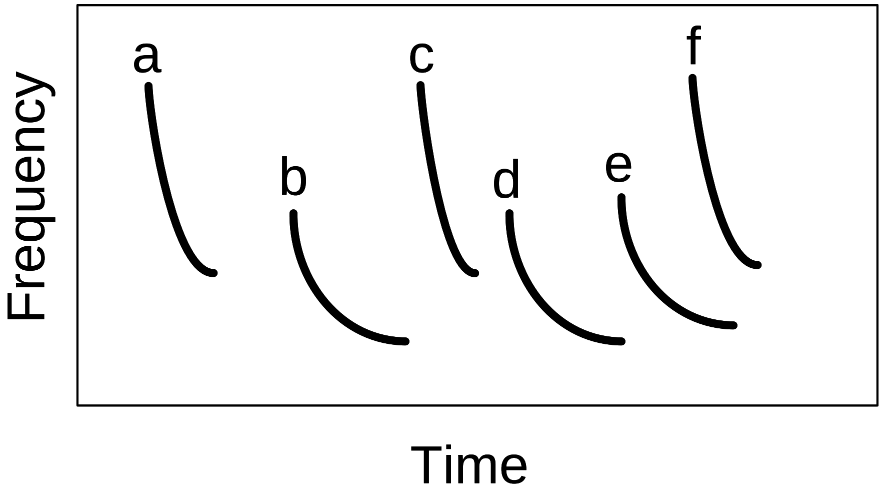

Figure 1.1 Schematic spectrogram of echolocation calls emitted by two different bats. Different letters mark different calls. Calls a, c and f tend to be grouped into the same auditory stream and the other three calls into another stream.

1.1.4 Possible factors influencing echolocation behavior

A bat dynamically adjusts its vocalizations to adapt to a continuously changing environment. In this thesis, two experimental conditions were created to study how big brown bats adjust their echolocation behavior to adapt to these changes. One condition is the modification of the bat's external ear to modify spectral cues the bat uses for sound localization. The other condition is adding another individual into the same room with the bat to investigate how its presence affects the bat's echolocation behavior.

Modifying cues for sound localization has been demonstrated to disrupt the sound localization accuracy in humans (Van Wanrooij and Van Opstal, 2005). However, human subjects also showed that they were able to adapt and localize sound sources correctly with changed cues after a short period of time. Similar manipulations can be introduced to the bat's external ear and used to study how the echolocating bat adjusts to its "new" ear. Deflecting the tragus of the big brown bat disrupted its vertical sound localization accuracy (Wotton and Simmons, 2000). Therefore, it is reasonable to deduce that tragus deflection affects the bat's sound localization, especially in the vertical plane. The bat may modify its echolocation call design, such as bandwidth, duration or pulse interval, to compensate for changes in acoustic information, produced by tragus deflection. Alternatively, the bat may not change its echolocation behavior in response to ear manipulation, but instead adjust other behaviors, such as flight attack angle, to adapt to the new condition.

Insectivorous bats use echolocation to navigate and forage in the wild, and they commonly fly in groups. Therefore, it is important for one bat to avoid interference with another bat's echolocation calls when two or more bats fly and forage in proximity. The prey capture behavior of bats is affected by echolocation calls produced by other bats (Dunning and Roeder, 1965). Acoustic interference experiments on *Noctilio albiventris* (Roverud and Grinnell, 1985a, 1985b) and *Rhinolophus rouxi* (Roverud, 1989) have reported that the distance discrimination ability of these two species was disrupted by artificial signals which were similar to the bat's own sonar vocalizations. The degree of interference is related to the similarity between the artificial signal and the bat's echolocation calls. In addition, the timing of the interference signals relative to echo arrival could affect the bat's ranging ability as well. Previous studies have demonstrated that vocalizations from conspecifics disrupt the bat's prey capture or range determination, and the level of influence depends on the similarity between the interfering signal and the bat's echolocation calls. Ranging ability of *E. fuscus* is impaired by the signal from another bat's emission (Masters and Raver, 1996). Evidence shows that bats adjusted the spectral or temporal features of echolocation calls when foraging in groups (Habersetzer, 1981; Ibáńez et al., 2004; Obrist, 1995; Ratcliffe et al., 2004; Schmidt and Joermann, 1986; Ulanovsky et al., 2004).

Similarity in call design can cause interference between the bat's echolocation calls and the possible adaptations the bat may use in its echolocation behavior may be comparable to another group of active sensing animals, such as weakly electric fish. Jamming avoidance response (JAR) describes weakly electric fish's behavior to modify its self-generated energy to avoid signal interference from conspecifics (Heiligenberg, 1991). Two types of electric fish, wave-type and pulse-type, use different strategies to avoid signal jamming. The wave-type electric fish shifts the discharge frequency away from another conspecific to avoid signal jamming (Kawasaki, 1996; Watanabe and Takeda, 1963; Zakon et al., 2002). The fish with the higher frequency signal shifts its EOD upward and the fish with the lower frequency signal shifts its frequency downward to maximize the difference between their EOD frequencies. The pulse-type electric fish responds to another fish's EOD by increasing or decreasing the pulse interval to reduce the possibility of coincident discharges (Baker, 1980; Capurro et al., 1999; Heiligenberg, 1974; Heiligenberg et al., 1978; Westby, 1979). Although bat echolocation behavior is not as regular and periodic as the organ discharge in electric fish, strategies which the fish adopt in JAR could still be a valuable reference for studying how the bat avoids jamming with conspecifics. Similar modifications in call design when echolocating bats are flying with conspecifics can also be regarded as a strategy to increase differences in call design and improve auditory stream segregation. A possible result of this study is that the bat adjusts its echolocation call design, spectral and/or temporal features, to cope with the complex acoustic environment. The alternative outcome is that the bat does not change its echolocation behavior at all, but instead uses naturally occurring differences between calls from different individuals to avoid call interference.

1.2 Flight Behavior

Echolocating bats are flying animals and some of their flight behaviors may be comparable to other flying animals that use vision rather than audition to guide their flight. How the bat adapts its flight behavior to capture prey with modified external ears or in the presence of a competitor in a large flight room is investigated here. Human subjects show changes in their motor behavior when their vision is distorted by prisms. Bats may exhibit similar modifications in their flight behavior when the sound localization cues are manipulated. Another conspecific may also affect the bat's flight trajectories and its ability to capture prey.

1.2.1 Interaction between two individuals

In the presence of other animals, flight behavior of one animal can be affected in many ways. Behaviors, such as chasing, following, prey capture or escaping, are commonly observed in several animal species. For example, a male fly chases another male to defend its territory and pursues another female for mating. The most common interactions between heterospecifics are predator-prey pursuit. The roles of pursuer and pursuee may be reversed in conspecific pursuit but these roles in heterospecific chases are usually stable.

How one animal tracks, locks on and intercepts a target is an important aspect in pursuit behavior. A male housefly chases another female housefly for mating and the change in its error angle (the angle between the fly's velocity and the vector between it and the target) is linearly related to its angular velocity with a time delay (Land and Collett, 1974). A dragonfly keeps a constant absolute angle, rather than a constant error angle, when approaching its prey (Olberg et al., 2000). The same strategy is used by echolocating bats when pursuing a tethered mealworm (Reddy, 2007) or flying mantis (Ghose et al., 2006). An animal relies on visual, auditory or other sensory cues to track other individuals. For examples, houseflies use visual cues to track others (Wagner, 1986a; 1986b) while echolocating bats use sonar to pursue targets (Ghose and Moss, 2003). A male mosquito tracks and follows the sound of the female's flapping wings (Gibson and Russell, 2006).

1.2.2 Possible factors influence the flight behavior

Left-right or up-down reversal prisms disrupt the visual input of human subjects, but they adapt to the new input by adjusting their motor control after a period of practice (Stratton, 1896; 1897a; 1897b). Sound localization cue changes may induce similar adaptive behavior in echolocating bats. For example, although the bat may miss a direct attack on the target, but following external ear manipulation, it may manage to acquire the correct position of the target through its tactile sense or olfaction. Upon subsequent approaches to a prey item, the bat may adjust its flight trajectory to compensate for its estimate of target location and intercept the prey successfully. Modifications in flight behavior, especially prey capture behavior, are expected following manipulation of the bat's external ear. The alternative result is that the bat does not change its flight behavior but changes its sonar call features to adapt to the modification of its external ears. A combination of these two strategies is also possible.

The presence of another conspecific can alter a bat's flight path; however, such adaptive behavior in echolocating bats has not been previously explored. Big brown bats use a constant absolute target direction (CATD) strategy to pursue prey (Ghose et al., 2006; Reddy, 2007), but whether they use the same strategy to interact with conspecifics is a question under study in this thesis. Other pursuit strategies will also be examined here to determine which strategy the bat may use when interacting with conspecifics. Limiting the food source may increase the competition between two bats and force them to adjust their flight behaviors to access a single prey item in the shortest time. Pursuit behavior and some aggressive behaviors are expected to be seen in paired foraging bats because of the competitive environment. The predicted result is that the bat employs the same pursuit strategy (CATD) it uses to chase its prey when interacting with conspecifics. However, other pursuit strategies, such as classical pursuit (CP) or instantaneous optimal bearing (IOB), may be employed by bats due to the difference in behavioral tasks.

1.3 Adaptive Biosonar System and Flight Control

1.3.1 Research questions

Microchiropteran bats produce ultrasound and use returning echoes to localize targets and to navigate in space. The echolocation behavior of the bat engaged in prey capture is composed of three phases: approach, track and terminal, and these phases are characterized by time-frequency parameters of individual signals and by pulse intervals (Simmons, 1989). Changes in these call parameters as the bat detects, localizes, approaches and captures insect prey reflect a dynamic and adaptive biological sonar imaging system.

The echo information received and processed by the bat is ever changing as it flies, and the sensorimotor feedback system that is integral to bat echolocation supports both obstacle avoidance and prey capture. This study will focus on adaptive echolocation and flight behaviors required for prey capture in the insectivorous big brown bat, *Eptesicus fuscus*. The study employs two experimental conditions: (1) Alteration of the bat's external ear to change the acoustic cues it uses for sound localization; (2) Acoustic interference from the sonar signals of conspecifics. The effect of the external ear manipulation on the sound localization will be examined by deflecting the tragus of the bat's external ear. The acoustic interference is created by pairing two bats together and letting them compete for a single prey item. Both experiments are designed to investigate adaptive behaviors, including echolocation and flight behaviors, on prey capture in free flying bats.

The main purpose of this study is to find out how the big brown bat modifies its echolocation and flight behavior to adapt to the internal (*i.e.* the tragus manipulation) and external (*i.e.* acoustic interference from the other bat) changes in acoustic signals.

1.3.2 Behavioral experiments and outlines of dissertation

Two behavioral experiments were conducted in this study. The animal subjects were big brown bats, *Eptesicus fuscus*, and they were trained to capture a tethered mealworm in a large flight room.

The first experiment explored the role of the bat's external ear in vertical sound localization. Prey capture behavior of the bat was tested in three experimental conditions, baseline (intact ear), tragus-deflected and recovery (intact ear again). The echolocation and flight behaviors were analyzed to examine how the bat adjusted these behaviors to adapt to its "new" ear. Results of this experiment are presented in

Chapter 2. Principle findings from this experiment were that the bat changed its flight trajectories to approach the prey in the vertical but not horizontal plane. No significant change was found in the call design of the bat's echolocation calls following tragus manipulations, which suggests no modification in the echolocation behavior. Although the tragus deflection lowered the bat's prey capture performance, most bats recovered from the tragus-deflection within one day. The influence of tragus deflection on the bat's auditory perception was compared with the effect of distorted vision on visual perception inhumans.

The second experiment investigated the influence of conspecifics on echolocation and/or flight behavior. Bats were tested in three experimental conditions, baseline, two-bat and recovery. Adjustments made by the bats in echolocation behavior are discussed in Chapters 3 and 4, and flight behavior adjustments are discussed in Chapter 5.

Chapter 3 describes a silent strategy the bat used to avoid call interference from conspecifics and discusses the role of passive hearing, which is often overlooked in studies of animals that rely on active sensing. The bat stopped vocalizing for more than 0.2 s (200 ms) when its distance to the other bat was short. This is the first study to report silent behavior in echolocating bats, and this finding could help explain several observations that involve multiple bats, such as swarming, group foraging and cooperative sonar.

Modifications in echolocation call design and possible factors that may influence the bat's call adjustments are discussed in Chapter 4. In general, the bat modified its echolocation call design when another bat was present in the flight room.

The call design was described by five parameters, which were start and end frequencies, duration, bandwidth and sweep rate. The bat increased separation in call design between its own calls and another bat's vocalizations when flying together. A detailed across successive vocalizations was used to examine the flexible adjustment the bat applied in its call design. Auditory stream segregation in echolocating bats is discussed in this chapter to consider why the bat increased differences between its echolocation calls and others when flying with another conspecific.

Chapter 5 describes the flight behavior when two bats flew in pairs and competed for the same prey item. Flight direction, inter-bat distance and angle between paired bats show that bats tended to follow each other and the bat that flew behind the other bat successfully captured the prey more often. Flight behaviors suggest that the trailing bat in fact chased the other bat to strategically intercept the only food source. Three pursuit strategies, classical pursuit (CP), instantaneous optimal bearing (IOB) and constant absolute target direction (CATD), were used to examine the flight behavior of paired bats, especially following flight. CP is the strategy the bat used most often to pursue the other bat in this study. The result is different from the previous study on prey capture behavior in big brown bats, which suggests that the bat may use more than one strategy to track a target. The pursuit-evasion game is discussed in this chapter to explain how big brown bats competed with another bat in order to gain access to the prey.

Chapter 6 draws conclusions from these two experiments and points out possible future experiments that can be conducted to further investigate how the bat adapts its echolocation and flight behavior to cope with a dynamic acoustic environment.

1.4 Overview of Dissertation

Overall results in this thesis show that the big brown bat is capable of adjusting its echolocation and/or flight behavior to cope with two different experimental conditions, *i.e.* the modification of external ears and the influence of signals produced by conspecifics. Tragus deflection affected the sound localization ability of the big brown bat. The bat did not change its echolocation calls, but adjusted its flight speed and approaching angle when capturing its prey in the tragus-deflected condition. In comparison to the external ear manipulations, the presence of another conspecific caused greater modifications in echolocation and flight behavior in big brown bats. The bat's echolocation is affected by the presence of another conspecific and the big brown bat in this study either went silent or adjusted its call design to avoid signal jamming caused by another bat. In addition, the occurrence of silent behavior and the magnitude of vocal adjustments were influenced by the similarity in call design between paired bats. Paired big brown bats also tended to engage following behavior when flying in a large flight room and competing for the same prey item. The bat which flew in the rear usually captured the worm in more trials than the one flew in the lead. The trailing bat often adopted a classic pursuit strategy, which means the heading of the trailing bat pointed to the position of the leading bat. In summary, these experimental findings suggest that the echolocation and flight behavior of big brown bats are highly adaptive to different situations.

Paper title	The role of the external ear in vertical sound localization in the free flying bat, *Eptesicus fuscus*
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Chapter 2: The role of the external ear in vertical sound localization in the free flying bat, *Eptesicus fuscus*

The role of the external ear in sonar target localization for prey capture was studied by deflecting the tragus of six big brown bats, *Eptesicus fuscus*. The prey capture performance of the bat dropped significantly in the tragus-deflection condition, compared with baseline, control and recovery conditions. Target localization error occurred in the tragus-deflected bat, and mainly in elevation. The deflection of the tragus did not abolish the prey capture ability of the bat, which suggests that other cues are available used for prey localization. Adaptive vocal and motor behaviors were also investigated in this study. The bat did not show significant changes in vocal behaviors but modified its flight trajectories in response to the tragus manipulation. The tragus-deflected bat tended to attack the prey item from above and had lower tangential velocity and larger bearing from the side, compared with baseline and recovery conditions. These findings highlight the contribution of the tragus to vertical sound localization in the free-flying big brown bat, and demonstrate flight adaptations the bat makes to compensate altered acoustic cues.

2.1 Introduction

Echolocating bats produce ultrasonic vocalizations and listen to echo returns to localize prey items and obstacles. They rely on biological sonar to accurately localize insects in a dynamic acoustic environment in which predator and prey are in continuous motion. Sound localization in bats, like other mammals, is accomplished largely via auditory computations on direction-dependent acoustic signals. Horizontal sound localization depends on binaural comparisons, such as interaural level difference (ILD), interaural time difference (ITD), while vertical sound localization relies largely on spectral cues generated by the external ear.

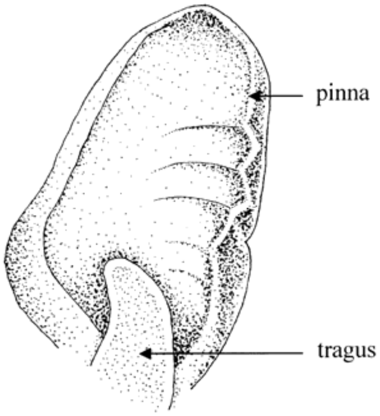

Figure 2.1 Drawing of the external ear of *Eptesicus fuscus*, including the pinna and the tragus (Drew by Kweelen Lee).

The external ear of echolocating bats serves as a receiver to collect sound and is important to localize auditory targets. The external ear of most bat species consists of two major parts, the pinna and the tragus (Figure 2.1). The tragus is a piece of skin that stands in front of the ear canal and may affect the incoming acoustic signal. The size of the tragus varies across bat species but is typically a prominent structure, particularly compared with other mammalian ears.

It is generally believed that the tragus can generate spectral cues for vertical sound localization. Spectral notches in the head-related transfer function (HRTF) are elevation-dependent, as reported in several bat species (*Phyllostomus discolor* - Firzlaff and Schuller, 2003; *Pteronotus parnellii* - Firzlaff and Schuller, 2004; *Antrozous pallidus* - Fuzessery, 1996; *Eptesicus fuscus* - Aytekin et al., 2004; Müller, 2004; Wotton et al., 1995, 1997). Previous studies have shown that spectral cues produced by the external ear are important for vertical sound localization in humans (Batteau, 1967; Bloom, 1977; Carlile et al., 2005; Fisher and Freedman, 1968; Middlebrooks and Green, 1991; Oldfield and Parker, 1986) as well as other animal species (Heffner et al., 1996; Parsons et al., 1999).

Several studies have addressed the functional contribution of the tragus to elevation-dependent spectral cues. Grinnell and Grinnell (1965) removed the contralateral tragus of the ear of *Plecotus townsendii* and recorded the evoked potential from the inferior colliculus (IC). Wotton et al. (1995) measured elevation-dependent changes in acoustic signals at the tympanic membrane of the big brown bat, *E. fuscus*, both before and after tragus removal. These two studies each reported sound elevation effects of tragus deflection, which occur below the bat's eye-nostril plane. Aytekin et al. (2004) found that tragus removal produced no change in elevation-dependent spectral notches of the big brown bat's HRTF in the frequency range of 30 to 50 kHz, as Wotton et al. (1995) reported. Instead, they found that the tragus contributed to the gain and directionality of the HRTF at 70 to 90 kHz. A similar HRTF study on another species, *Phyllostomus discolor*, reported that tragus deflection produced a significant decrease in the depth of a spectral notch at about 55-60 kHz (Firzlaff and Schuller, 2003). All studies to date reported some degree of change in the spectral characteristics of the HRTF when the tragus is removed. However, the nature and extent of change varies across studies and bat species. No research findings suggest that tragus removal abolishes elevation-dependent spectral notches, indicating that alter sources of spectral cues may play a role in vertical sound localization, even if they must be relearned following changes to the external ear.

Psychoacoustic experiments on *E. fuscus* have also suggested that the tragus contributes to vertical sound localization, particularly below the horizon. The bat's ability to discriminate vertical angle deteriorates when the tragus is deflected (Lawrence and Simmons, 1982b). Vertical angle acuity (VAA) in tragus-deflected bats is impaired for positions below the horizon, but not above the horizon (Wotton and Simmons, 2000). While past studies on the role of the tragus on vertical sound localization are suggestive, none have directly examined its importance in natural behaviors, namely on the precise localization required for insect capture.

Another question that remains to be answered is the extent to which an animal can adapt to modifications of the external ear that alter the acoustic cues used for vertical sound localization. Plasticity of sound localization has been studied in a broad range of animal species, including humans. Several studies demonstrate that plasticity can take place in adulthood, as long as a sufficient practice period is allowed (Hofman et al., 1998; King et al., 2000; Knudsen, 1994; Linkenhoker and

Knudsen, 2002; Van Wanrooij and Van Opstal, 2005). In addition, the degree and time period of adaptation in spatial hearing depends on the sound localization tasks.

There are two purposes of this study, first to investigate the influence of tragus deflection on prey capture behavior, with a particular emphasis on target localization in the vertical plane, and second to measure adaptive motor behaviors in response to changes in the acoustic cues believed to contribute to vertical sound localization.

2.2 Materials and Methods

2.2.1 Experimental animals

Six big brown bats, *E. fuscus*, were used in the experiment. They were housed in an animal colony room at the University of Maryland, College Park, United States. The temperature and humidity in the facility were maintained at 24-28 °C and 30-50%, respectively. The light/dark cycle was reversed and maintained at 12 hrs, with lights off at 7:00 am so that bats were run in experiments during their active period. Bats were housed in small groups with two to four individuals in one cage, with free access to fresh water. They were maintained at approximately 80% of *ad lib* feeding weight and ate only when they successfully took tethered mealworm during experimental trials.

2.2.2 Behavioral experiment

Experiments were run between May and September when *E. fuscus* were most active. All the experimental trials were conducted in a large carpeted flight room (7 x 6 x 2.5

m) with walls and ceiling lined with acoustic foam (Figure 2.2). In order to eliminate the bat's use of visual cues, long-wavelength lighting (>650 nm) was used as the only light source in the flight room (Hope and Bhatnagar, 1979). Each bat was trained inside the flight room to catch tethered mealworms hung in random locations from the ceiling and with different string lengths (0.5, 0.75, 1, 1.25 and 1.5 m) to present insect prey at variable elevations. The data collection began after the bat performed the task at a minimum success rate of 75%.

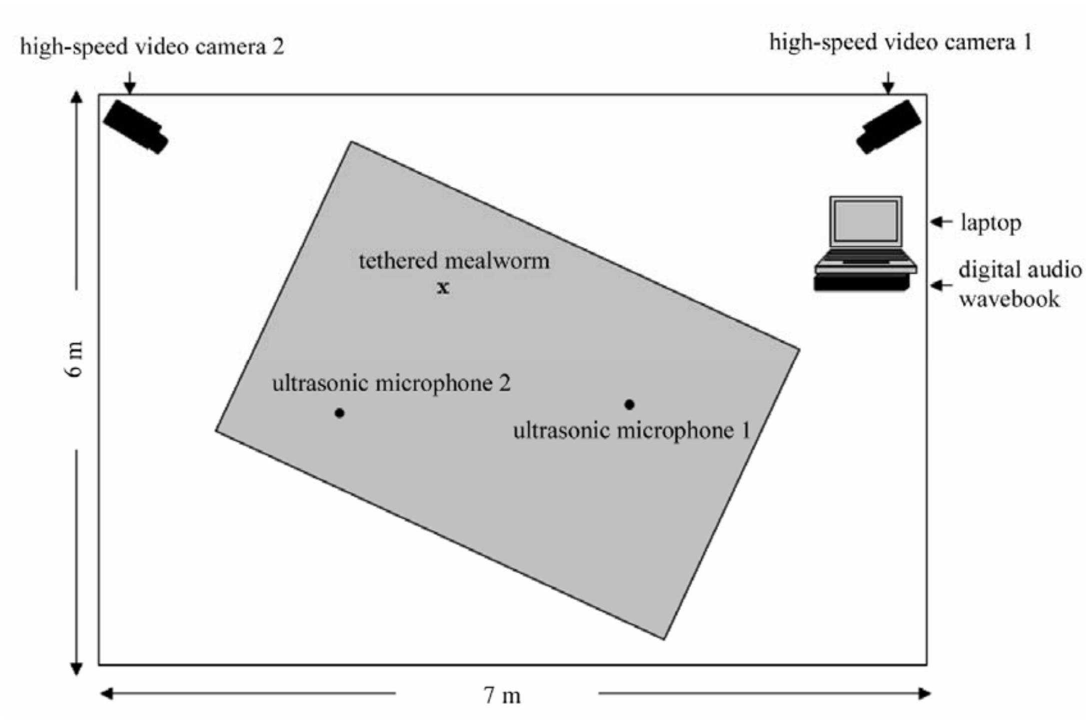

Figure 2.2 Schematic of setup for video and sound recordings of tethered prey captures by echolocating bats. Two high-speed IR cameras (Kodak MotionCorder Analyzer, 240 frames per second) were mounted in the room to permit 3D reconstruction of the bat's flight path. Video recordings were synchronized with audio recordings taken with two ultrasonic microphones delivering signals to an IOTech Wavebook.

2.2.3 Data collection

Audio recordings

Two ultrasound microphones (UltraSound Advice, London) were placed on the floor to pick up vocalizations of the bat and stored digitally in a Wavebook (IOTech, sample rate 250 kHz per channel). These audio recordings were analyzed off-line using a custom MATLAB program to measure spectral and temporal features of echolocation calls produced by the bat performing the insect capture task.

Video recordings

Two high-speed video cameras (Kodak MotionCorder Analyzer, Model 1000, 240 frames per second) were mounted on two corners of the flight room to capture the motion of the flying bat. Video recordings from these two cameras were then digitized and analyzed off-line using commercial hardware and software (Peak Performance Technologies and MATLAB) to reconstruct the 3-D flight path of the bat.

Audio-video synchronization

Audio and video recordings were triggered simultaneously by the experimenter when the bat made or attempted contact with the mealworm and the preceding eight seconds of data were stored.

2.2.4 Tragus manipulation

Alteration of acoustic signals received at the bat's tympanic membrane was accomplished by gluing the tragus forward to the side of the head by Vetbond (3M) or Prosthetic Adhesive (Ben Nye). The glue was applied every day before the experiment started and served to hold down the tragus for approximately three hours (two hours after completion of experimental trials). There were four distinct experimental conditions: baseline, control, tragus-deflection and recovery. Each condition was run over four successive days, except the control condition, which was run one day, and the entire experiment involved a total of 13 test days for each bat.

The behavioral task was identical in all four conditions. The baseline condition tested the prey capture performance of the individual bat with unmanipulated external ears. In the control condition, a drop of water was applied to the tragus, using the same procedures as the tragus-deflection condition without actually gluing down the tragus. The purpose was to determine if any change in the prey capture performance could be attributed to disturbance created by touching the bat's external ear. The tragus-deflection condition examined changes in the bat's prey capture performance when both tragi were glued down. The recovery condition was run after both tragi came up, and documented the bat's behavior after the experimental manipulation to the external ears. The position of the tethered mealworm was changed every trial to prevent the bat's use of spatial memory rather than echolocation to perform the insect capture task.

2.2.5 Data analysis

Several parameters acquired from audio recordings were used to measure the bat's vocal behavior and are listed as follows: (1) Spectral features of echolocation calls: start frequency (the highest frequency of the fundamental), end frequency (the lowest frequency of the fundamental) and bandwidth (the frequency range of the entire fundamental); (2) Temporal features of echolocation calls: duration (the duration of the fundamental) and pulse interval (the time interval between the onset of two successive calls); (3) Terminal buzz duration, defined as the sound segment prior to insect capture or attempted capture with pulse intervals less than 8 ms.

Previous studies have shown that the tragus may play a role in vertical sound localization; thus the analysis of motor behavior was emphasized in the plane of elevation. Flight behavior was measured from video recordings and the following parameters were used: (1) Trial time: from the moment the bat took off to when the bat made contact with the mealworm; (2) The elevation difference between the bat and the prey (Figure 2.3A); (3) The tangential velocity of the bat in the vertical plane (Figure 2.3B)(side view); (4) The bearing in the vertical plane (Figure 2.3C): The bearing is the angle between two vectors, which are the vector of the bat's tangential velocity and of the bat-worm vector (vector from the bat to the mealworm). The first vector represents the actual direction the bat is heading, and the second one is the direction from bat to the worm.

All vocal and motor behavior analyses were carried out for trial segments within one second before contact with the tethered mealworm. In addition, only the vocal and motor behaviors of the direct target hit trials were included to study adjustments of these behaviors following the tragus manipulation. Repeated measurement ANOVA was used to test statistical differences in data across conditions. Bonferroni adjustments were used to correct for additive errors associated with multiple tests in post-hoc analyses, *e.g.* 0.05/n, where n = 10.

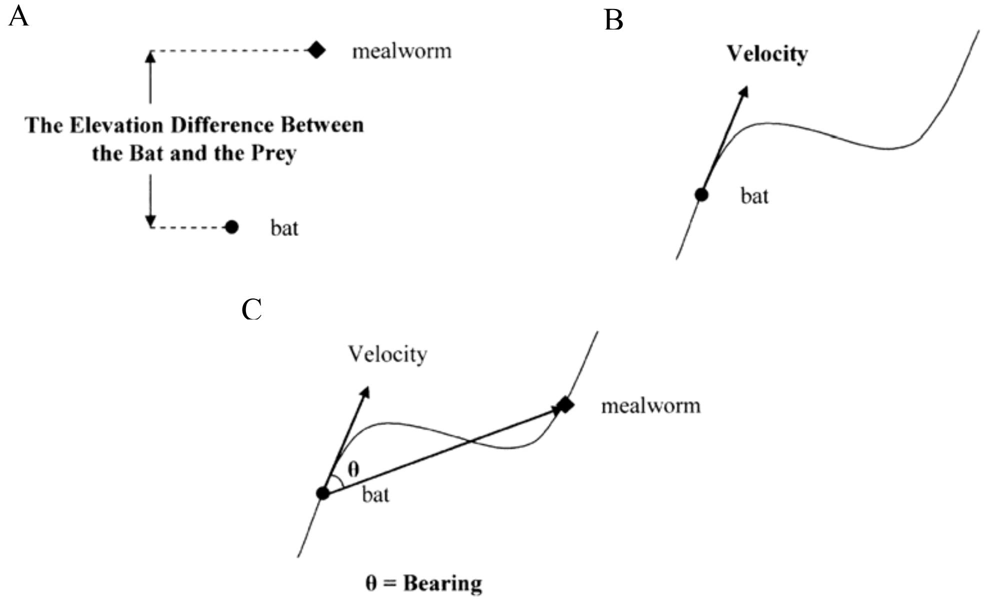

Figure 2.3 The schematic of motor behavior parameters, (A) the elevation difference between the bat and the prey; (B) the velocity of the bat from the side view; (C) the bearing from the side view.

2.3 Results

2.3.1 Performance

Three insect capture behavior patterns were categorized from video recordings, *i.e.* direct target hit, target contact and far miss. Direct target hit was the most typical pattern in the prey capture behavior. The bat approached the mealworm and used its tail membrane to scoop up the mealworm. Target contact was recorded when the bat attempted insect capture with a body part other than tail membrane (such as left/right wing, mouth, etc.). The bat may successfully grab the tethered mealworm or drop it in the contact behavior described above, but in either case the bat made physical contact with the target. Far miss occurred when the bat failed to hit the actual target. The first pattern characterizes the bat's precise localization of its prey. The second and third patterns show localization errors of different magnitudes.

The prey capture performance of all six bats is shown in Figure 2.4. The Fisher exact test (Zar, 1996) was used to analyze the performance change across days and conditions. Within the same condition, there is no significant difference in performance across different days ($p < 0.05$, Figure 2.4A). Direct target hit is the most frequent behavior pattern across all four experimental conditions and target contact and far miss trials increase in the tragus-deflection condition. The direct target hit trials remain at around 80% in the baseline condition. The performance of the control condition is comparable to that of the baseline condition. There is a drop in the percentage of direct target hit trials and a rise in target contact and far miss trials on the first day of the tragus deflection condition; performance in the tragus manipulation condition gradually returns to the baseline level. The percentage of direct target hits is higher on the first day of recovery compared with the tragus-deflection condition but lower than in baseline trials. The performance of the following three days of recovery data is similar to the baseline condition. Collapsing data across days, the percentage of direct target hit trials in the tragus-deflection condition is the lowest, and the percentage of target contact and far miss trials are the highest (Figure 2.4B).

We also analyzed the interaction position of the bat with respect to the insect across conditions. The moment the bat made contact with the mealworm is defined as interaction time. The bat's position at this time is referred to as the interaction position, and the distance between the bat and the prey at the interaction time is defined as the interaction distance. Because the bat can catch the mealworm using not only its tail membrane but also the wing, the range of capture is defined by the wingspan and body length of the bat (Figure 2.5). The wingspan (30 cm) determines the horizontal range (x- and y-planes) and the length between the center of the body and the tip of the tail (10 cm) determines the vertical range (z-plane) that the bat can reach. To examine in detail how the tragus manipulation influences interaction distance of the bat, the number of trials that exceed this range is shown in Table 2.1 across conditions. The interaction distance exceeds the range of capture in the z-plane in significant more trials when the tragus was glued down compared with baseline and recovery conditions. However, the tragus manipulation has no effect on the interaction distance in x- and y-planes.

2.3.2 Adaptive vocal behavior

The terminal buzz duration (Figure 2.6) in both tragus-deflection and recovery conditions is significantly longer than in the baseline condition (one-way ANOVA, $p<0.05$). The features of vocalizations were analyzed in 100 ms time blocks during the final 1000 ms before the bat captured the prey item. Only direct target hit trials were included in the analysis of adaptive vocal behavior to examine if the bat modified its echolocation calls in order to catch the prey successfully. No reliable pattern of change in the vocalizations emerged from these analyses when comparing the baseline, tragus-deflection and recovery conditions.

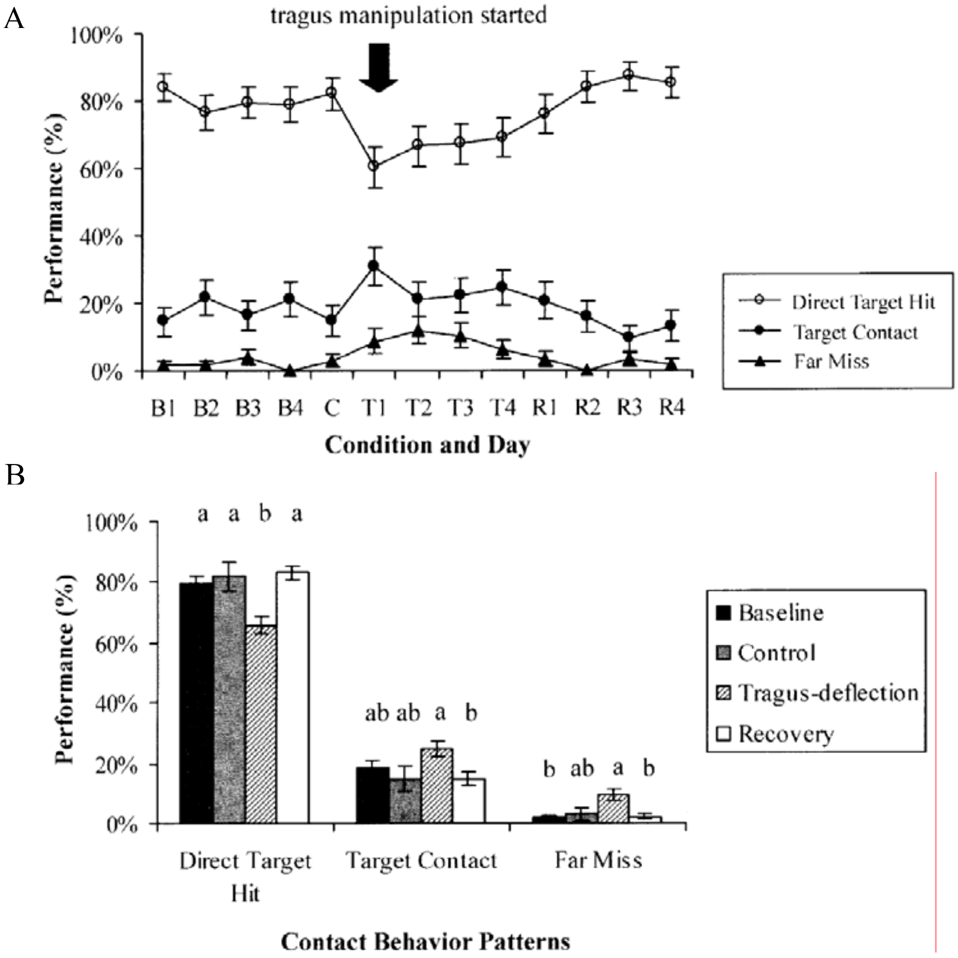

Figure 2.4 (A) Prey capture performance under different conditions over repeated test days. The open circle summarizes direct target hits, the closed circle shows target contacts and the closed triangle shows far misses. The x-axis represents the conditions (B as baseline, C as control, T as tragus-deflection and R as recovery) and the number refers to test days one to four. (B) Prey capture performance under different conditions. The letters above the histograms represent the rank of the performance. The same letter means no significant difference.

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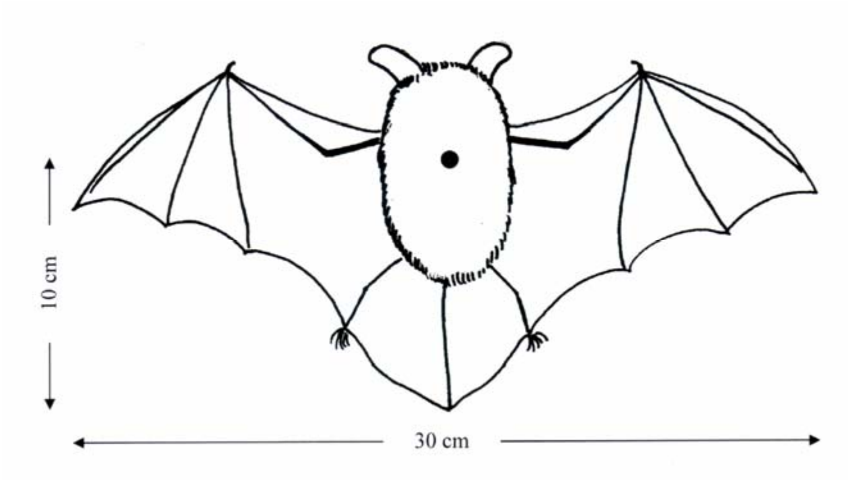

Figure 2.5 The range of capture measurement in *E. fuscus*. The black dot on the bat's body is the center of the bat

Table 2.1 The interaction distance under three different tragus conditions.

Dimension	Tragus condition	Trials exceed (x or y > 15 or z > 10)	Percentage	*p*	Post-hoc test
x-plane	Baseline	2	0.74%		
	Tragus-deflection	3	1.14%		
	Recovery	1	0.41%	n.s.	
y-plane	Baseline	4	1.48%		
	Tragus-deflection	3	1.14%		
	Recovery	1	0.41%	n.s.	
z-plane	Baseline	3	1.11%		b
	Tragus-deflection	12	4.56%		a
	Recovery	5	2.07%	< 0.05	ab
Distance (3-D)	Baseline	3	1.11%		b
	Tragus-deflection	14	5.32%		a
	Recovery	5	2.07%	< 0.01	ab

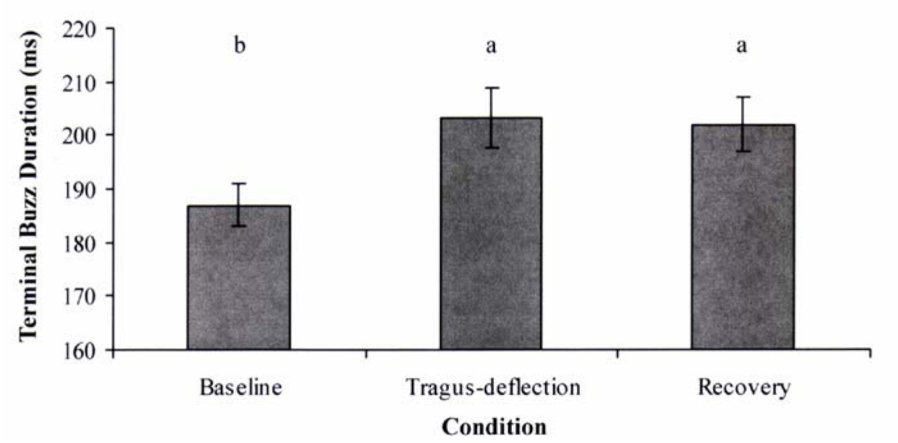

Figure 2.6 Sonar buzz duration across the three different conditions, baseline, tragus-deflection and recovery. The letter in the histogram represents the rank of the buzz length.

2.3.3 Adaptive motor behavior

There is no significant difference in trial time from release to capture across baseline (17.78±1.78sec), tragus-deflection (19.94±2.42sec) and recovery conditions (16.84±1.88sec). Although the tragus-deflection condition shows the largest average trial time compared with the other two conditions, the difference is not statistically significant (one-way ANOVA, $p>0.05$).

The adjustment of distance (between the bat and the prey) and bearing in tragus-deflection condition is shown in Figure 2.7. The magnitude of adjustment is computed from the distance and bearing difference between baseline and tragus-deflection conditions (the mean distance/bearing in tragus-deflection condition subtract by the mean distance/bearing in baseline condition). The distance (Figure 2.7A) and bearing (Figure 2.7B) differences in the vertical plane is similar to differences the horizontal plane in the last half second, but show larger differences in the vertical plane than in the horizontal plane before 0.5 second before contact. The modifications of flight path in the tragus-deflection condition are more prominent in the vertical than the horizontal plane.

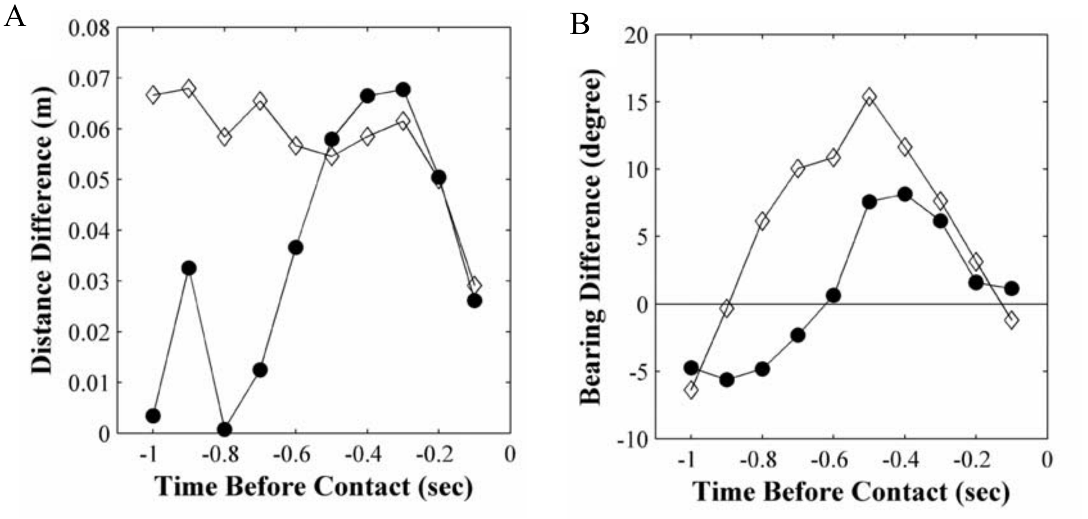

Figure 2.7 The adjustment of flight path in different planes in the tragus-deflection condition. (A) Distance difference and (B) bearing difference in the vertical (closed circle) and horizontal (open diamond) planes. The difference is computed from the difference between mean values in baseline and tragus-deflection conditions in every time segment.

The bat tended to attack the mealworm from above when tragi were glued down. The elevation difference between the bat and the prey in the tragus-deflection trials is significantly larger than the baseline condition during the entire last second before contact (Figue 2.8A. The recovery condition shows the smallest elevation difference between the bat and the prey and even smaller than the baseline condition for half the time segments (five out of 10 time segments). The bat flew slower in the tragus-deflection condition (Figure 2.8B). In the tragus-deflection condition, the bat first shows higher side tangential velocity than in the baseline condition and lowers the velocity and then raises the tangential velocity again in the very last moment of contact. The side tangential velocity in the recovery condition shows no significant difference compared with the baseline condition in most segments, except three (0.7, 0.6 and 0.1 second, $p < 0.005$), and the differences between baseline and recovery conditions are not as large as the differences between tragus-deflected and recovery conditions. The bearing from the side view is larger in the tragus-deflection than in the baseline condition during 0.8 to 0.2 second before contact ($p < 0.005$, Figure 2.8C). The recovery of the bearing is not complete and in three time segments (0.4 to 0.2 second before contact, $p < 0.005$), the bearing is significantly different from the baseline condition.

The prey capture performance dropped most dramatically on the first day of the tragus-deflection condition. Therefore, the motor behavior data in the first day was analyzed in detail. The motor behavior of different attack patterns, direct target hit and target contact, was also compared here. Far miss trials were excluded from this analysis due to the small sample size. To simplify the description of the following results about adaptive motor behaviors in the first day of tragus-deflection, we summarized the findings separated for the baseline condition direct target hit (B-DH) trials, the first day tragus condition direct target hit (1st T-DH) trials and the first day tragus condition target contact (1st T-C) trials.

Comparing these three different data sets provides information about how the bat modified its motor behaviors to enable insect capture. We hypothesize that the bat adapted its motor behaviors in response to changed acoustic input as a result of the tragus manipulation.

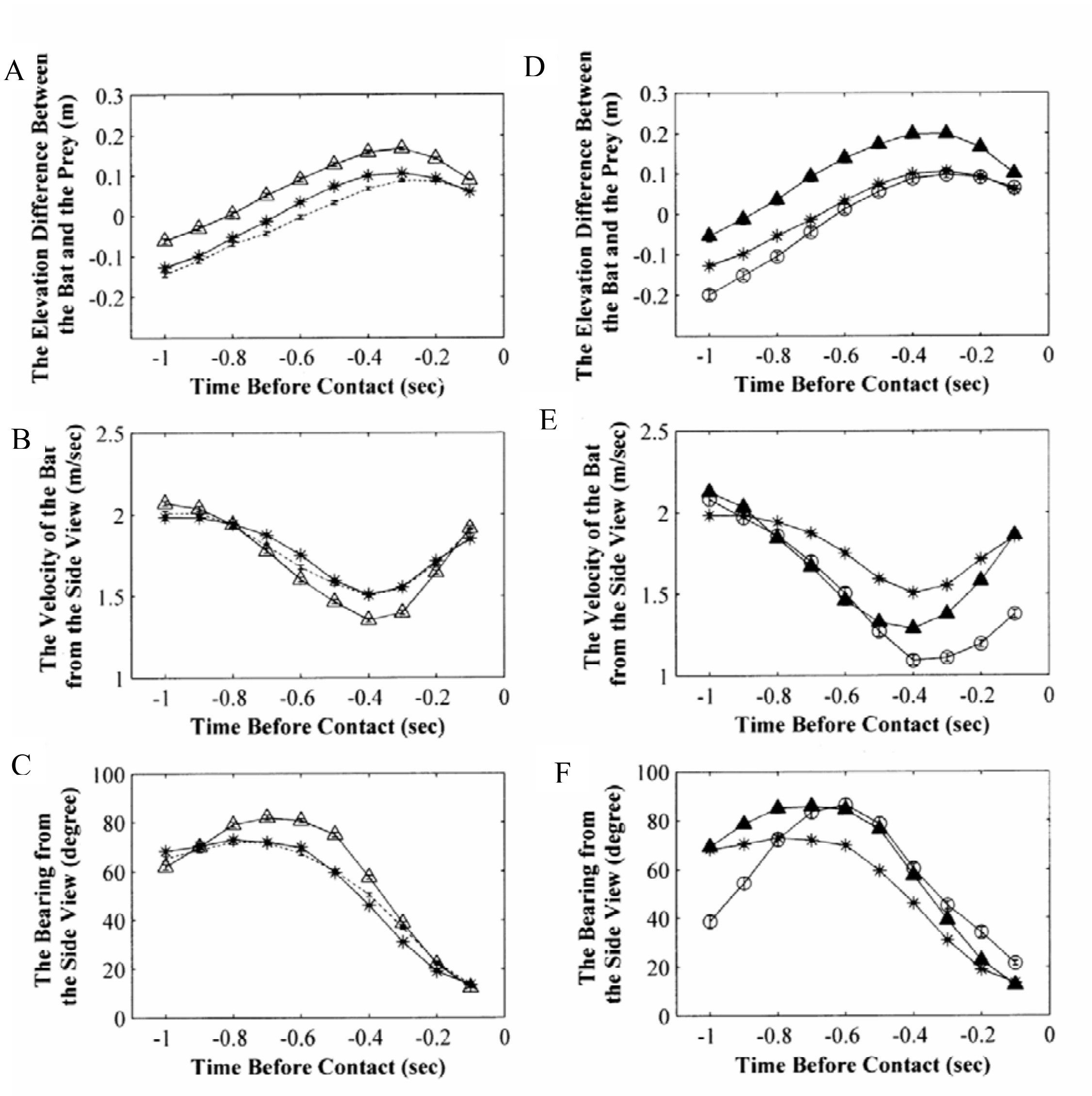

Figure 2.8 The bat's adaptive motor behavior, (A) the elevation difference between the bat and the prey; (B) the velocity of the bat from the side view; (C) the bearing from the side view, of three conditions direct hit trials, baseline (asterisk), tragus-deflection (open triangle) and recovery (dot). The bat's adaptive motor behavior, (D) the elevation difference between the bat and the prey; (E) the velocity of the bat from the side view; (F) the bearing from the side view, of three conditions, baseline condition direct target hit (B-DH) trials (asterisk), the first day tragus condition direct target hit (1st T-DH) trials (closed triangle) and the first day condition target contact (1st T-C) trials (open circle). The error bar represents the standard error.

Following the tragus manipulation, the bat maintains almost the same elevation difference in 1st T-C trials, compared with B-DH trials in the last 0.7 sec before prey capture (Figure 2.8D). On the other hand, 1st T-DH trials show significantly larger elevation differences between the bat and the prey than the other two conditions ($p < 0.005$). This result is consistent with our hypothesis stated above. The bat shows significantly lower side tangential velocity in 1st T-C and 1st T-DH trials compared with B-DH trials in the last 0.7 second before capturing the prey ($p < 0.005$, Figure 2.8E). The 1st T-C trials have the lowest side velocity across three data sets ($p < 0.005$). In the last 0.1 second before prey capture, the bat shows the same side velocity in both 1st T-DH trials and B-DH trials. The tragus-deflected bat only made contact with the tethered mealworm when the side velocity at the last moment did not reach the baseline level. The 1st T-DH trials show significantly larger bearing from the side view than B-DH trials in the entire final second before prey capture ($p < 0.005$), except the beginning and end of this period (Figure 2.8F). The 1st T-C trials show smaller bearing in the beginning of the last one second before contact (-1 and -0.9 second) and the bearing increases significantly over B-DH trials ($p < 0.005$), but is similar to 1st T-DH trials ($p > 0.005$). The bearing in 1st T-DH trials is closer to B-DH trials than 1st T-C trials in the final 0.1 sec before prey capture. The difference in bearing across conditions in the final 0.1 sec of a trial seems critical to the outcome of prey capture, *i.e.* direct target hit or off-axis contact of the prey item. Although these results on the velocity and bearing do not statistically support our hypothesis, adjustments of motor behaviors in the very last moment have immediate consequences on prey capture success.

2.4 Discussion

2.4.1 The influence of tragus deflection on prey capture performance and sound localization

Tragus deflection reduced sound localization accuracy and decreased successful prey capture performance of the big brown bat, with the largest effect on the first test day after the experimental manipulation of the external ear. Similar performance in control and baseline conditions demonstrates that the drop in the prey capture performance under the tragus-deflection condition is caused by changes in acoustic cues used for prey localization. Over test days, the bat adapted to the changes in acoustic cues introduced by tragus deflection and successfully captured tethered prey after some experience with altered external ears. This result suggests that the bat can adapt quickly to altered acoustic cues for prey localization. The recovery and baseline conditions did not show significantly different performance, which suggests that the bat can switch back to using baseline acoustic cues for sound localization. These results are consistent with human studies: Introducing new spectral cues to the human ear via pinna molds increased sound localization error, particularly in the vertical plane (Fisher and Freedman, 1968; Hofman et al., 1998; Oldfield and Parker, 1984; Van Wanrooij and Van Opstal, 2005). However, subjects regained the vertical sound localization ability after a few days of experience, and the newly learned cues did not interfere with the old ones (Hofman et al., 1998; Van Wanrooij and Van Opstal, 2005).

In the present study, the percentage of trials exceeding the range of capture is used as an index of sound localization error. The more trials exceeding the range of capture, the more consistent is the error. In the vertical plane, the most trials exceeding the range of capture occurred in the tragus-deflection condition compared with baseline and recovery conditions. Tragus deflection produced no effect on interaction distance in the other two planes. This indicates that the tragus deflection has the largest effect on vertical sound localization. Previous behavioral studies of vertical localization in *E. fuscus* also came to similar conclusions with different experimental designs (Lawrence and Simmons, 1982b; Wotton and Simmons, 2000).

The bat's prey capture performance decreased after tragi were glued down. The performance dropped significantly but did not drop below 50 %, which suggests that prey capture ability of *E. fuscus* is not heavily dependent on the contribution of the tragus. This result is consistent with HRTF studies on the echolocating bat, which show some spectral disruption following tragus deflection, but the disruption is not very dramatic (Aytekin et al., 2004; Firzlaff and Schuller, 2003; Grinnell and Grinnell, 1965; Müller, 2004; Wotton et al., 1995). Müller et al. (2006) demonstrates that the tragus, as well as the lower ledge of the pinna rim, introduces similar contributions to the directivity patterns in *Nyctalus plancyi*. It is suggested that the spectral cues introduced by the tragus can facilitate sound localization in the vertical plane. However, the contribution of the tragus is limited, and the present study demonstrates that the bat can adapt to changes in the filtering characteristics of the external ear. Although the big brown bat does not have a prominent lower ledge of the pinna rim, other parts of the external ear, such as the ridge along the pinna, may also contribute to sound localization. Human and bat studies have shown that auditory cues for horizontal and vertical sound source localization are not independent (human: Butler and Humanski, 1992; Gardner, 1973; bat: Aytekin et al., 2004; Fuzessery, 1996). Therefore, changes in certain spectral cues caused by tragus-deflection may be compensated by other cues. Therefore, the tragus can contribute to the acoustic cues for vertical sound localization, but they are not exclusive.

2.4.2 Humans visual-motor adaptation and bats audio-motor adaptation

Two highly inter-related systems, sensory and motor, are required for successful prey capture in the echolocating bat. The bat must localize the source of echoes reflected from prey and use this spatial information to guide motor systems to enable appropriate commands for prey capture. The bat relies upon precise sound localization of prey through binaural and monaural acoustic cues. The effect of the tragus on vertical sound localization has already been described above. Successful prey capture also depends on accurate motor control of the body. Distorted acoustic information about object location is expected to elicit errors in motor behaviors.

Since humans rely heavily on vision and bats on audition to perceive their spatial surroundings, there may be some relevant parallels to explore in sensory-motor adaptations. Several human studies have introduced distorted or rotated visual information to subjects who are required to produce movements to accomplish task-specific goals (Abeele and Bock, 2001; Cunningham, 1989; Cunningham and Welch, 1994; Imamizu et al., 1998; Kagerer et al., 1997; Marotta et al., 2005; Martin et al., 2002; Stratton, 1896, 1897a, 1897b; Van Beers et al., 2002; Yoshimura, 2002). Redding et al. (2005) indicates that prism exposure involved three adaptive processes, which are postural adjustments, strategic control and spatial realignment. All these studies demonstrate that humans show plasticity in visual-motor control and are capable of selecting the suitable locomotion to adapt to distorted visual cues. A study on rhesus monkeys reported that nonhuman primates acquire and generalize visual-motor transformations as do humans (Paz et al., 2005).

In the present study of altered sensory input, the big brown bat attacked from higher elevation in the tragus-deflection condition than the baseline condition. In addition, the trials in which the bat contacted the target show similar flight path characteristics to the baseline condition, suggesting that modifying the flight path can increase the prey capture performance of the bat. The bearing from the side view also shows a larger bearing in the tragus-deflection condition than the tragus-intact condition, including baseline and recovery. These flight path modifications are the most robust and consistently significant changes in the bat's motor behavior in response to altered acoustic cues for vertical sound localization in the bat. Similar trajectory modification has also been reported in human visual-motor adaptation studies (Abeele and Bock, 2001; Contreras-Vidal et al., 2005; Cunningham, 1989; Seidler, 2005; Wolpert et al., 1995a).

Altered acoustic cues for sound localization in this study are analogous to altered visual spatial cues in human studies. Human subjects wearing prisms that shift or rotate visual input showed hand trajectories that deviate from the original when asked to point to a target, but they also corrected the hand trajectory after some practice with feedback. Visual feedback is important for motor behavior adaptation (Redding and Wallace, 1994). A forward model predicts the outcome of the motor behavior and an inverse model records the signals, which are derived from the error between predicted and real outcomes, used to choose a proper motor command to reduce performance error. The trajectory change is the result of a motor learning process. The forward and inverse models are tightly coupled together and capable of explaining motor learning in humans (Kawato, 1999; Kawato and Wolpert, 1998; Wolpert and Kawato, 1998; Wolpert et al., 1995b).

The same internal model can be applied to explain the bat's motor behavior adaptation in this study. The forward model in the bat predicts the target position and initiates suitable motor commands for the animal to successfully intercept the mealworm. The bat typically captures the prey by positioning itself just above the prey item to scoop it up with the tail membrane. When a localization error occurs, the bat may still be able to make contact with the target, but with the wing or the mouth instead of the tail membrane. Through contact with the prey, the bat acquires information about the real target position. The discordance between the estimated and actual target positions generates a motor error. The motor error signal is conveyed to the inverse model and permits further correction in the next motor command, by adjusting the flight path approach (the elevation difference between the bat and the prey) and angle (the bearing from the side view). Therefore, even when the bat makes an error in localizing the tethered mealworm position in the tragus-deflection condition, it can still use dynamic auditory feedback to correct its motor behavior and initiate a proper motor command to successfully intercept the target.

Other human visual-motor research shows that decreasing the reaction time increases the performance error. There is a trade-off between reaction time and accuracy of pointing to the target localization (Fitts, 1966). Although the trial time of the bat in this study did not show any significant difference across baseline, tragus-deflection and recovery conditions, the approaching side velocity did show significant difference across these three experimental conditions. The result of lowering the side velocity suggests a tradeoff between speed and accuracy. A slower velocity may provide the bat with the additional time needed to compensate for the alteration of information from the experimental manipulation. The slower side velocity in the first day contact trials suggests that the bat slowed down to correct its approach for attempted insect capture.

Redding and Wallace (2002) proposed two adaptation processes in human visual prism experiments: strategic calibration and spatial alignment. Prism goggles disrupt the relationship between extrinsic and intrinsic space, and a new visual-motor transformation is needed for visually guided reaching or pointing. The strategic calibration is a faster motor modification to adjust to a change in visual-motor mapping. The spatial alignment is a slower process and requires re-mapping the visual and motor relation. Similar adaptation processes have been reported by Shinn-Cunningham (2001) for the auditory system. Short-term training changes the perceived sound source location and long-term training may activate a new neural pathway to extract spatial information from altered acoustic cues. The motor adaptation in the tragus-deflected condition of this study suggests that the bat applies a strategic calibration to adapt to new spectral cues introduced by the external ear manipulation. The spatial alignment between the auditory and motor mapping may happen after long-term training.

2.5 Conclusions

In conclusion, our results suggest that the tragus plays a role in vertical sound localization for prey capture in the free-flying big brown bat, but the bat can quickly adapt to altered acoustic cues for sound localization. Tragus deflection does not completely disrupt prey capture ability of the echolocating bat, which suggests that other cues can be used to compensate the effect of changing acoustic cues for target localization in the vertical plane. This is consistent with the report by Aytekin et al. (2004) that binaural cues are available to the bat for estimates of vertical sound localization. Moreover, in this study we provide evidence that the bat adapts its flight path in response to altered acoustic cues for target localization. A big brown bat with defective external ears is occasionally found in the wild. Whether the defect is congenital or acquired, this study demonstrates that this animal could successfully compensate for altered acoustic cues for prey localization by modifying its motor behavior.

Paper title	Flying in Silence: Echolocating bats cease vocalizing to avoid sonar jamming
Authors	Chen Chiu, Wei Xian and Cynthia F. Moss
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Chapter 3: Flying in Silence: Echolocating bats cease vocalizing to avoid sonar jamming

Although it has been recognized that echolocating bats may experience jamming from the signals of conspecifics, research on this problem has focused exclusively on time-frequency adjustments in the emitted signals to minimize interference. Here, we report a surprising new strategy employed by bats to avoid interference, namely silence. In a quantitative study of flight and vocal behavior of the big brown bat (*Eptesicus fuscus*), we discovered that the bat spends considerable time in silence when flying with conspecifics. Silent behavior, defined here as at least one bat in a pair ceasing vocalization for more than 0.2 s (200 ms), occurred as much as 76% of the time (mean of 40% across seven pairs) when their separation was shorter than 1 m, but only 0.08% when a single bat flew alone. Spatial separation, heading direction, and similarity in call design of paired bats were related to the prevalence of this silent behavior. Our data suggest that the bat uses silence as a strategy to avoid interference from sonar vocalizations of its neighbor, while listening to conspecific-generated acoustic signals to guide orientation. Based on previous neurophysiological studies of the bat's auditory midbrain, we hypothesize that environmental sounds (including vocalizations produced by other bats) and active echolocation evoke neural activity in different populations of neurons. Our findings offer compelling evidence that the echolocating bat switches between active and passive sensing to cope with a complex acoustic environment, and these results hold broad implications for research on navigation and communication throughout the animal kingdom.

3.1 Introduction

Active sensing enables a wide range of animal species to orient and forage under conditions where light levels are low or absent (Nelson and MacIver, 2006). Self-produced acoustic or electric signals give rise to information about the environment that is used to guide a variety of behaviors. Echolocating animals produce ultrasonic signals and determine the direction, distance and features of objects in the environment from the arrival time, amplitude and spectrum of sonar reflections (Thomas et al., 2004). Electric fish generate discharges from an electric organ in the tail, and sense the location and features of nearby objects from amplitude and phase changes in the electric field (Heiligenberg, 1991).

With the benefits of active sensing also come challenges, namely the potential for interference from signals produced by neighboring conspecifics. Past research has uncovered strategies by which echolocating bats and electric fish avoid jamming through active adjustments in the signals they produce to probe the environment. Wave-type weakly electric fish modify the electric organ discharge frequency, and pulse-type weakly electric fish change the timing of electric organ discharge to avoid interference from the signals of neighbors (Heiligenberg, 1991). In echolocating bats, spectral and/or temporal adjustments in the characteristics of sonar vocalizations, which yield acoustic separation between signals of conspecifics, have been reported in several species (Bates et al., 2008; Obrist, 1995; Ulanovsky et al., 2004). None of the studies of jamming avoidance in bats measured the relative positions of animals when they made the reported vocal adjustments, and none have uncovered the finding that bats often go silent to minimize interference from the signals of conspecifics.

In bats, relative spatial position and flight direction influence the magnitude of acoustic interference from vocalizing conspecifics. Since spherical spreading loss and excess attenuation of ultrasonic frequencies produce a decrease in acoustic energy with distance (Lawrence and Simmons, 1982a), one would predict a negative correlation between interference level and inter-bat spatial separation. In addition, the bat's sonar radiation pattern (Ghose and Moss, 2003; Hartley and Suthers, 1989) and head related transfer function (HRTF) receiver are directional (Shimozawa et al., 1974; Aytekin et al., 2004). Thus, the angle between two bats' heading directions would also be expected to impact interference level and concomitant adjustments in sonar behavior.

Exploiting technological advances, we were able to quantitatively analyze strategies that an echolocating big brown bat, *Eptesicus fuscus*, uses to avoid signal interference when flying with a conspecific in a complex environment. Taking 3-D high speed video and sound recordings, we quantified the relation between flight path and vocal behavior, and importantly, identified which bat produced each vocalization in a stream of calls. Analyses of these data led to the discovery that bats flying in pairs go silent for extended periods of time (over 0.2 s), covering distances of at least 0.6 m when flying at a speed of 3 m/s, and the prevalence of silent behavior depends on the flight pattern of the bats and the baseline similarity of their sonar calls.

3.2 Results

To examine how the echolocating bat changes its behavior in response to the presence of a conspecific, 8 big brown bats, *E. fuscus*, were trained to fly in pairs and compete for a single prey item in a laboratory flight room. In these experiments, bats exhibited a significant amount of silent time, defined as no vocalizations from at least one bat for over 0.2 s (200 ms), when paired together (28 % of the time collapsed across all inter-bat separation distances; 40% of the time when the inter-bat separation was less than 1 m). However, bats almost never exhibited silent times longer than 0.2 s when flying alone (0.08%). Silent time indicates a period during an entire trial segment when one or both bats ceased vocalizing for more than 0.2 s, while vocal time refers to periods when both bats were continuously vocalizing (Figure 3.1A). Total trial time is the duration of each analyzed trial and also the sum of vocal and silent times. Figure 3.1B, D shows examples from selected trials, illustrating that silent behavior is related to the flight configuration of paired bats (see Table 3.1 for definitions). Figure 3.1C, E shows the timing of each bat's vocalizations and the silent/vocal times for the two trials in Figure 3.1B, D. One bat stopped vocalizing at 1.28 s in the first example (Figure 3.1B, C); the total trial time for this trial is 1.8 s, vocal time is 1.28 s and silent time is 0.52 s. Both bats were continuously vocalizing for the entire trial in the second example; therefore, the total trial time is equal to the vocal time for this trial (Figure 3.1D, E). Across trials, the silent time ranged from 0.2 to 2.55 s, and the mean silent time duration was 0.5 s. The average flight speed of bats in this experiment was 3.23 m/s; therefore the estimated distance the bat flew in silence ranged from 0.6 to 8 m, with an average of 1.6 m. However, the bat neither collided with the other bat nor exhibited signs of disorientation during prolonged silent times.

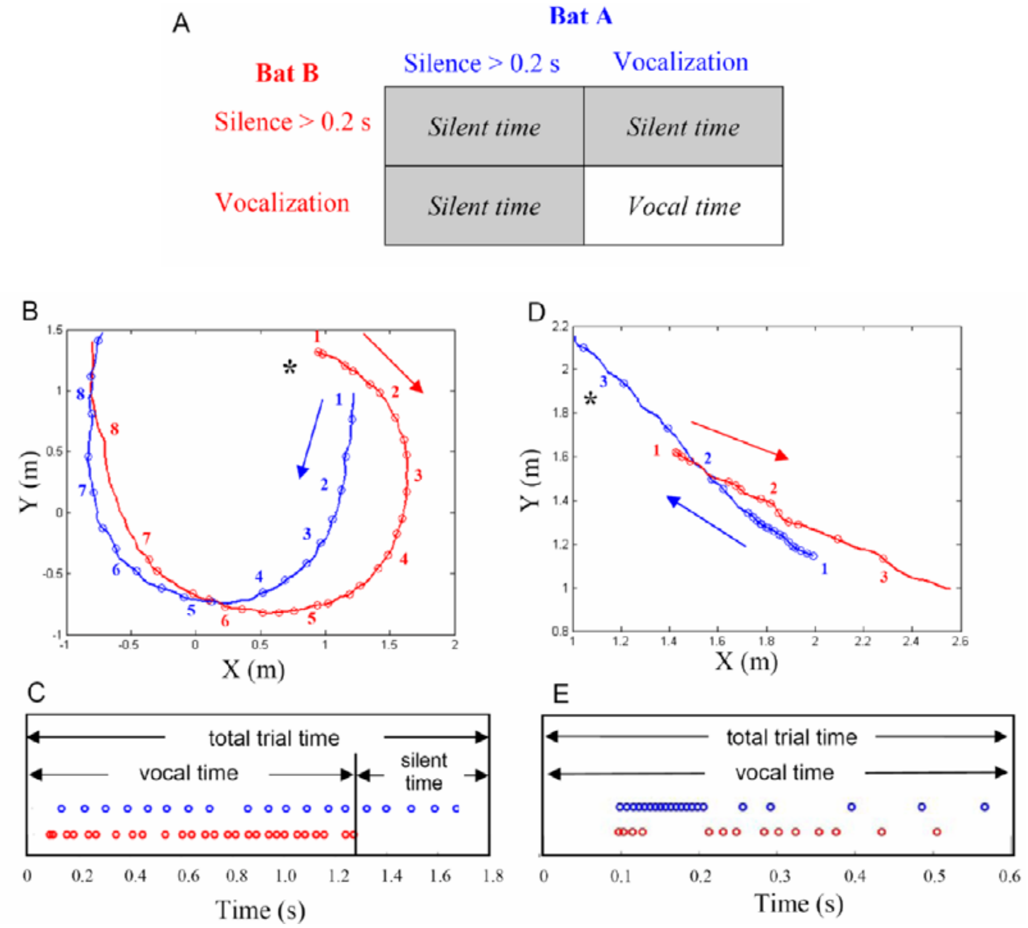


Figure 3.1 Definitions of silent/vocal times and flight trajectories of paired bats in different flight configurations from selected trials. (A) Two possible behaviors: (1) Silence: the bat stopped vocalizing for more than 0.2 s; (2) Vocalization: the bat was vocalizing continuously, with intervals between two consecutive pulses always shorter than 0.2 s. Silent time is defined as when one or both bats went silent for over 0.2 s, and vocal time is defined as when both bats were vocalizing continuously. (B), (D) Each circle represents an echolocation call and the asterisk marks the position of the target (tethered mealworm) in each trial. The time index "1" beside each flight path represents the starting point and the time interval between successive numbers is 0.5 s. (B) Following flight for time indices "1-5" is 30°-60° following flight and for time indices "6-8" is 0°-30° following flight. The bat whose behavior is shown in red, stopped vocalizing after time index "7." (D) Before time index "2" is converging flight and after this point is diverging flights. The bat (data shown in blue) produced a series of short duration and short pulse interval calls (avoidance buzz) between time indices "1" and "2". (C), (E) The silent time, vocal time and total trial time. Each circle represents one vocalization and different colors represent different bats. Plots in (B) and (C) are based on one trial and plots in (D) and (E) are based on another trial.

The results of this study were obtained by first training individual bats to intercept a tethered mealworm in a large laboratory flight room illuminated with dim, long-wavelength lighting (> 650 nm). The floor was carpeted and the walls/ceiling were lined with acoustic foam (Sonex-1). Data recordings began after all bats learned the prey capture task. Three ultrasound sensitive microphones were placed on the floor to record echolocation calls, and two high-speed infrared sensitive video cameras were mounted in adjacent corners of the flight room to permit reconstruction of 3-D flight paths. Synchronized sound recordings with a 16 microphone array on three walls of the room (Ghose and Moss, 2003) were used to substantiate that all sonar calls produced by the bats were recorded. Call assignment to individual bats was accomplished through joint analysis of video position and sonar pulse travel times to the three microphones (Materials and Methods, supporting information (*SI*) *Text* and Figures S3.1-S3.3).

The occurrence of silent times appears to be related to the level of call interference, which is influenced by the distance between two bats. When paired bats flew less than a meter apart, silence was observed as much as 76% of the time, with a mean across seven bat pairs of 40%. Figure 3.2 shows that the percentage of silent time decreased as the inter-bat separation increased. The average percentage of time spent in silence was negatively correlated with the inter-bat distance (Pearson's $r = -0.77$, $p < 0.0001$). The correlation between distance and silent time was even stronger for inter-bat distance shorter than one meter (Pearson's $r = -0.99$, $p < 0.0001$).

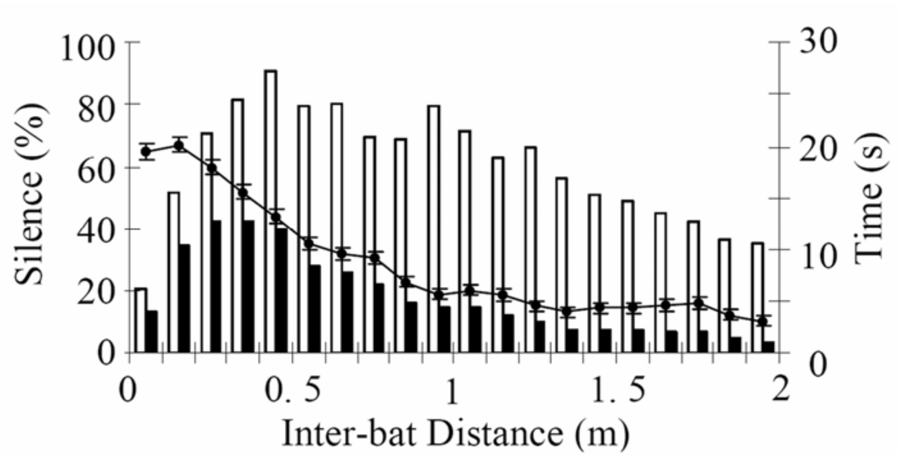
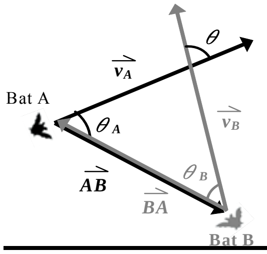


Figure 3.2 The relationship between the percentage of silent time and inter-bat distance. The percentage of silent time was calculated by dividing total duration of silent time by total trial time. Data, taken from a total of 441.27 s across 152 trials with seven pairs of bats are included. Error bars represent standard errors of the mean. The percentage of silent time as a function of inter-bat distance (filled circles, left ordinate). The histogram shows on the right ordinate the total trial time (white) and duration of silent times (black).

Table 3.1 Paired bats' flight configurations, which were categorized by the bearing of each bat and the inter-bat angle. A diagram on the left shows the bearing of each bat (θ_A and θ_B) and the inter-bat angle (θ).

Definitions (θ_A, θ_B and θ)	**Flight Configurations**	**Bearing of Each Bat (θ_A, θ_B)**	**Inter-bat Angle (θ)**
	*Converging*	Both are acute angles	0°~180°
	Diverging	Both are obtuse angles One is acute and the other is obtuse	0°~180°
	0°-30° Following	One is acute and the other is obtuse	0°~30°
	30°-60° Following	One is acute and the other is obtuse	30°~60°
	60°-90° Following	One is acute and the other is obtuse	60°~90°

We used the bearing of each bat to describe the relative position of paired bats and defined three major flight patterns: converging, diverging and following (Table 3.1). Following flight was the most common configuration, and we further divided this flight pattern into three groups according to the inter-bat angle. Figure 3.3A shows that one-third of the time one bat in a pair flew behind the other bat in the same general direction (0°-30° following) and another one-third of the time in different directions (30°-60° and 60°-90° following). The rest of the time both bats either flew toward or away from each other (converging or diverging), with the time paired bats spent in diverging flight double that of converging flight.

Figure 3.3B-F shows the distribution of inter-bat distance during silent and vocal times in various flight patterns. The y-axis is the duration of silent (red bars) and vocal (blue bars) times at various inter-bat separations. The average inter-bat distance in silent times was always shorter than in vocal times, which shows that the silent behavior typically occurred when the spatial separation between two bats was small. Silent and vocal times were almost equivalent when two bats approached each other (converging flight) at short inter-bat distances (Figure 3.3B). When paired bats flew away from each other (diverging flight), silent times were greater than vocal times only when the inter-bat distance was shorter than 0.4 m (Figure 3.3C). In following flight (0°-30° inter-bat angle) and at short inter-bat distances, silent times were more frequent than vocal times (Figure 3.3D). The ratio of silent to vocal times decreased as the inter-bat angle increased at the same inter-bat distance (Figure 3.3D-F).

The similarity in call design, determined by discriminant function analysis (DFA), between one bat and another bat in a pair also influenced silent behavior. We compared the call designs of each bat in a pair and found that the incidence of silent behavior was related to differences between paired bats' echolocation call designs, *i.e.* duration, bandwidth, start/end frequencies and sweep rate of the frequency

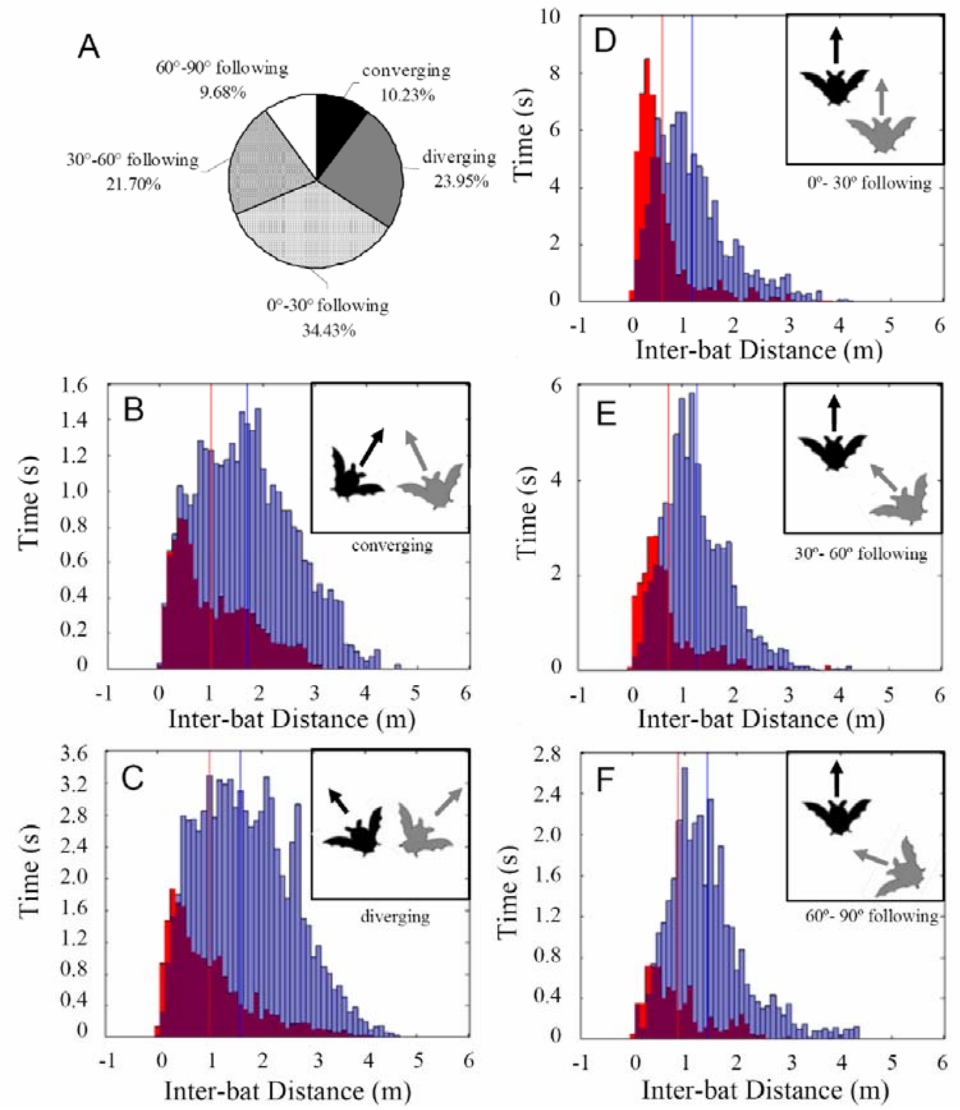


Figure 3.3 The proportion of each flight pattern and the inter-bat distance histogram of five different flight patterns. (A) Pie chart shows the percentage of time bats spent in each flight pattern. About 65% of the time one bat followed the other bat and more than half of the time, bats maintained an inter-bat angle smaller than 30°, which indicates that one bat was following another bat in a similar direction. (B-F) The x-axis is the inter-bat distance (m) and the y-axis represents the duration of silent and vocal times. Red bars represent the silent times and blue bars represent the vocal times at specified inter-bat distances. If the bat was silent more than vocal, the red bar exceeds the blue one. If the bat was vocal more than silent, the blue bars exceed the red. Overlap regions are indicated by purple bars. Note that the y-axes in panels (B-F) do not show equal scales. The upper right inset shows the geometric configuration of each flight pattern, and arrows represent the flight direction of each bat. (B) When the bearing of both bats is at an acute angle, the flight pattern is referred to as converging flight. (C) When the bearing of both bats is at an obtuse angle, the flight pattern is referred to as diverging flight. (D-F) When the two bats are flying in the same general direction, the flight pattern is called following flight. We divided following flight into three separate patterns according to the inter-bat angle between paired bats. (D) Inter-bat angle between 0° and 30° is called 0°-30° following. (E) Inter-bat angle between 30° and 60° is called 30°-60° following. (F) Inter-bat angle between 60° and 90° is called 60°-90° following.

modulated call, when flying alone. Discriminant function analysis was applied to determine how well these five call features can correctly distinguish the echolocation calls from each individual. Calls that are correctly assigned to one bat in a pair can be classified as distinctly different from those of the other bat. A negative correlation was found between the silent behavior of a bat in a pair and the percentage of correct classifications by discriminant function analysis (Pearson's $r = -0.83$, $p < 0.05$). The similarity of call design between two bats in a pair reliably predicted the prevalence of silent behavior (Figure 3.4A; $R^2 = 0.69$, $p < 0.05$). When a bat was paired across different sessions with different individuals, it showed more silent behavior when paired with an individual whose signals were more similar to its own (Figure 3.4B). The greater the similarity in call design between paired bats, the more silent behavior each exhibited.

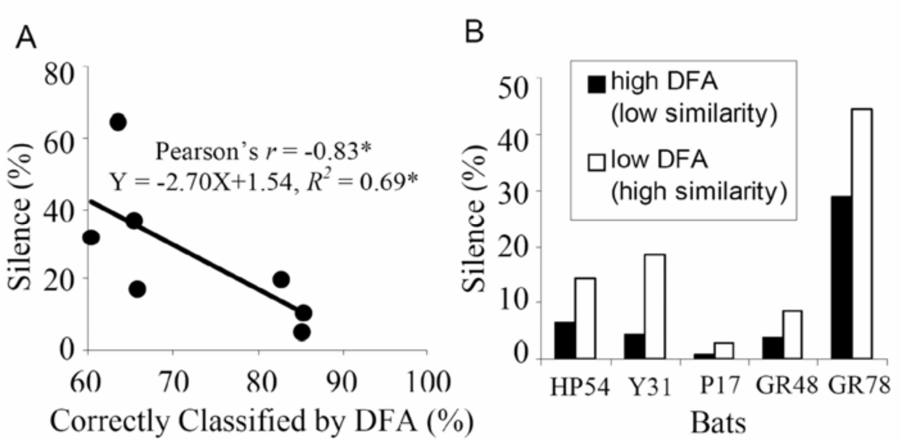


Figure 3.4 The correlation between sonar signal discriminant function analysis (DFA) and silent behavior. (A) Each data point represents a pair of bats and a total of seven pairs of bats were used in this study. Five call features, start/end frequency, duration, bandwidth, sweep rate, were used in DFA to classify calls from different individuals. The percentage correctly classified represents how well these five features could distinguish an individual's echolocation calls. The more separation in the time-frequency structures of a bat pair, the less silent behavior they showed in this study. * indicates $p < 0.05$. (B) An individual bat's silent behavior depended upon the similarity of its calls and the bat with which it was paired. Data shown for the five bats that were paired with more than one individual. Black bars represent the percentage silence of a bat when paired with another bat whose signals show a high DFA. White bars represent the percentage silence of a bat when paired with another bat whose signals show a low DFA. High DFA indicates low similarity between paired bats in call design, while low DFA indicates high similarity. All bats tested in multiple pairings showed an increase in silent behavior when paired with an individual whose signals were more similar to its own.

Only one prey item was presented in every trial, so only one individual captured the tethered prey. We examined the timing of silent behavior for the bat that caught the worm to determine whether silent behavior immediately preceded the feeding buzz that always accompanied prey capture. The bat that captured the prey showed significantly fewer silent times than the one who did not capture the worm during the last 0.5 seconds before the a start of the feeding buzz ($\chi^2 = 11.8$, $p < 0.001$), but there was no significant difference in silent behavior between the catching and non-catching bats during other time intervals (Figure 3.5). The bat that caught the prey started its echolocation at least 0.24 seconds before initiating the feeding buzz.

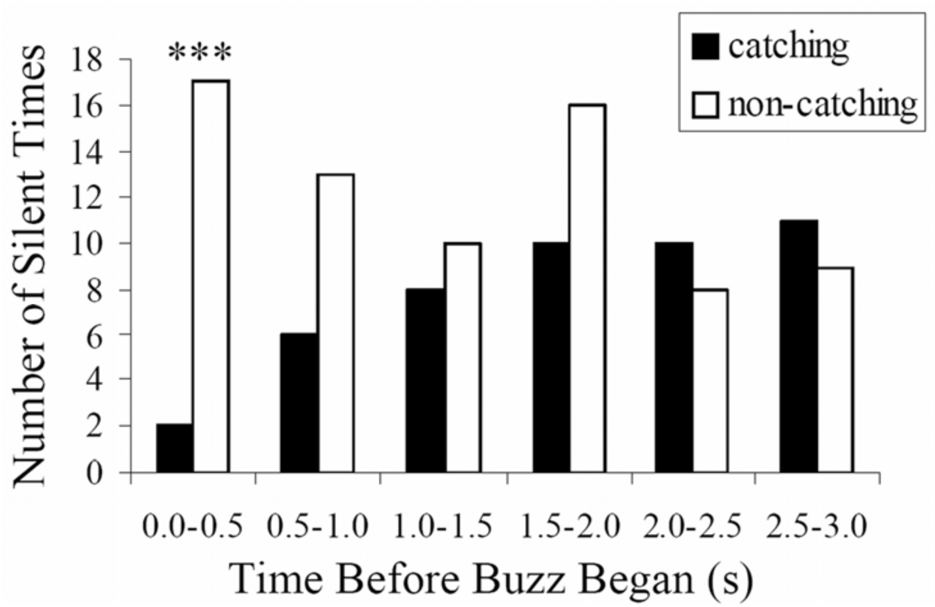


Figure 3.5 The relationship between prey capture and silent behavior. The number of silent times before the feeding buzz for both the bat that captured the worm and the bat that did not capture the worm. The x-axis is the time a silent time ended before the beginning of the feeding buzz and y-axis is the number of silent times. Black bars represent the bat that caught the worm and white bars represent the bat that did not catch the worm. Chi-square test is applied to examine the difference of silent behavior between these two bats and *** means $p < 0.001$.

3.3 Discussion

The results of this study suggest that echolocating big brown bats employ a surprising jamming avoidance strategy, silence. The relation between the occurrence of silent behavior and the spatial separation and heading of the paired bats indicates that one bat stopped vocalizing in order to avoid interference with another bat's echolocation (Figures 3.2, 3.3). This interpretation is bolstered by the observation that silent behavior is most prevalent in pairs of bats that produce similar echolocation calls when flying alone (Figure 3.4).

Short inter-bat distance and/or small angular separation in heading directions of paired bats occurred most often with silent times. When two bats approached each other, the acoustic interference between them is greater than in the diverging flight configuration, because the intensity of the bat's sonar vocalization is strongest directly in front of the animal (Hartley and Suthers, 1989). The bats did not show greater silent times in converging flight, but instead produced a series of calls with short duration and short pulse interval (Figure 3.1B, the path marked with blue between time indices "1" and "2"). This series of calls suggests an avoidance buzz, with intervals close to those observed in the feeding buzz (Ulanovsky et al., 2004), and we infer that the bat's vocal behavior in this situation served to increase its spatial resolution to avoid collision with the other bat. The ratio of silent to vocal times decreased as the inter-bat angle increased for a given inter-bat distance for pairs engaged in following flight, demonstrating that silent behavior is affected by the angular separation of paired bats' flight directions. Large angular separations in flight direction between bats reduce acoustic interference between individuals, as both sonar transmission and reception are directional (Aytekin et al., 2004; Ghose and Moss, 2003; Hartley and Suthers, 1989; Shimozawa et al., 1974).

The big brown bat produces individual-specific echolocation calls, which differ in the details of signal features (Masters et al., 1995) and personalized call design may help a bat to segregate its own signals from those of conspecifics (Masters et al., 1991). Psychophysical experiments have demonstrated that interference signals most similar to a bat's own call caused the most severe disruption to its target ranging performance (Masters and Raver, 1996). Bats using similar call design could interfere with each other's sonar target localization; therefore, increased silent behavior may serve to minimize disorientation.

Previous studies of acoustic communication in other animal species, such as birds (Ficken et al., 1974) and frogs (Schwartz, 1993), have reported the use of temporal separation of signals to avoid acoustic interference from conspecifics or noise. In birds and frogs, social communication calls are sometimes interrupted, presumably to avoid acoustic interference, but this silent behavior would not disrupt spatial orientation in these animals. However, echolocating bats use vocalizations for both communication and spatial orientation. Our results suggest that the echolocating bat engages in silent behavior to avoid interference from conspecifics, and we speculate below on how the bat can orient without producing sonar cries.

Although bats can use spatial memory to reference the position of obstacles in a familiar flyway (Jensen et al., 2005; Mueller and Mueller, 1979; Schnitzler et al., 2003), we exclude the possibility that the silent bat oriented entirely by spatial memory in this study. It may be possible for a bat to use spatial memory instead of echolocation to avoid fixed obstacles; however, the unpredictable movement of a conspecific eliminated the possibility that the silent bat could rely on spatial memory to avoid in-flight collision. The bat's use of vision was excluded by the low level infrared lighting in the room, which fell outside the spectral sensitivity of the bat's retina (Hope and Bhatnagar, 1979).

Multiple sonar sources produce signal interference, but can also potentially provide useful information about the surroundings to other listening individuals (Kuc, 2002; Simmons et al., 2004). There has been speculation that a silent bat can acquire information about the environment, locate another bat, and avoid collision by passively listening, rather than actively echolocating; however this has not been previously addressed with quantitative kinematic and acoustic analysis. The big brown bat can passively localize sound sources (Koay et al., 1998), but its accuracy is not as high along the azimuthal axis (Koay et al., 1997; 1998) and has not been measured along the range axis, compared with active echolocation (Simmons, 1973). In addition, studies of other animal species, such as dolphins and birds, suggest that acoustic signals may aid in determining the relative distance between individuals (Holland et al., 1998; Mercado et al., 2007), but this has not been previously studied in bats. Even man-made radar systems, such as multi-static radar, passive radar and passively guided missiles, monitor signals generated by other sources to localize targets, suggesting that echolocating bats may do the same. Our finding that the bat could orient without producing echolocation calls suggests the possibility that vocalizations from other bats may convey spatial information to a silent animal about the position of obstacles in the dark. Moreover, our data shows that around 70% of silent times came from the trailing individual in following flight. This implies its possible use of the leading bat's echolocation calls for spatial orientation.

A few studies with animals that are capable of active sensing have reported the use of passive sensing for stealth strategies, object discrimination, prey localization and orientation when encountering conspecifics. For example, a subordinate electric fish ceases its electric organ discharge for longer than 0.2 s when passing by the territory of a dominant conspecific (Hopkins, 2005; Moller et al., 1989; Scheffel and Kramer, 1997; Werneyer and Kramer, 2002). Dolphins and whales can passively listen to echolocation signals of their companions to navigate and discriminate different objects (Gotz et al., 2006; Lammers and Au, 2003; Xitco and Roitblat, 1996). Gleaning bats, which take prey from substrate, can passively listen to prey-generated sound to localize their prey (Russo et al., 2007). Although it has been observed that active sensing animals are capable of using passive sensing, little is known about whether aerial hawking bats, which rely heavily on echolocation most of the time for prey capture and navigation, can also use passive sensing for the same purposes.

Gleaning pallid bats, which echolocate but also rely on passive listening to prey-generated sounds for foraging, cannot process sonar and prey-generated sounds concurrently (Barber et al., 2003). Therefore, when listening to prey-generated sounds, a gleaning bat stops producing sonar vocalizations (Russo et al., 2007). Although the big brown bat is not known to rely on passive listening to find its prey, it may experience difficulty in simultaneously processing two auditory streams of information, similar to that reported for the pallid bat. When the disadvantage of echolocation outweighs the advantage, a bat may choose to cease echolocation and process only one auditory stream from conspecific-generated sounds for orientation.

The bat that caught the mealworm in each trial of this study stopped its vocalization less often (2/158 trials) than the other one (17/158 trials) in the 0.5 seconds before producing the feeding buzz, which suggests that echolocation is essential for prey localization. Feeding buzzes were recorded in all insect capture trials, indicating that the bat requires this series of self-generated calls with high repetition rate to accurately localize its prey. The bat might roughly localize the position of its prey by listening to conspecific-generated echoes, but more precise localization of the target is required for interception.

Neurophysiological recordings from the midbrain of the bat suggest that separate populations of neurons may be specialized for passive listening to acoustic signals in the environment and active listening to sonar echoes. Tonic and chopper neurons in the inferior colliculus of the little brown bat (*Myotis lucifugus*), with long integration times, long latencies and robust responses to sinusoidal amplitude modulation, exhibit response characteristics that would be best suited for processing sounds generated in the environment; whereas onset neurons, with relatively short and stable response latencies, high best frequencies and poor responses to sinusoidal amplitude modulation, would be best suited for processing self-generated echolocation signals and sonar returns (Condon et al., 1996).

Two population of neurons have been identified in the superior colliculus of the big brown bat (*E. fuscus*), one that responds selectively to acoustic stimulation at a particular azimuth and elevation (2-D neurons) and one that responds selectively to acoustic stimulation over restricted azimuth, elevation and distance (3-D neurons) (Valentine and Moss, 1997). The population of 2-D neurons responds to single frequency-modulated (FM) signals and would be well suited for passive localization of sound sources, but not for precise distance measurements required for prey capture. The population of 3-D neurons is selectively activated by a high amplitude FM sweep (pulse) followed by a weaker FM sweep (echo), and responds to pulse-echo pairs over a limited delay window. It is believed that echo-delay-tuned neurons are important for target ranging in bats (Dear et al., 1993a; 1993b; Suga and O'Neill, 1979), and activity of echo-delay-tuned neurons in the bat superior colliculus also depends on the azimuth and elevation of stimulation. The population of 3-D neurons in the bat superior colliculus therefore exhibits response characteristics that could support active localization by echolocation. We hypothesize that environmental sounds, including vocalizations from other bats, evoke activity in 2-D neurons, and echolocation evokes activity in 3-D neurons. Two-dimensional localization is sufficient for estimates about the azimuth and elevation of a sound source (*e.g.* the position of another vocalizing bat), but precise 3-D localization is required for prey capture.

This paper reports a newly discovered silence strategy employed by echolocating bats to avoid call interference. Additionally, the silent bat can potentially trace another bat's position by passively listening to the other bat's vocalizations and resulting echoes. The silence strategy provides new perspectives on swarming and chasing behavior, as well as navigation and communication, in a variety of animals.

3.4 Materials and Methods

3.4.1 Animals

Eight big brown bats, *E. fuscus*, were used in this study and formed seven pairs. Five bats were tested in pairings with more than one individual bat. Bats were collected in Maryland and housed in a colony room at the University of Maryland, College Park. All experiments were approved by the University of Maryland's Institutional Animal Care and Use Committee.

3.4.2 Behavioral Experiments

Experiments were run between June and August in 2005, 2006. All bats were trained first in a large flight room (7x6x2.5 m) to catch tethered mealworms. Baseline (one bat alone) and two-bat data (paired bats competing for a single tethered prey item) were collected on four different days per pair. We analyzed 30 baseline trials/bat and 20 two-bat trials/pair. Light in the room was long-wavelength filtered (>650 nm), to prevent the bat from using visual cues for orientation and prey capture (Hope and Bhatnagar, 1979).

3.4.3 Data Recording

Audio recordings were acquired by three ultrasound sensitive microphones (UltraSound Advice, London) on the floor, amplified (UltraSound Advice, London) and stored digitally (Wavebook, IOTech), sampled at 250 kHz/channel) and a 16 microphone array positioned on three walls of the room (Ghose and Moss, 2003).

Video recordings were taken by two high-speed cameras (Kodak MotionCorder Analyzer, Model 1000, 240 frames/s) mounted in two corners of the room, permitting off-line 3-D reconstruction of the bats' flight paths. Audio and video recordings were simultaneously end-triggered after one bat made contact with the prey, and the preceding eight seconds of data were stored. Audio and video data were later analyzed by two custom MATLAB programs.

3.4.4 Call Assignment

The assignment of sonar calls to individual bats flying in pairs was accomplisted following the steps outlined in Figure 3.6. Briefly, three microphones (separated by 2 to 3 m) ensured pick-up of all sonar calls, and at least one microphone was always ≤ 2 m from each bat flying in the video-calibrated space. Time waveforms and spectrograms of the audio recordings from the three separate channels were examined to select two channels with good signal to noise ratio Spectrographic displays of signals in the selected channels were marked manually by the investigator using a custom MATLAB program, and signals in the unselected channel were also examined to ensure that no vocalizations were missed. The actual audio delay of each echolocation call was determined by computing the temporal offset of call onset times in two different channels from spatially separated microphones. Call duration recorded from the strongest channel was used to calculate onset of vocalization in the two other weaker channels (*SI Text*). Position data of each bat and the microphones were digitized (accuracy ~1.5 cm) by another custom MATLAB program and used for frame-by-frame measurement of 3-D inter-bat separation and bat distances to the microphones. The estimated audio delay was the difference between the pulse travel times to two selected microphones, computed from sound travel time in air (346 m/s) and bat position data. The actual and estimated audio delays should be equal (within 0.5~1 ms margin of error) if the association between calls and bats was correct. We included the third microphone and the 16 microphone array to ensure detection of all sonar calls and to increase the reliability of assigning each call to the vocalizing bat. Details of call assignment, correction for onset of vocalizations and several trial examples are presented in *SI Text* and Figures 3.7-3.9.

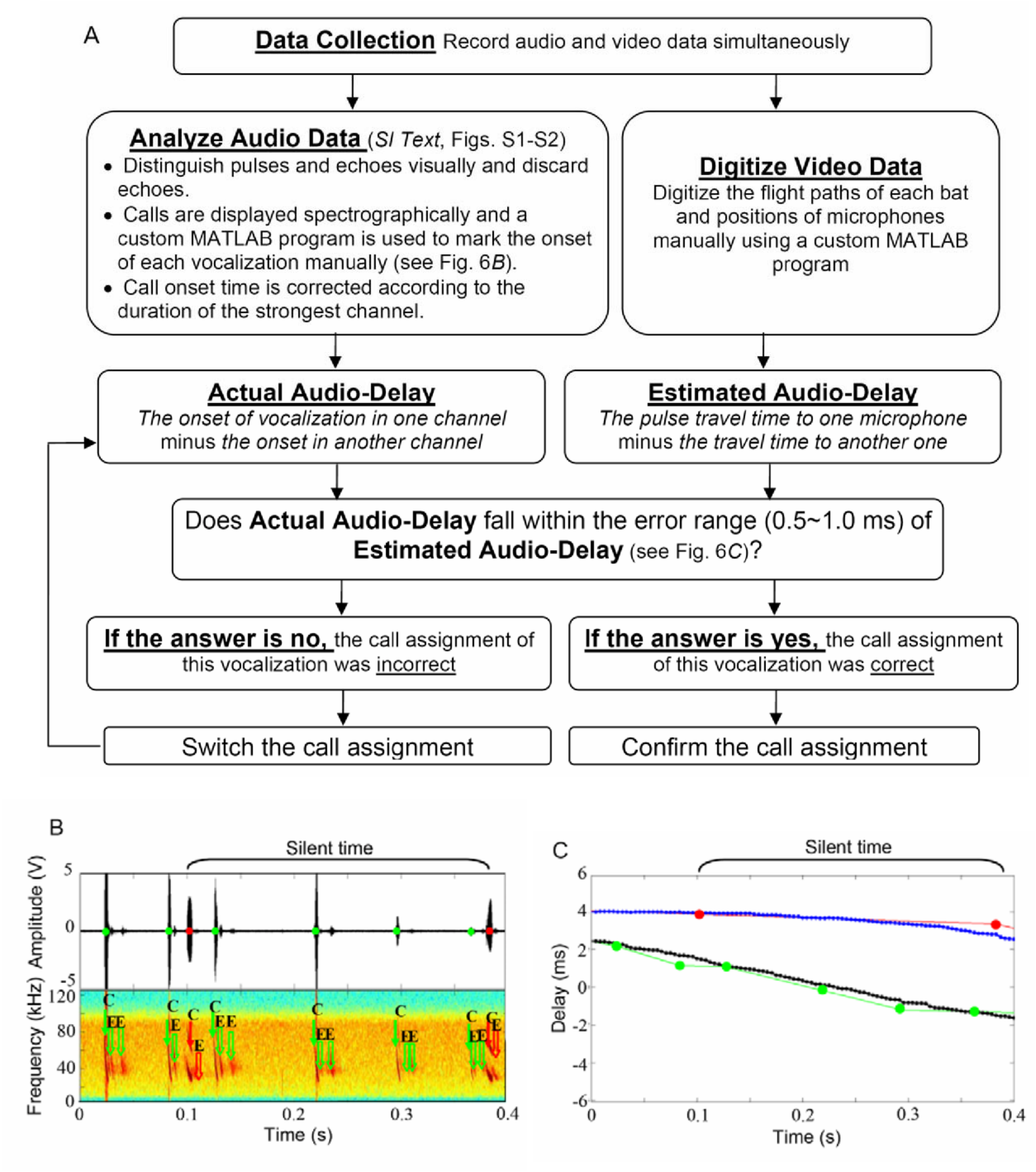


Figure 3.6 A flow chart illustrating how each call in a stream was assigned to the vocalizing bat in a pair and an example of call assignment to different bats. (A) Steps for analyzing video and audio recordings. (B) Manual call assignment in one of the three channels. Letters "C" and "E" refer to sonar call and echo, respectively. Red (Bat A) and green (Bat B) dots in (B) and (C) mark vocalizations that belong to each of the two bats. (C) Comparison between actual and estimated audio delays. Blue (Bat A) and black (Bat B) lines in (C) are estimated audio delays, while red (Bat A) and green (Bat B) dots are actual audio delays. Note that estimated and actual delays for the two bats' vocalizations coincide.

3.5 Supporting Information

The reliability of assigning echolocation calls to individual bats depends on the following:

1) detection of all sonar calls produced by each bat,

2) precision in marking the onset of the arrival times of vocalizations at each of the microphones and

3) accurate 3-D localization of the two bats and their spatial separation as they fly. Below are details on each of these measurements:

3.5.1 Call detection

Three ultrasound microphones were used to pick up all vocalizations from bats and at least one microphone was within 2 m distance to each bat. The investigator first visually inspected audio recordings in all three channels, and identified pulses and excluded echoes. Although only the two strongest channels were typically selected for call analysis, spectrographic displays of signals recorded by the third microphone was visually examined as well to make certain that no vocalization was missed (Figure 3.7). A 16 microphone array on three walls of the flight room was also used to confirm that no vocalization was produced by one or both bats during the silent time. The microphone array was tied to the same trigger as the three floor microphones and the video acquisition system.

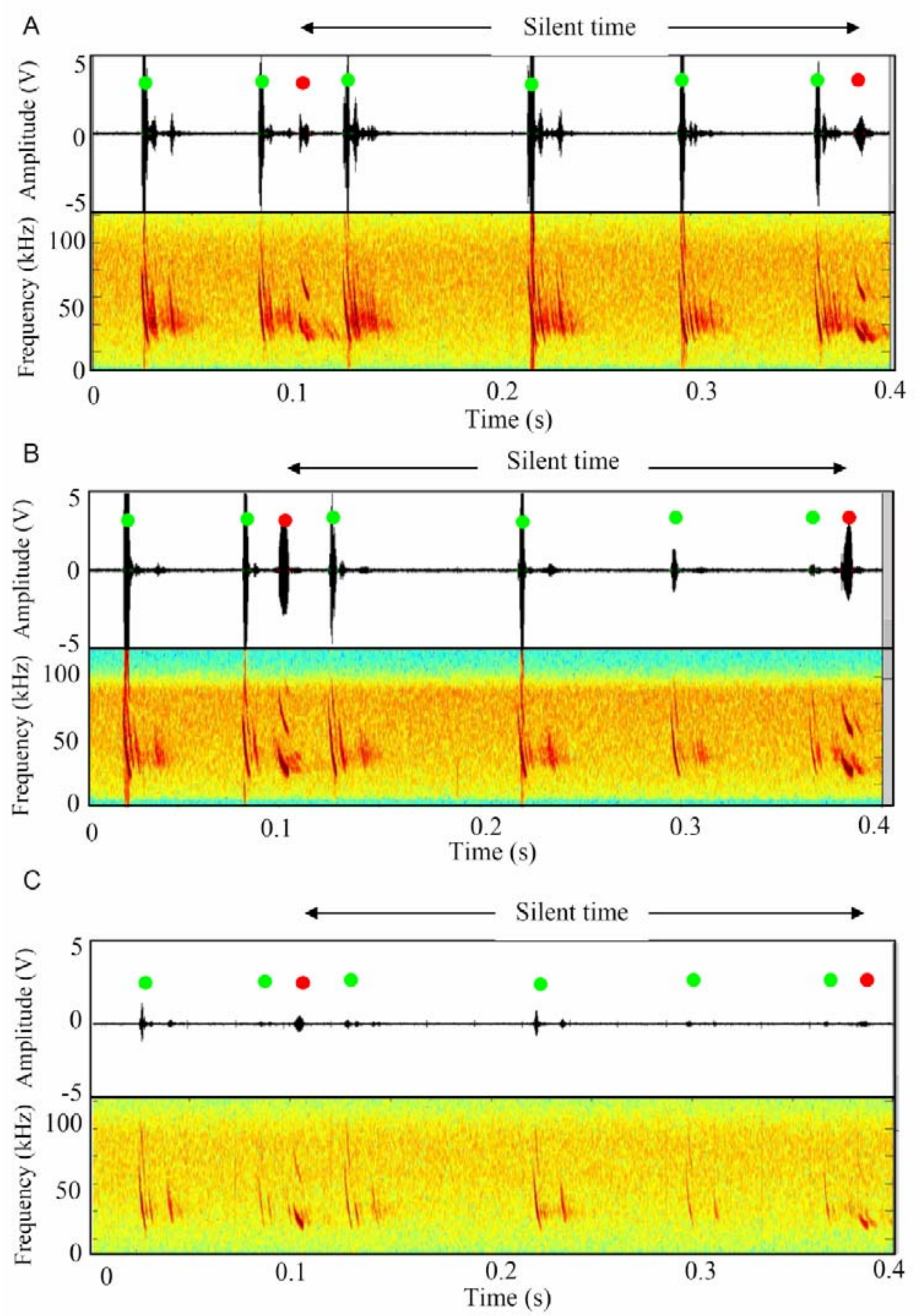
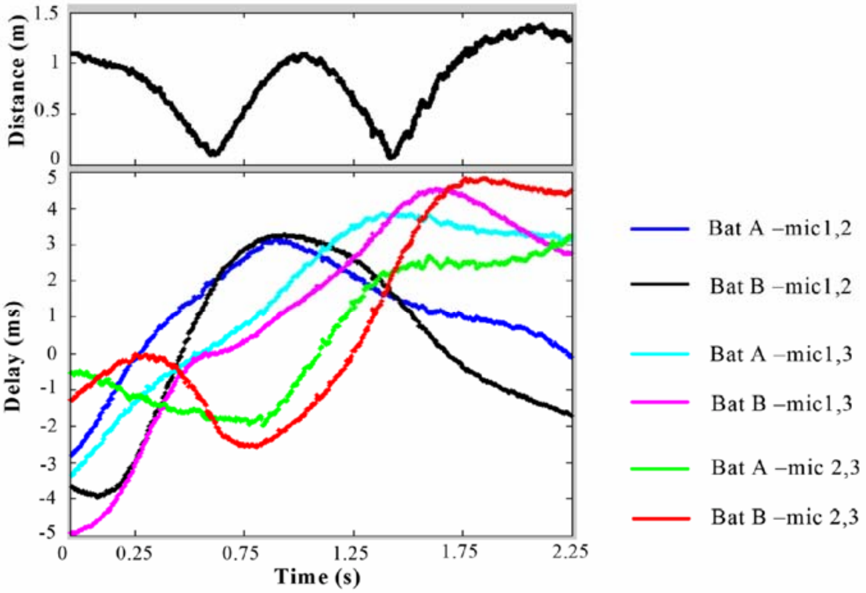


Figure 3.7 Audio recordings in three different channels. (*A*) Channel 1, (*B*) Channel 2, and (*C*) Channel 3. Red and green dots represent vocalizations from different bats. Each panel shows both waveforms (above) and spectrograms (below) of a sequence of vocalizations from bats flying together. The x-axes for both waveforms and spectrograms are time (s). The y-axis is amplitude (V) in the upper panel and frequency (kHz) in the lower panel. In this example, the bat flew closer to microphones 1 and 2, so the amplitude is strong in these two channels. A silent time occurred between 0.1 and 0.4 s. One bat (sonar calls marked by red dot) stopped vocalizing for more than 0.2 s and the other bat (sonar calls marked by green dot) did not cease its vocalizations. Before and after the period when one bat went silent, its calls show high signal-to-noise ratio, which minimizes the possibility that silent time was due to signals falling below the noise floor of all three microphones.

3.5.2 Call onset time at the fixed microphones

Because high frequency sound attenuates more rapidly than low frequency, measurement of the bat's FM sonar call onset time at each of the microphones is subject to error. We address this problem by comparing each sonar call received at the three microphones and use the signal with the highest signal to noise ratio to measure its duration. We then use this measurement of call duration to calculate vocal onset time at the other two microphones with weaker signals. For example, if a call in channel 1 is stronger than in channel 2, the duration of the call is measured by manually marking the start and end times of the call in channel 1 and taking the difference. We use this duration measurement to calculate the start time of a weaker recording in the other microphone channel, by lining up the spectrograms of the calls acquired in the different channels. This correction allows us to make a more precise measurement of call onset times across microphone channels, which is used to compare the measured (from audio recording data) and estimated (from video position data) audio-delays at the spatially separated microphones.

Two of three microphones were typically used to calculate acoustic delay and determine whether the real and estimated audio-delays were the same. The coincidence of real and estimated audio delays allowed us to verify the assignment of a given call to a particular bat, based on the bat's 3-D position in the room with respect to the microphones. However, when the possibility of confusing one bat's signals with another's was high (at short separations), we also included recordings from the third microphone to increase the reliability of our analysis. Figure 3.8 shows that we can minimize error of call assignment by calculating delay to all three microphones. This figure illustrates that ambiguity in call assignment arises when inter-bat distance is short. When using only microphone 1 and 2, there would be ambiguity in the assignment of bat calls between -1.6 and -0.7 s of the trial, because the estimated audio-delays for these two bats were similar at these two microphones. However, the use of audio delays between microphones 1 and 3 or 2 and 3 disambiguates the call assignment.



Bat A – mic 1, 2 equals (pulse travel time from Bat A to Mic 1) minus (pulse travel time from Bat A to Mic 1)

Figure 3.8 Acoustic delay measurements taken from different microphone pairs helps to disambiguate call assignment. The upper panel plots the inter-bat distance as a function of time (s) and the bottom panel shows estimated audio delays (ms) from each bat to each microphone as a function of time (s). The actual audio delays should be the same as the estimated audio delays if the call assignment is correct.

We considered call assignment to be reliable if the difference between actual and estimated audio-delay was less than 1 ms for inter-bat spacing greater than 0.5 m and less than 0.5 ms for inter-bat spacing less than 0.5 m. Figure 3.9 shows several examples of call assignment based on the joint analysis of video position and microphone delay data. If video position data were not available for one or both bats, the corresponding vocalization data were discarded from the analysis. In addition, if vocal data could not be reliably assigned to a particular bat in a trial segment, it was also discarded from the analysis.

3.5.3 Precision of marking bat position

High speed video data (240 frames/s) were analyzed from two fixed cameras with overlapping fields of view. Each bat's position was marked in each video frame and used to reconstruct its flight path, and the resulting 3-D position data were used to validate measurements of acoustic arrival time at each of the two microphones for each bat vocalization. The accuracy of our video localization system is ± 1.5 cm in 3-D.

3.5.4 Additional information about our analyses

Individual signature

Past research has shown that individual *Eptesicus fuscus* show individual call design (Kazial et al., 2001; Masters et al., 1995), and studies on multiple bats have used the similarity in call design to distinguish vocalizations from different individuals (Obrist, 1995; Ulanovsky et al., 2004). We used this information to supplement our quantitative measures of bat position and acoustic delay as we tracked echolocation behavior over time.

Silent behavior at long distances

Silent behavior was not limited to short inter-bat spacing only. When bats were separated by larger distances (> 1 m), when call assignment to the individual bats was extremely clear and call intensity adjustments to nearby objects (e. g. the other bat) were minimized, we observed silent behavior as well.

Silent behavior depends on bat pairing

The prevalence of silent behavior in a given bat depended on the similarity of its baseline call characteristics to the bat with which it was paired on a given set of trials.

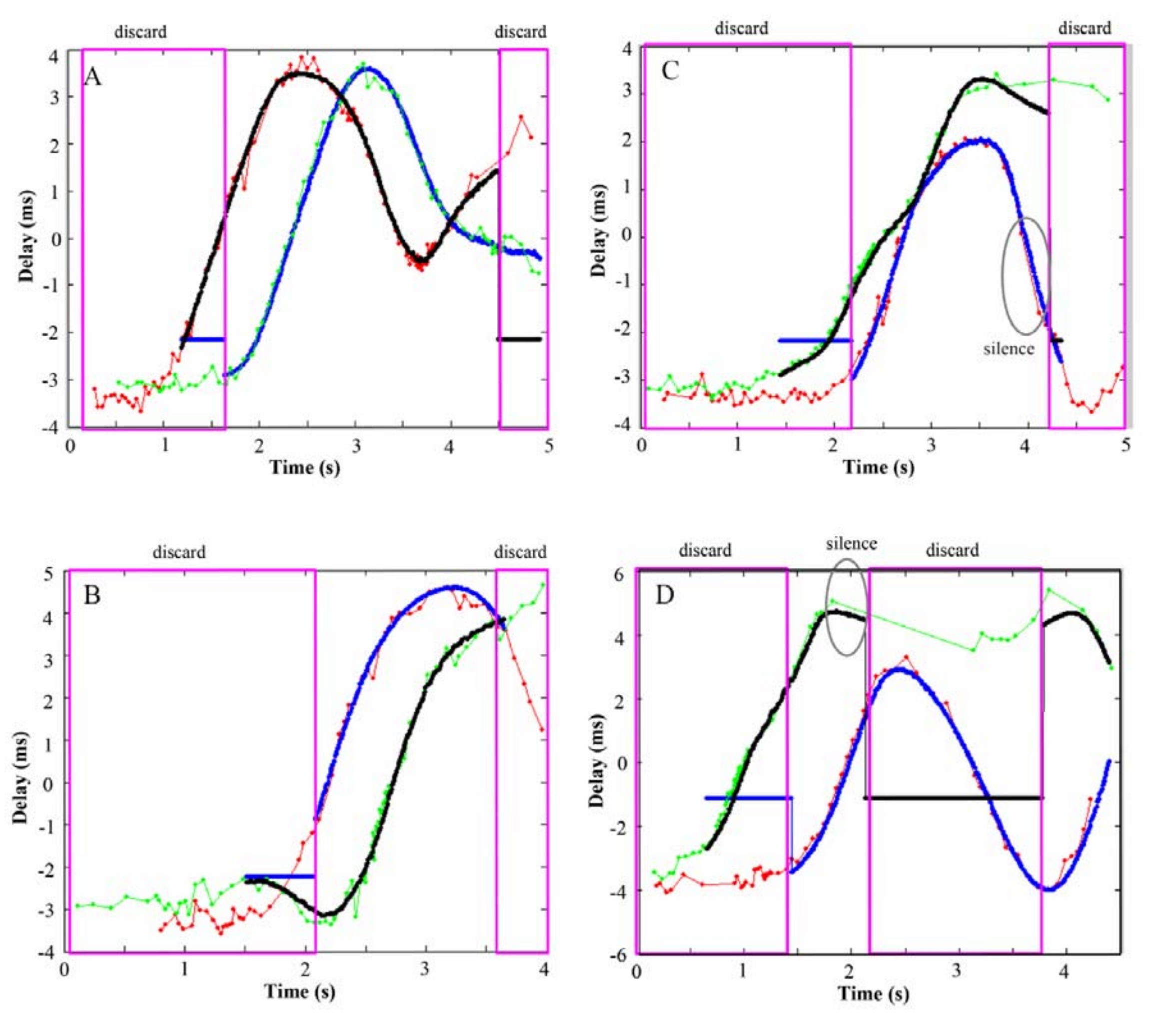


Figure 3.9 Examples of call assignment when comparing actual and estimated audio delays. The x-axis shows time and the y-axis refers to audio delays, both actual and estimated (ms). Each panel shows data from on trial segment. The magenta squares mark the segments which were discarded due to unreliable call assignment. Blue (Bat A) and black (Bat B) lines represent the estimated audio delays, which were calculated from position data. Red (Bat A) and green (Bat B) lines are the actual audio delays between floor microphones, and each red/green dot refers to one vocalization. The gray circles in (*C*) and (*D*) show silent periods.

Chapter 4: Adaptive echolocation behavior in bats, *Epetsicus fuscus*, in the presence of conspecifics

Echolocating bats emit ultrasonic pulses and listen to returning echoes to probe their surroundings. Bats adapt their echolocation call design to cope with dynamic changes in the acoustic environment, including habitat change or the presence of nearby conspecifics/heterospecifics. Seven pairs of big brown bats, *Eptesicus fuscus*, were tested in this study to examine how they adjusted their echolocation calls when flying and competing with another individual for food. Results showed that differences in five call parameters, start/end frequencies, duration, bandwidth and sweep rate, significantly increased in the two-bat condition, compared with the baseline data. In addition, the magnitude of spectral separation of calls was negatively correlated with the baseline call design differences in individual bats. Bats with small baseline call frequency differences showed larger increases in call frequency separation when paired than those with large baseline frequency differences. Bats are able to avoid signal jamming through pre-existing differences in time-frequency structure of calls if their baseline separation in call design is large. Call design differences were also influenced by physical spacing between two bats. Calls of paired bats exhibited the largest design separations when inter-bat distance was shorter than 0.5 m, and the separation decreased as the spacing increased. All individuals modified at least one baseline call parameter in response to the presence of another conspecific. Dissimilarity between the time-frequency features of sonar calls produced by different individuals aids each bat in segregating echoes from its own sonar vocalizations and acoustics signals produced by neighboring bats.

4.1 Introduction

Auditory scene analysis is the process that allows listeners to segment, integrate and segregate sounds in a complex acoustic environment into meaningful streams (Bregman, 1990; Hulse, 2002). For example, when a sentence spoken by one person, together with background noise from the environment, arrives at a listener's ear, the listener must segment the acoustic signals, integrate meaningful segments, and segregate these sounds from background noise. The ability to analyze complex auditory scenes is exhibited by humans and other animal species, such as birds and frogs, which rely heavily on acoustic communication.

Bregman (1990) provides numerous examples demonstrating that a human listener can separate and identify auditory objects by listening to differences in the pitch, timbre, melody and temporal pattern of a sound sequence. Auditory signals that fall in different frequency bands, for example, can provide a cue for a human listener to segregate sounds into separate auditory streams. A listener tends to segregate acoustic signals with large frequency differences into separate auditory streams, and to group those with small differences in frequency into the same auditory stream (Carlyon, 2004; Darwins et al., 1997; Moore and Gockel, 2002).

Spectral or temporal cues used by human listeners can be applied to the understanding of auditory scene analysis in animal models as well. Previous studies have demonstrated that frequency separations and differences in temporal patterns of acoustic stimuli are important factors that affect auditory stream segregation in fish, anurans and birds. Goldfish can segregate two sequences of pulses according to the differences in repetition rates and spectral features (Fay, 1998, 2000). Separation in spectral features of vocalizations and call timing are crucial factors that affect auditory scene analysis in frogs (Farris et al., 2005; Greenfield and Rand, 2000; Narins, 1992; Schwartz, 1993) and birds (Hulse et al., 1997; Wisniewsky and Hulse, 1997).

It is particularly important for echolocating bats to perceive and interpret auditory scenes, because they generate sonar pulses and listen to the features of echoes reflected from objects to perceive their surroundings. Their ability to orient, capture prey and avoid obstacles all depend on correctly grouping and segregating echoes from sonar targets in a complex environment and on differentiating their own calls/echoes from those produced by other bats in their surrounds.

Background noise and calls/echoes from other animals may influence a bat's perception of auditory objects. Past studies have reported that bats modify the spectral-temporal features of their vocalizations in response to conspecifics. Field recordings have shown that bats flying in groups produce calls with different frequencies and/or temporal patterns than those flying alone (Obrist, 1995; Ulanovsky et al., 2004). A playback experiment showed that *Tadarida brasiliensis* raised the end frequency of the frequency modulated (FM) sweep in response to playback jamming signals, whose frequencies were equal to the average end frequencies of this species' sonar calls (Gillam et al., 2007). It has been hypothesized that the bat modifies its call design in order to avoid interference from the vocalizations of conspecifics and improve localization of auditory objects.

Most studies of echolocation behavior in the presence of conspecifics have been conducted in the field, and lacked records of the 3-D positions of individual bats and call design changes in identified individuals. Differences in call design measured in most previous studies could have been evoked by the presence of conspecifics, but could also have been pre-existing inter-individual differences prior to the introduction of conspecifics. Only one study so far has demonstrated a shift of the bat's call frequency in response to the broadcast of jamming signals in unidentified bats in the field (Gillam et al., 2007).

We paired bats in a large flight room, presented a single prey item and recorded each bat's echolocation calls before (baseline) and during (two-bat) pairing. Recordings from ultrasound sensitive microphones and high speed stereo video enabled us to track vocalizations and flight behavior in individual bats. The question of whether differences in baseline call design of each bat in a pair are sufficient to avoid signal interference is also addressed here. We further consider how the similarity in call design and the inter-bat spacing affected the time-frequency structure adjustment in paired bats' sonar vocalizations. This is the first detailed study to address changes in sonar call design of identified echolocating bats in response to vocalizing conspecifics as a function of inter-bat separation. Results of this study extend our understanding of the echolocating bat's active vocal control in the analysis of auditory scenes.

4.2 Materials and Methods

4.2.1 Animals

We studied the vocal behavior of eight big brown bats, *Eptesicus fuscus*, and data from seven pairs are reported here. Bats were collected from different regions in Maryland **(**#SCO 42501**)** and kept in captivity in University of Maryland, College Park, USA. The animal housing facility maintained relatively stable temperature (24-28°C) and humidity (30-50%). The light/dark cycle in the room was reversed by 12 hrs to ensure that bats were at their most active periods during the behavioral experiment. The weight of each bat was between 14 and 16g, typical of an adult big brown bat. All animal care and experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Maryland, College Park.

4.2.2 Experimental setup

All eight bats were first trained to fly and capture a tethered mealworm in a large anechoic flight room (7 x 6 x 2.5 m) equipped with synchronized high speed audio and video equipment. After each bat reached the success capture rate of 80%, we began to record its echolocation calls and flight paths. During data recording, only long-wavelength lighting (>650 nm) was available, preventing the bat from using visual cues to localize the target and conspecifics (Hope and Bhatnagar, 1979).

Bats were tested in two experimental conditions, baseline and two-bat conditions, with 10 to 20 trials per day in each condition. Baseline data were recorded when a bat flew and captured a tethered mealworm alone in the room. Two-bat data were collected when paired bats flew and competed to capture a single tethered mealworm. Baseline and two-bat data were recorded on different test days. Ten trials per day over four test days were recorded in the baseline condition, yielding at least 40 baseline trials. Fifteen trials per day over a minimum of three test days, yielding at least 45 two-bat trials, were recorded in the two-bat condition after completely finished collecting baseline data. Only 20 to 30 trials per individual/pair with high quality audio and video recordings from each condition were selected for analysis.

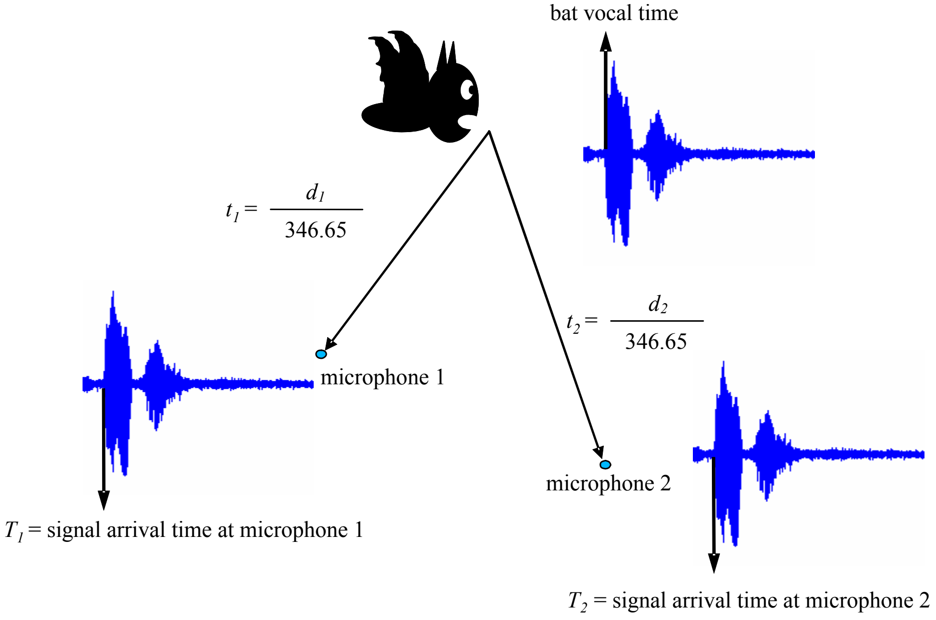
4.2.3 Data recordings

Audio data were recorded with three ultrasound sensitive microphones (UltraSound Advice, London) on the floor, and video data were recorded with two high-speed digital video cameras (Kodak MotionCorder Analyzer, Model 1000, 240 frames per second) mounted in two adjacent corners of the flight room, permitting 3-D reconstruction of the bat's flight path. An eight second circulating buffer of audio and video recordings was end-triggered synchronously by the investigator when the bat made contact with the tethered worm in each trial. The audio and video data from each trial were analyzed off-line using two custom MATLAB programs (see below).

4.2.4 Data analysis

A custom MATLAB program was used to analyze audio data, and five parameters were applied to characterize the call design of a frequency modulated (FM) sonar vocalization. These five parameters are duration (ms), bandwidth (kHz), start and end frequencies of the FM sweep (kHz) and sweep rate (kHz/ms), all taken from the fundamental. Sweep rate is calculated by dividing bandwidth by duration and describes the slope of the FM call. Data analysis of video recordings was accomplished by digitizing each bat's and microphone's position and reconstructing 3-D flight path via another custom MATLAB program.

Data analysis for audio recording in the two-bat condition was different from the one-bat condition, because the ultrasonic microphones recorded all vocalizations from both bats, and it was necessary to associate a given echolocation call with the individual bat that produced it. For the two-bat condition, we first visually inspected all echolocation calls in the three audio recording channels, and assigned calls manually to each bat according to differences in signature using the same custom MATLAB program employed to analyze the baseline audio data. Each call's onset times in two different microphones were marked in order to calculate the *actual audio delay* (Figure 4.1). Because the two microphones were positioned at different locations in the room, a call which was produced by a bat would reach these two microphones at different times. The *actual audio delay* of one call was calculated by subtracting the call start time in microphone one by the call start time in microphone two. The position of the two microphones and paired bats were already established by video data analysis. The *estimated audio delay* was computed by estimating the travel time differences in calls from the bat's position to each of the two microphones. When we assigned a given call to the vocalizing individual, we could confirm that the *actual* and *estimated audio delays* were identical. Therefore, by comparing the values of *actual* and *estimated audio delay*, we could unambiguously associate each echolocation call to the bat who vocalized. Detailed analysis methods were reported in Chiu et al. (2008).



Actual audio delay = $T_1 - T_2$

Estimated audio delay = $t_1 - t_2$

Actual audio delay = Estimate audio delay, if the call assignment is correct

Figure 4.1 Schematic of assignment of echolocation calls to individual bats. The sound speed is 346.65 m/s; T1, T2 are the time one signal arrived at each microphone; t1, t2 are the time one signal arrived at each microphone, which are estimated from video recordings; d1, d2 are the distance between bat and each microphone. Real audio delay is calculated from audio recordings and is equal to T1-T2. Estimated audio-delay is calculated from video recordings and is equal to t1-t2. Values of real audio delay and estimated audio delay are the same if a call was assigned to the correct bat.

4.3 Results

Call design modifications by one bat to increase the differences between its vocalizations and those of conspecifics flying in proximity could serve as a strategy to avoid signal jamming. Sequential calls made by different bats in a pair were analyzed to determine if the features of one bat's vocalizations are influenced by closely timed calls of another conspecific. Here we investigated possible factors driving call modifications, including baseline differences in call design and spatial separation between bats. Separation in call design during pairing (two-bat condition) was also compared with call design differences between the two bats before pairing (baseline condition) to determine if the signal separation in the two-bat condition was the consequence of another bat's presence. Analysis of baseline data revealed that some bats have more similar call designs when they flew alone; therefore we studied whether or not the similarity in baseline call design could predict call adjustments when individuals were paired. The effect of inter-bat spacing on sonar call adjustments is also examined in this study.

4.3.1 Sequential call analysis

Individual bats usually show differences in call design, and these differences may be used to avoid call interference from neighboring conspecifics. Figure 4.2 shows the flight trajectories, relative position and call design of each bat in a pair from two selected trials. One bat was following another bat in the first example and gradually shortened its distance to the other animal (Figure 4.2A, B). The separation in start frequency between paired bats' sonar calls increased as the inter-bat distance decreased. Small separations were observed in their end frequencies, and changes in the inter-bat spacing did not appear related to these separations. These two bats maintained a certain amount of separation in duration and sweep rate, but the separation also did not change with inter-bat spacing. Bats in the second example were flying toward and then away from each other (Figure 4.2C, D). Unlike the first example, the two bats in this trial showed similar call design until they flew close to each other. Differences between calls were the largest when the spatial separation between the two bats was the shortest. In this example, the magnitude of difference in call duration and sweep rate depended on spatial separation between paired bats.

The examples above suggest that differences in call design between two bats sometimes occurred only in a short period of time when the bats flew close together. Bat echolocation calls may also exhibit context-specific changes; therefore, we examined the call design differences between two consecutive vocalizations produced by different bats in pairs. Figure 4.3 shows two sequences of calls with various start frequencies from two different bats in a pair. Two consecutive vocalizations, produced by the same bat, were excluded in this analysis because the main focus here is to determine differences in call design between paired bats in response to the calls of the other. Sequential call analysis example in Figure 4.3 only includes the absolute differences between the following pairs of calls: A2-B1, B1-A3, A3-B2 and B4-A4. If the interval between two consecutive vocalizations from different bats was greater than 20 ms or one bat produced a vocalization before or while it heard another bat’s vocalization, these data were excluded from this analysis. The time interval of 20 ms was chosen, because the sound propagation distance in this time period is about 7 m, which is almost the length of the flight room (speed of sound is 346.65 m/s at 25°C). High repetition rate feeding buzzes, which are used by bats in the terminal phase of prey capture, were also excluded from this analysis, because the vocal adjustment during this period of time is due to the presence of prey rather than conspecifics.

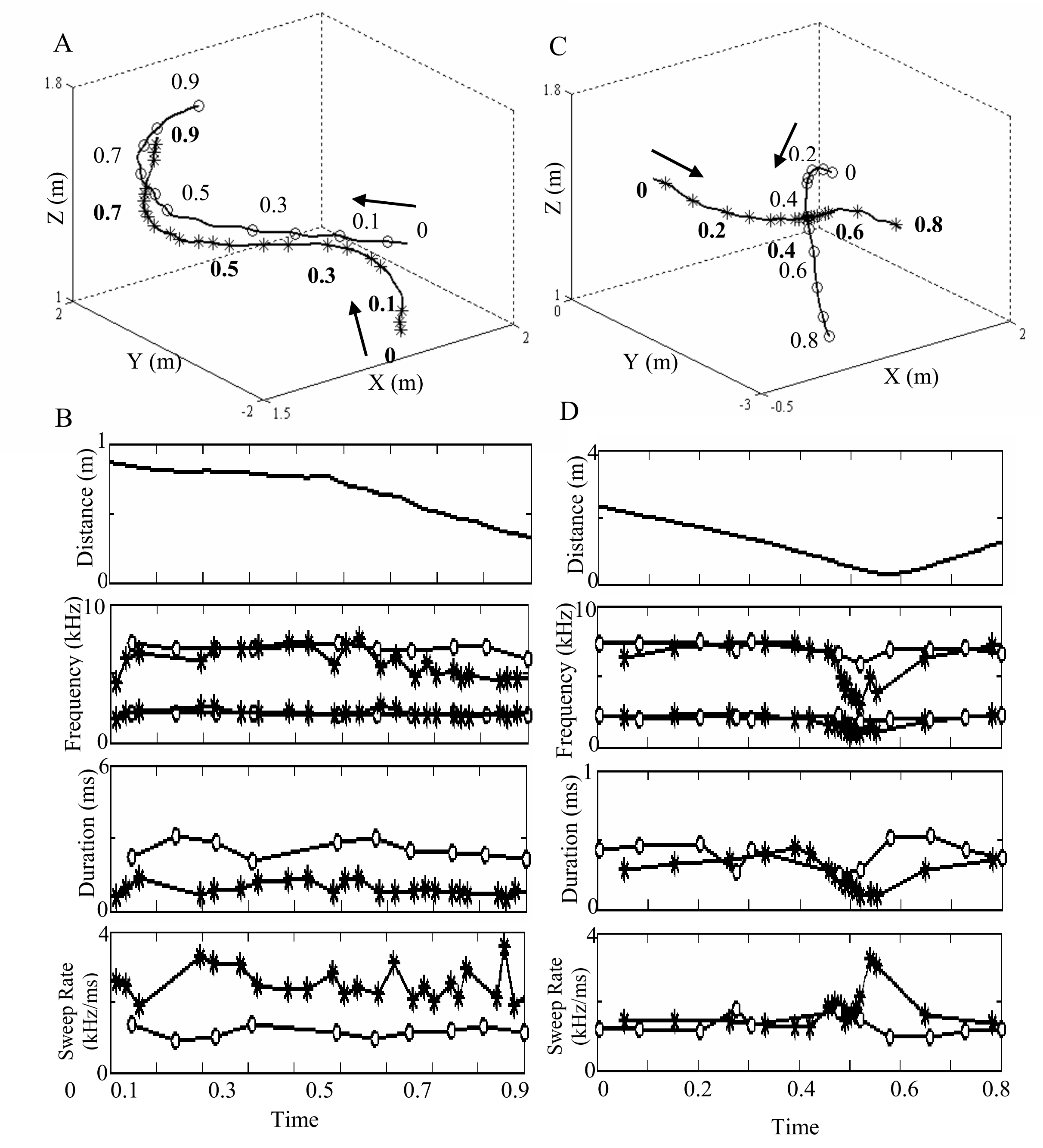


Figure 4.2 Two examples show the relative position of paired bat and the design of their vocalizations. The 3-D flight paths of each bat in (A) example #1 and (C) #2. The number beside each flight path is the trial time and matched the x-axis in panel (B) and (D), respectively. Each asterisk and open circle represent one vocalization from Bat A (asterisk) and Bat B (open circle). The inter-bat distance and call design of Bat A and B in (B) example #1 and (D) #2. The asterisk represents vocalizations from Bat A and the opened circle represents vocalizations from Bat B. From the upper to bottom panels are inter-bat distance, start/end frequencies (those two curves with higher values are start frequencies and the other two are end frequencies), duration, sweep rate.

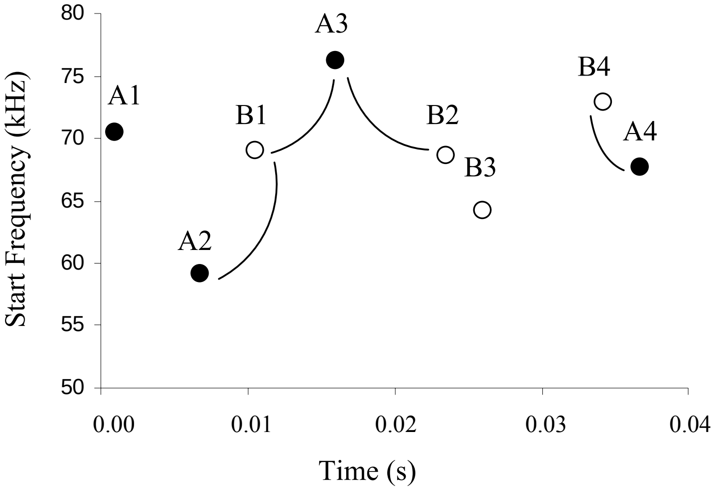


Figure 4.3 Schematic illustration of data analysis for sequential calls. Each point represents the start frequency of one vocalization and different letters means different bats. For example, A1 is the first call Bat A produced and B3 is the third call Bat B generated. The x-axis is time and y-axis is frequency of calls. Lines between two calls represent two consecutive vocalizations produced by different bats and absolute differences between these two sequential calls are used to analyze separation in paired bats' call design. Two consecutive calls, which were not connected by lines, were not included in data analysis because they were produced by the same individual.

We computed the absolute differences between two sequential vocalizations in calls produced by different bats across trials and found that separations in each call parameter were all significantly larger than zero and also significantly greater than call design separation prior to pairing (one sample *t*-test, $p < 0.0001$). Histograms of separation in each call parameter in the two-bat condition and their baseline separations are shown in Figure 4.4. Nearly 90% of vocalizations exceed the baseline separations in duration and sweep rate when two bats flew together, while over 60% of vocalizations in the two-bat condition show separations in start/end frequencies and bandwidth greater than baseline data. Overall, paired bats increased their call design separation when flying together, compared with their baseline differences in call design.

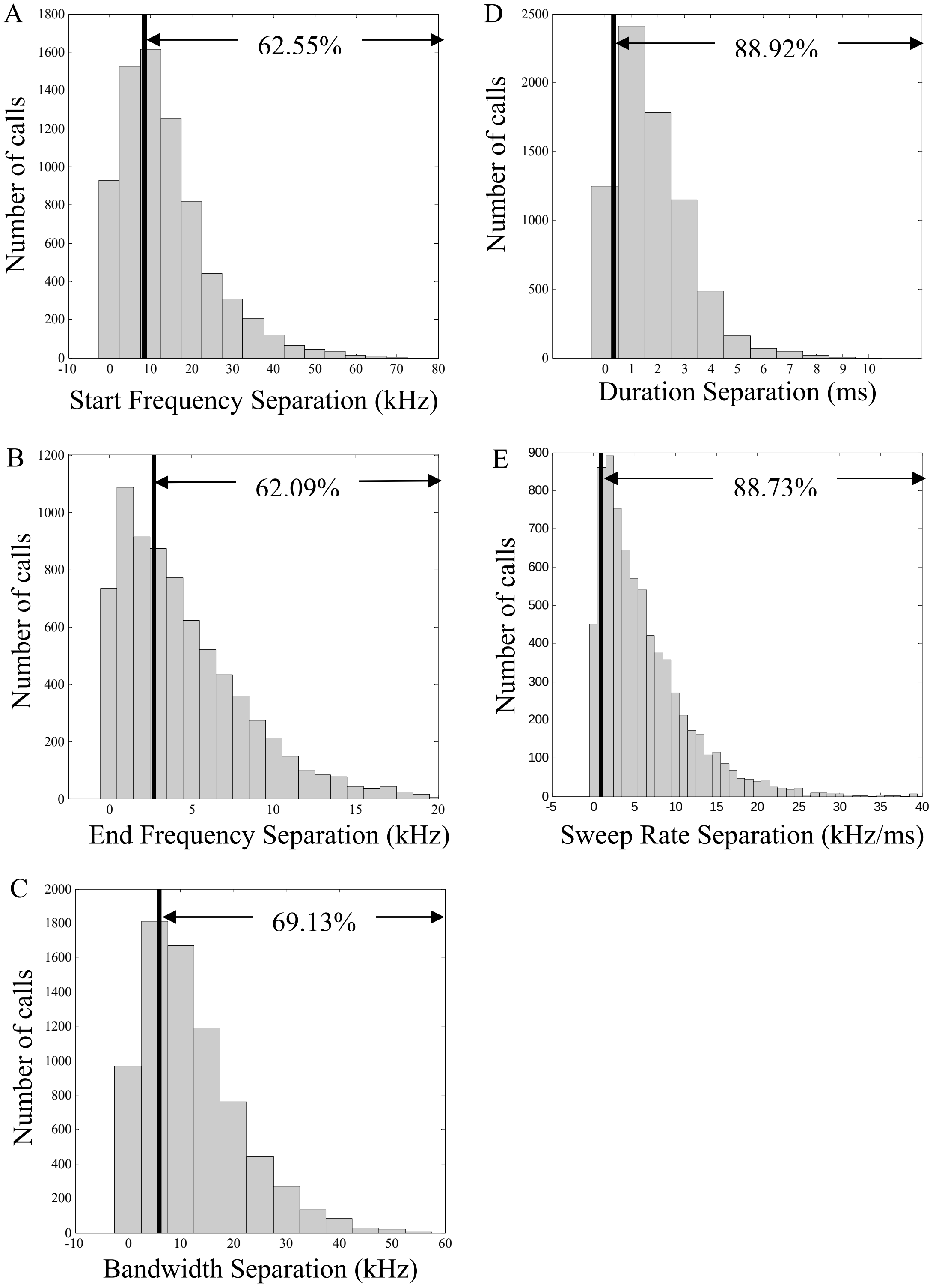


Figure 4.4 Distribution of call design separation between two sequential calls produced by different bats when flying together. The black line in each histogram indicates the baseline separation, which is the difference in call design between two bats when flying alone. The percentage marks the percentage of calls that exceed the baseline separation. Call parameters analyzed here are (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate.

4.3.2 Similarity in baseline call design

Individual bats in this study showed different amounts of separation in their baseline call design, and the similarity between paired bats' call design influenced how each bat adjusts its calls. The magnitude of call design adjustment represents the increase in call design separations between paired bats from the baseline to two-bat condition. It computes the absolute difference in separation between the baseline and two-bat condition. Three (Pairs 1, 3 and 4) out of seven bat pairs showed large baseline separation in start/end frequencies and bandwidth, and four others (Pairs 2, 5, 6 and 7) showed small baseline separation. A negative correlation was found between the baseline separation of spectral call features and the magnitude of call design adjustment under paired conditions (Figure 4.5A-C). Figure 4.5A-C show that the bat pairs with most similar baseline call frequencies (start/end) and bandwidth increased their differences in these parameters when they flew together and the magnitude of call adjustment varied with baseline call similarity. Changes in call duration and sweep rate in the two-bat condition were not predicted by baseline separation of these call parameters (Figure 4.5D, E).

Similarity in baseline call frequency was also related to how the bat adjusted its call frequency in response to nearby conspecifics. We calculated the proportion of one bat's vocalizations with higher start/end frequencies than the other bat in a pair, and selected the proportion belonging to the individual with higher baseline call frequency to plot as a function of the baseline frequency separation (Figure 4.6). A positive correlation was found between these two parameters, which means that for those bat pairs with greater start frequency separations in the baseline condition, most of the time the individual with the higher start frequency maintained this higher frequency in the two-bat condition. The same relationship also applies to call end frequency. Therefore, whether the bat called at a higher frequency than the other bat in the two-bat condition depended on baseline call frequency design.

4.3.3 Spatial separation

Differences in call design were affected by the spatial separation of paired bats. A one-way ANOVA was applied to test the effect of inter-bat distance in call design separation, and Scheffé's test as a post-hoc test to examine which spatial separation affected call differences significantly more than others. The largest separations in start and end frequencies, duration and bandwidth occurred when the inter-bat distance was shorter than 0.5 m (Figure 4.7). When the inter-bat distance was between 0.5 and 1 m, the sweep rate difference between paired bats was the greatest. The separation in call design generally decreased as the inter-bat distance increased. Differences in all call design when inter-bat distance was shorter than 0.5 m was always significantly greater than those when inter-bat distance was longer than 2 m. All differences in call parameters, although influenced by spatial separation between paired bats, were still larger than the baseline separation.

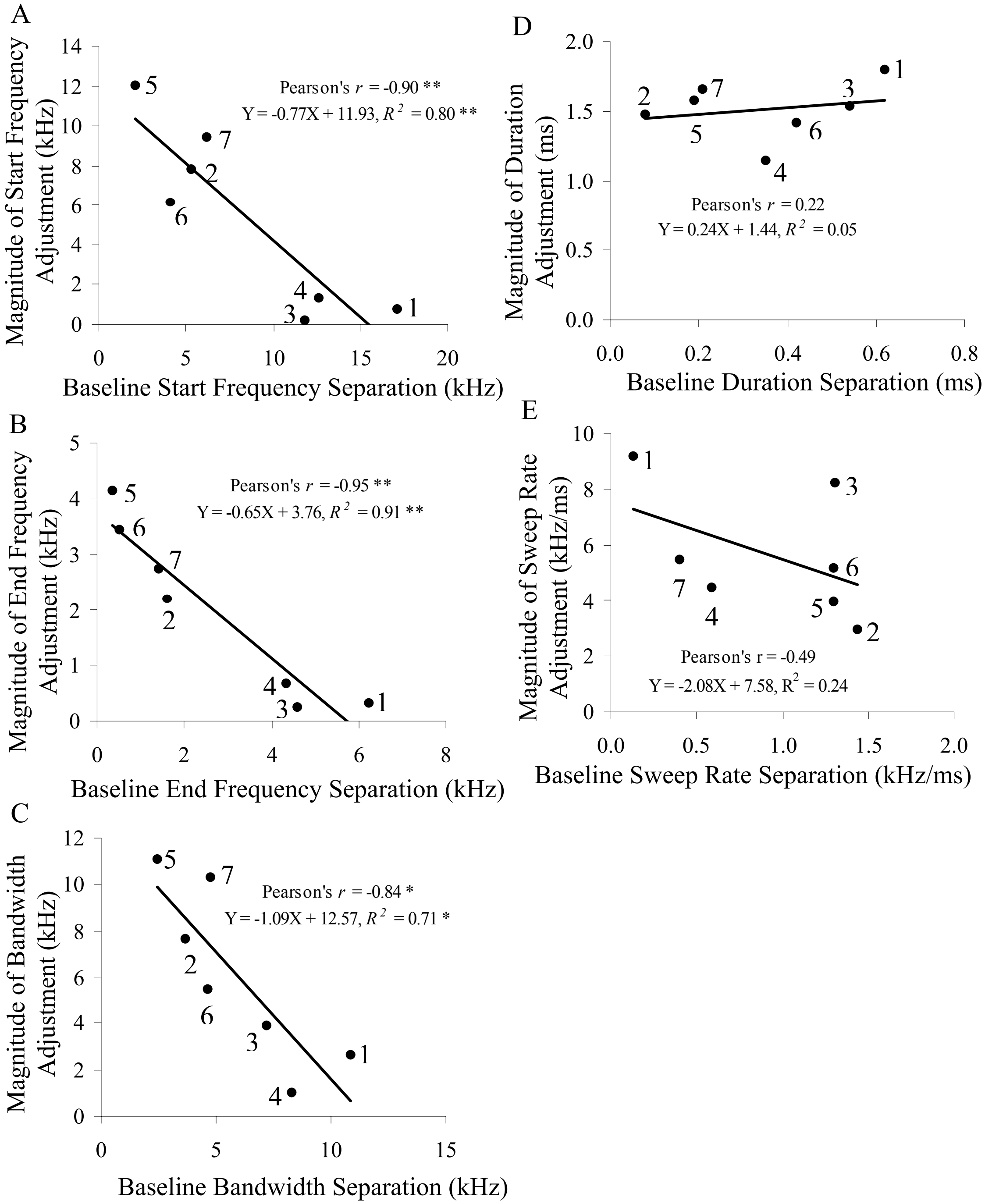


Figure 4.5 The correlation between each pair's baseline separation and the magnitude of adjustment from baseline to two-bat condition in (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate. * means $p < 0.05$ and ** means $p < 0.01$. Each data point represents one bat pair and the number next to each point refers to different bat pairs. Only spectral parameters, start/end frequencies and bandwidth, show significant negative correlation.

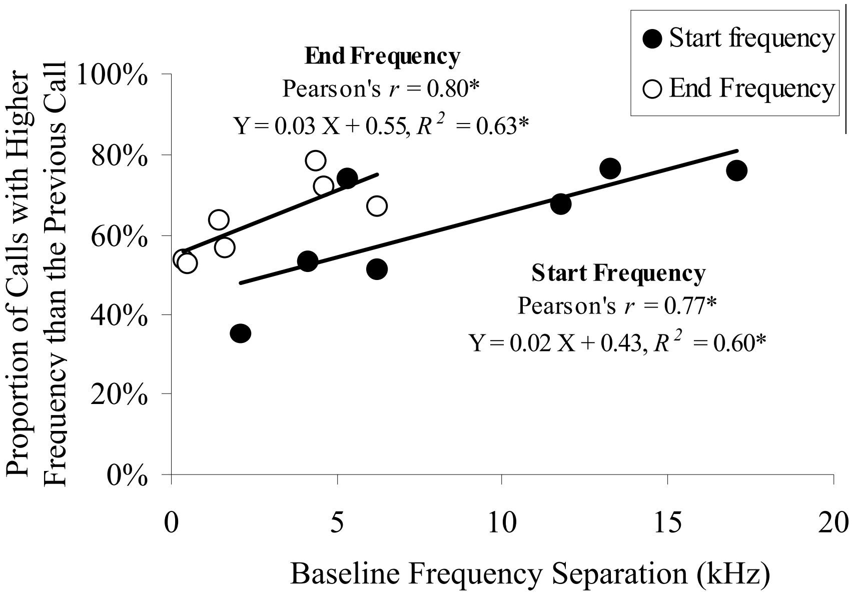


Figure 4.6 The correlation between start frequency or end frequency separation and proportion of calls with higher start frequency or end frequency than the preceding call. The closed circle represents start frequency and the opened circle means end frequency in each bat pair. The bat with higher start frequency tended to keep a higher frequency than the other bat in the pair when the start frequency separation is large for this pair. End frequency shows similar trend to start frequency.

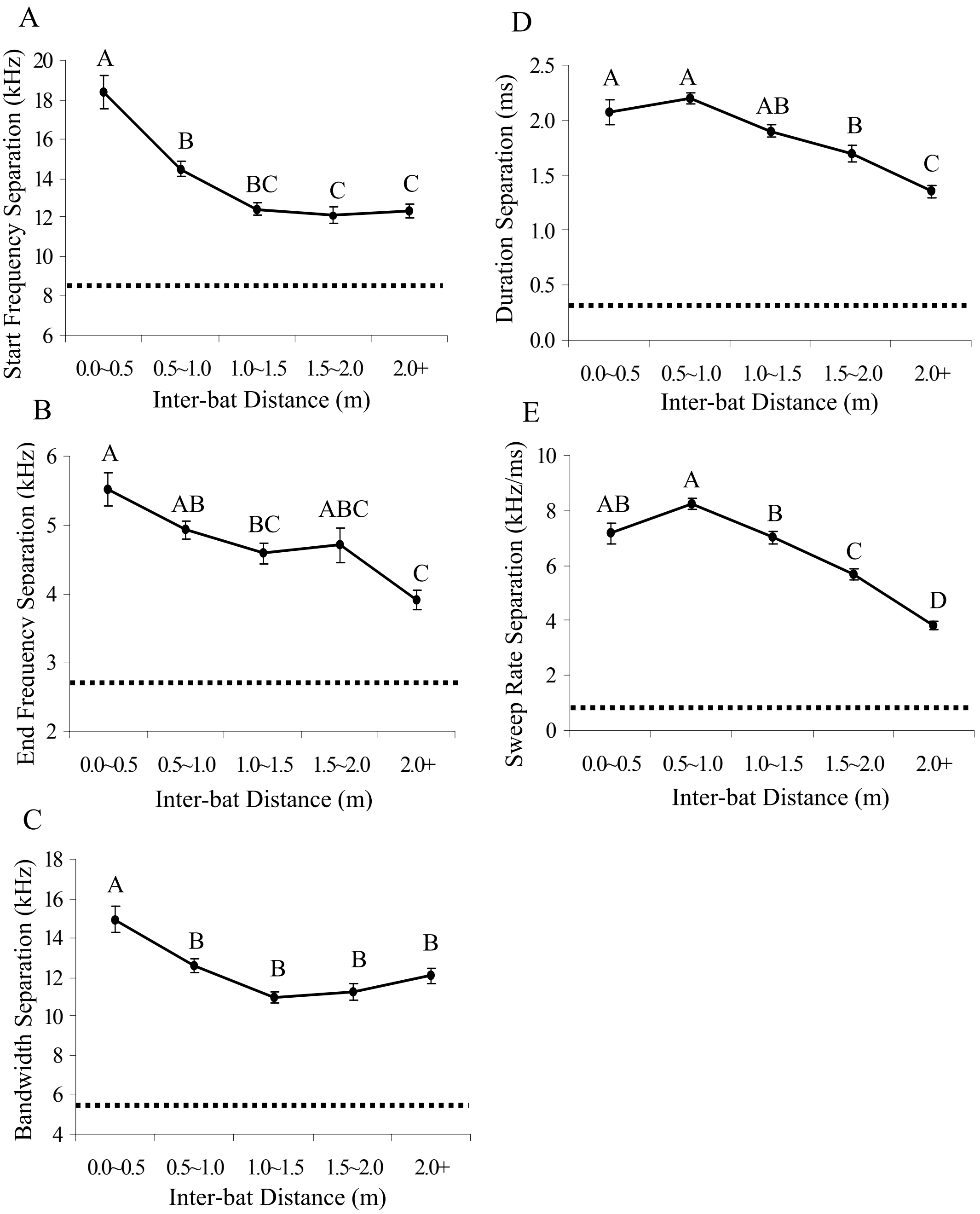


Figure 4.7 The mean comparison of each call design separation between two consecutive calls at different inter-bat distance by one-way ANOVA and error bars indicate standard error of mean. Different letters mean there is a significant difference between two values. The dot line in each panel shows the amount of separation in the baseline condition. Call designs are measured by five parameters: (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate.

4.3.4 Call modification

Sequential call analysis shows the dynamic and short-term call design changes in paired bats. Here we examine differences in vocalizations between baseline and two-bat conditions in each bat in a pair to determine general pattern of call structure adjustment in individual bats. Call design in the two-bat condition minus that in the baseline condition represented the amounts of change from the baseline condition, and all bats modified at least one call parameter when paired with another bat (Figure 4.8). Call design changes in different pairs examined by one sample *t*-tests revealed a significant decrease in start frequency and bandwidth in all individuals, except one bat in Pair 5. This particular individual in Pair 5 only modified its sweep rate when paired with another bat, but another individual in Pair 5 modified its start frequency, bandwidth and sweep rate. No consistent change was observed in the direction of sonar call's end frequency, duration and sweep rate, but most bats made either spectral or temporal adjustments in their call designs when paired with another individual. Five individuals did not show a significant increase in the end frequency of their vocalizations when paired, and both bats in Pairs 2 and 5 did not change the end frequency of their calls. When one individual in a pair shifted its call design, the other bat did not necessarily modify its call design in the opposite direction. Most bats adjusted their start frequency and bandwidth in the two-bat condition, and end frequency was the call parameter that exhibited the fewest changes.

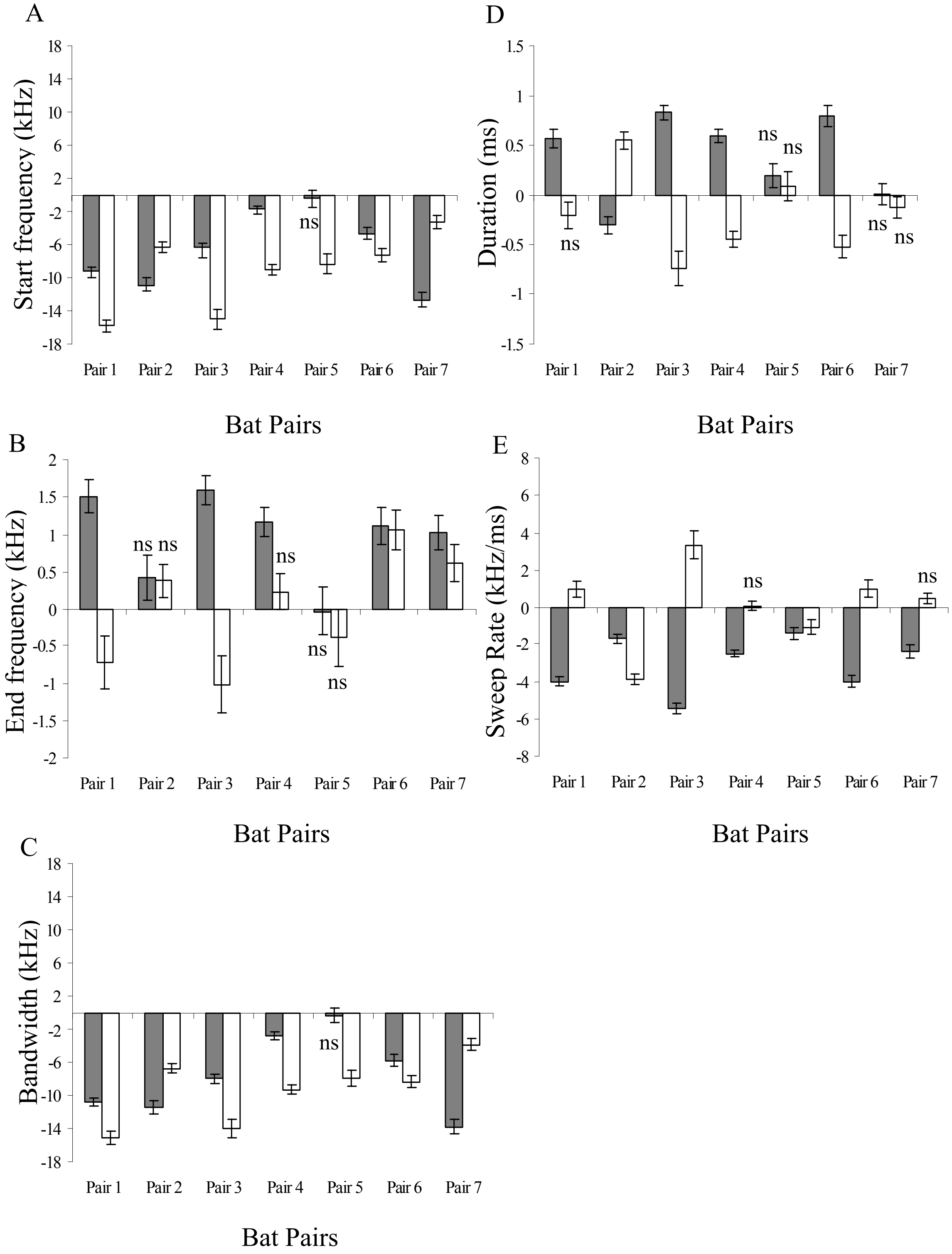


Figure 4.8 The amount of deviation from the baseline data for each bat in each pair. White and grey bars indicate data from different bats in a pair. Five call parameters were presented here (a) start frequency, (b) end frequency, (c) bandwidth, (d) duration and (e) sweep rate. All deviated amounts are either significantly larger or smaller than zero, except those marked with n.s. The x-axis shows bat pairs and these bat pair number corresponds to those in figure 5. Error bars represent standard error of the mean.

4.4 Discussion

Human and other animals can distinguish and make sense of auditory streams from complex acoustic scenes. This study explores how the echolocating bat orients in a dark flight room in the presence of another individual whose sonar signals are similar to its own. Results show that bats modified their call design significantly in the two-bat condition and paired bats enlarged the differences between the time-frequency structures of their vocalizations. These differences in call design were affected by the spatial separation between paired bats and by the baseline call design of the individuals. Distinct spectral features or temporal patterns can help bats integrate and segregate auditory streams in a complex environment (Bregman, 1990; Moss and Surlykke, 2001). The results of this study suggest possible acoustic cues, arising from call design differences, for echolocating bats to segregate echoes from their own sonar vocalizations, without confusion from those of conspecifics.

4.4.1 Rules for signal modification I: individual signature and similarity in call design

Signals with individual signature have been discovered in active sensing animals and one possible advantage of these personal signals is for animals to recognize the identity of conspecifics. Wave-type weakly electric fish produce an individual-specific electric organ discharge (EOD) frequency and are capable of discriminating signals generated by different individuals (McGregor and Westby, 1992). Adult female bats can identify their own pup’s isolation calls when many other pups are calling in the background simultaneously. Each pup produces isolation calls with spectral and temporal features distinct from others, and female bats may recognize their own pups by listening to these individual-specific calls (Balcombe, 1990; Gelfand and McCracken, 1986; Knörnschild et al., 2007). A psychoacoustic experiment shows that female greater spear-nosed bats, *Phyllostomus hastatus*, are capable of discriminating a specific pup's isolation calls from others (Bohn et al., 2007).

Not only do pups show individual signatures in their isolation calls but also adult bats. Similar inter-individual differences in call design have been observed in several bat species, with few exceptions (Siemers et al., 2005; Siemers and Kerth, 2006). Echolocation calls of *E. fuscus* show individual identity, age and group variation (Masters et al., 1995), and female bats recognize the gender of other bats by listening to their vocalizations (Kazial et al., 2001). Other bat species, such as *Molossus molossus*, *Myotis lucifugus*, *Nycticeius cubanus*, *Otomops martiensseni*, also produce distinct echolocation calls for those individuals from different groups (Fenton et al., 2004; Kössl et al., 1999; Mora et al., 2005; Pearl and Fenton, 1996).

Previous studies have demonstrated that conspecific bats often produce calls with different design features and bats are capable of discriminating call design differences at the individual level. Differences in these individual-specific calls may be enough for the auditory system to segregate acoustic streams from different sources. The negative correlation between call features of bats flying alone and the magnitude of change when paired indicates that echolocating bats can use personal signals to avoid call jamming from conspecifics, as long as the differences in these individual-specific signals are discriminable. In this study, each individual in a pair increased differences in their calling frequencies or bandwidth if their baseline vocalizations showed similar spectral features to the bat with which it was paired. Paired bats, whose calls already showed considerable amount of separation in the baseline condition, did not increase their differences in start/end frequencies and bandwidth. For those pairs with less similar baseline calling frequencies, the bat with the higher frequency vocalizations tended to maintain higher calling frequencies.

The estimated amount of separation required for paired bats to distinguish their own calls/echoes from those of a conspecific can be inferred from this study. The average separations in call design of paired bats when flying together were 13.51 kHz for start frequency, 4.62 kHz for end frequency, 1.83 ms for duration, 12.05 kHz for bandwidth and 6.11 kHz/ms for sweep rate. These average values here provide an estimate of discriminable spectral and temporal feature separations in call design of paired big brown bats. Two pipistrelle bats, *Pipistrellus pipistrellus* and *P. pygmaeus*, produce calls with peak frequencies of 45 and 55 kHz, respectively. Their call design changed when they flew with conspecifics, but their calls remained the same when flying with heterospecifics (Bartonička et al., 2007). The authors of this study suggested that call difference between these two pipistrelle species, which is 10 kHz, is enough to avoid jamming among heterospecifics. Separation of 10 kHz in the peak frequencies of pipistrelle bats is between the average start frequency (13.51 kHz) and end frequency (4.62 kHz) separation in this study. These findings suggest a reference for conducting further psychoacoustic experiments on the bat's ability to discriminate signals with different time-frequency structures.

4.4.2 Rules for signal modification II: spatial separation

We analyzed in detail vocal changes the bat made in response to the presence of the other bat at a particular spatial separation, because recording and analysis methods permitted us to associate each call with an identified individual and its 3-D position with respect to the animal. Short term changes in vocalizations can be detected by a sequential call analysis, since the bat may enlarge differences between its calls and those of the other bat for a short period of time when the call interference is large. We discovered that the separations in call design are dependent on the inter-bat distance. Start/end frequencies, duration and bandwidth of the FM sweep showed larger differences between paired bats when the inter-bat distance was shorter than 0.5 m. The magnitude of call interference became large when paired bats flew close to each other and one bat in a pair sometimes stopped vocalizing for more than 0.2 s to avoid signal jamming from conspecifics. Silence is a strategy for the echolocating bat to avoid call interference when flying with conspecifics, as we reported in an earlier publication (Chiu et al., 2008). When both bats vocalized at short inter-bat distances, the separation of their call features increased as well. Our data suggest that bats increased their call feature separations to avoid interference caused by another bat nearby and greater inter-bat distances could help bats resolve the problem of conspecific sonar interference. Other animal species have been found to use spatial separation to avoid call interference, such as male frogs in a chorus, which typically maintain a minimum distance (Gerhardt and Huber, 2002).

4.4.3 Call modification

Big brown bats changed features of their echolocation calls when flying with conspecifics. The question of whether the observed differences in call design are the result of active jamming avoidance or simply due to individual-specific call design can be resolved here by comparing call modifications in the two-bat condition with baseline vocalization data. Call modification can be attributed to the presence of conspecifics, because most individuals in pairs showed significant changes in each call parameter when flying alone compared with flying with another conspecific. Call design separation is affected by the spatial separation of paired bats and baseline similarity in call design, which further suggests that the bat actively adjusts its call design to avoid signal interference from conspecifics.

Animals constantly adjust their call frequencies and timing when conspecifics are in proximity. Several bat species, including *Rhinopoma hardwickei, Balantiopteryx plicata, Tadarida brasiliensis* and *T. teniotis*, have been reported to adjust their call frequencies when flying in groups (Bartonička et al., 2007; Habersetzer, 1981; Ibáńez et al., 2004; Ratcliffe et al., 2004; Ulanovsky et al., 2004). Some bat species modified temporal features rather than spectral features of their vocalizations to avoid call interference from conspecifics (Obrist, 1995). Ulanovsky et al. (2004) and Gillam et al. (2007) have reported end frequency adjustments in vocalizations of two bat species, *T. brasiliensis* and *T. teniotis*, when flying with conspecifics. Although big brown bats, *E. fuscus*, in this study also showed call modification in end frequency, the amount of adjustment in start frequency is more notable than end frequency. Another study has discovered a larger call frequency separation in start frequency than end frequency in *E. fuscus* and *Lasiurus cinerus*, but not in *L. borealis* and *Euderma maculatum*. Previous and present research findings suggest interspecific variation exists in call modification of echolocating bats.

Research on other animal species has also reported modification in spectral and temporal features in the presence of conspecifics. Wave-type electric fish, which also rely on active sensing for orientation, shift frequencies of their electric organ discharge (EOD) to avoid signal jamming with conspecifics (Bullock et al., 1972; Watanabe and Takeda, 1963). Pulse-type electric fish increase or decrease the discharge rate of their electric organ to avoid signal overlap with another fish (Heiligenberg, 1991). Similar temporal and spectral modifications in signals used as a strategy to avoid signal interference have also been reported in other animals, which do not rely on active sensing (Egnor et al., 2007; Farris et al., 2005; Ficken et al., 1974; Greenfield and Rand, 2000; Serrano and Terhune, 2002).

Animals adopt different strategies to achieve a separation in signals and avoid jamming. Previous studies in electric fish have proposed some strategies about how two fish adjust their EODs to increase differences between their signals. For example, wave-type electric fish modify the frequencies of their EOD, and the one with the higher frequency increases its frequency and the other shifts its frequency in the opposite direction (Bullock et al., 1972; Watanabe and Takeda, 1963). No similar rule has been reported so far about how two or more bats adjust their call design to reach a sufficient separation to minimize interference from signals of conspecifics. Past research has reported an overall upward shift or downward shift in call frequencies of several bat species in response to neighboring conspecifics (Habersetzer, 1981; Ibáńez et al., 2004; Kössl et al., 1999; Miller and Degn, 1981; Ratcliffe et al., 2004; Surlykke and Moss, 2000). Gray sac-winged bats, *Balantiopteryx plicata*, shifted their peak frequencies slightly upward when flying in groups (Ibáńez et al., 2004) and *T. brasiliensis* shifted their end frequencies upward when a playback bat call was broadcast (Gillam et al., 2007). Bates et al. (2008) reported that the big brown bat shifted calling frequencies upward when lower jamming frequencies were broadcast and made downward shifts when higher jamming frequencies were broadcast. By contrast, the present study reports an overall downward shift in start frequency and bandwidth of the big brown bats' vocalizations when they flew in pairs, except one individual in Pair 5 maintained the same baseline start frequency and bandwidth. No clear modification pattern was found in three other call parameters, end frequency, duration and sweep rate. Although no clear overall vocal adjustment pattern was found when comparing each individual's call design changes in baseline and two-bat conditions, paired bats were still able to establish a large enough separation of its signals from another bat to avoid interference by dynamically changing call structure. The fact that paired bats did not collide with each other or show any sign of disorientation demonstrates that big brown bats have employed efficient strategy to avoid signal jamming from conspecifics.

The overall start frequency drop could be the consequence of detecting a nearby object (another flying bat in this case) at a close distance, since bats using FM signals tend to employ lower start frequency and shorter bandwidth calls when approaching a target (Schnitzler et al., 2003; Simmons et al., 1979). A possible explanation is that the bat may deliberately lower its call intensity to avoid call interference when flying with conspecifics and therefore our recording devices did not receive the high frequency parts of calls, due to the excess attenuation high frequency sounds (Lawrence and Simmons, 1982). Call intensity decrease due to the presence of conspecifics could be one vocal adjustment strategy the bat uses to avoid signal jamming. A reliable measurement of the bat's call intensity is required in the future to confirm whether bats decrease their call intensity or frequency to avoid signal jamming.

4.4.4 Auditory stream segregation

Gestalt psychologists suggest that several principles, such as similarity, proximity and closure influence human visual perception. For instance, humans tend to group visual objects together according to similar characteristics, such as color or shape. Bregman (1990) suggests that the same principles can be applied to auditory stream segregation and integration. The principle of similarity enables the auditory system to segregate and integrate complex sounds. Echolocating bats may apply these principles to distinguish its emissions/echoes from those of others, and to track echoes from moving target in a complex acoustic environment (Moss and Surlykke, 2001).

Increase in call design separation when flying with another bat provide a demonstration that the bat may use the principle of similarity in call design to integrate its own signals/echoes and segregate them from a conspecific's signals/echoes. Sweep rate separation increased in the two-bat condition, suggesting that the big brown bat changed the shape of its FM sweep to maximize differences from conspecifics' calls. A series of psychophysical experiments on range discrimination performance in the big brown bat demonstrate that the bat's range discrimination performance in phantom target experiments was impaired when the playback echo was replaced by signals of other bats with different call designs (Master and Raver 1996). They also tested range discrimination performance of the big brown bat when various interference signals were broadcast with target echoes. They reported that the degree of interference was affected by the similarity between interference signals and the target echoes. The echolocating bat needs echoes with similar time-frequency structure and FM sweep curvature to signals it produces to perform accurate ranging. Several altered echo models were also used to test if the bat's ranging ability would be affected by altered echoes, and results showed that sweep curvature differences in signals compromised the ranging ability of the bat (Masters and Raver, 2000). Another study in *Pipistrellus pipistrellus* reported that clicks from arctiid moth species did not affect the bat's range discrimination ability when broadcast randomly with respect to echo arrival times (Surlykke and Miller, 1985). However, big brown bats' range discrimination performance deteriorated when the click of ruby tiger moth (*Phragmatobia fuliginosa*) was broadcast within 1.5 ms before the echo return (Miller, 1991). Results from these studies suggest that calls that share similar time-frequency structure disrupt the bat's ranging ability the most. Therefore, minimizing the similarity in call design from conspecifics seems to be an appropriate strategy for the bat to avoid jamming and analyze auditory scenes when flying with conspecifics.

4.4.5 Two jamming avoidance strategies: vocal adjustment and silence

A recent research has uncovered that paired big brown bats tend to cease vocalizing at short inter-bat distance (Chiu et al., 2008). The present study on the same species with identical experimental setup suggests that big brown bats also tended to adjust their vocalizations in order to increase call design separations. Both studies have demonstrated that similarity in call design and spacing between paired bats are two important factors to affect bats' employment of these two strategies. These two factors also influence the interference level of vocalizations from conspecifics; therefore, these behaviors appear to function to minimize signal interference from conspecifics.

Sound intensity caused by another bat's echolocation calls becomes so intense when the bat flies near conspecifics that one bat goes silent to allow processing of acoustic signals from the environment. An echolocating bat shows sign of disorientation when it is prevented from using echolocation (Griffin, 1958), but a silent big brown bat is capable of orient in space when another bat is vocalizing in proximity (Chiu et al., 2008). The listening animal needs to be close to the vocalizing animal in order to use another bat's vocalization for orientation (Kuc, 2002; Xitco and Roitblat, 1996). An echolocating bat risks losing the ability to orient when shut off its echolocation but gains the advantage of avoiding severe signal jamming. Vocal adjustment seems to be a safer strategy for the bat to avoid signal jamming because the bat can still use echolocation for orientation, and silence can be viewed as a strategy to avoid extremely large interference caused by short inter-bat spacing with conspecifics.

Another advantage of silence strategy could be that it can resist signal jamming from a large number of conspecifics. A bat does not always fly alone in nature and it often encounter conspecifics/heterospecifics. Assume that vocal adjustment is the only strategy the bat uses to avoid signal jamming, then the bandwidth that is not interfered by other bats becomes narrower as the number of bats increases. Consider the fact that a bat usually flies out of its roost with many other individuals, it is reasonable to imply that bats have strategy other than vocal adjustment to avoid jamming. Silence seems to be a more likely strategy for a bat to employ when many conspecifics are flying around.

In summary, silence is a better strategy when interference from conspecifics is strong, whether it is caused by short inter-bat spacing to another individual or multiple conspecifics vocalizing at the same time; while vocal adjustment is superior when signals from conspecifics cause interference but cannot be used as cues for orientation.

4.5 Conclusion

A big brown bat encounters and interacts with conspecifics frequently in nature (Simmons et al., 2001). Flying with other bats does not disrupt the bat's ability to use echolocation for spatial orientation so the bat must develop some strategies to deal with possible signal interferences from conspecifics. An echolocating bat produces ultrasonic pulses to probe the environment, and it receives relevant information, such as returning target echoes, and irrelevant auditory streams, such as vocalizations from conspecifics/heterospecifics, clutter echoes and environmental noise. The results from this study show increases in call design separation when *E. fuscus* fly in pairs. Dissimilarity in time-frequency structure enables the bat to segregate auditory streams of its calls and echoes from a neighboring conspecific's. The big brown bat combines silence and call design modifications to avoid call interference from neighboring conspecifics. This study enhances our understandings of the echolocating bat's auditory scene analysis.

Chapter 5: Effects of competitive prey capture on flight behavior in paired big brown bats, *Eptesicus fuscus*

Flight behavior in animals is influenced by the interaction among different individuals, as they mate, defend territory and compete for food. Here we studied flight behavior of paired big brown bats, *Eptesicus fuscus*, when they competed for a single prey item in a laboratory flight room. Following flight was the most frequently observed behavior when two bats flew together. Cost function of three pursuit strategies, classic pursuit (CP), instantaneous optimal bearing (IOB) and constant absolute target direction (CATD), were applied to investigate the conspecific pursuit behavior in echolocating bats. When the baselines, the vector from pursuee to pursuer, are parallel, the bearing is also an optimal value; thus, the IOB is the same as CATD strategy under this condition. The difference between these two strategies is that the pursuer controls its bearing close to optimal value by using IOB strategy and it tries to maintain the baseline parallel by using CATD strategy. Paired bats often remained a nearly CP states (Λ was close to 1) when following another bat. The histogram of cost function Φ also showed a peak at -1, which suggests that the pursuer bat tried to maintain an optimal bearing when pursuing the other bat. Roles of pursuer and pursuee were sometimes reserved. A pursuer can detect and anticipate the movement of the bat it is following; while the advantage of being in the lead is gaining access to the prey first. The pursuer bat in this study was more successful in accessing the prey than the leading bat.

5.1 Introduction

Animals interact frequently with conspecifics and heterospecifics in nature. Small scale interactions, such as an animal tracking its prey for foraging and chasing conspecifics for mating or defending territory, and large scale interactions, such as animals aggregating for migratory purposes, are commonly seen in many animal species. Flight behavior in echolocating bats contains both small and large scale interactions. Insectivorous bats pursue insect prey and several bat species have been observed to chase conspecifics in the field (Hickey and Fenton, 1990; Simmons et al., 2001). In addition, gregarious bat species often fly out from their roosts at dusk in large groups, and some species migrate over hundreds of kilometers (Fenton and Thomas, 1985).

When a predator seeks to intercept a prey item or a male pursues a female, the pursuer uses an appropriate pursuit strategy to make contact with its prey or mate efficiently. A pursuer needs to predict the trajectory of the pursuee and to adjust its own movement to match the target. Here we examine three pursuit strategies, classical pursuit (CP), instantaneous optimal bearing (IOB) and constant absolute target direction (CATD) that the big brown bats, *Eptesicus fuscus*, may apply when pursuing conspecifics. The CP strategy means the pursuer always points its velocity toward the position of the pursuee (Klamkin and Newman, 1971; Wei, 2007; Wei et al., 2008). The IOB strategy is based on another pursuit strategy called constant bearing (CB), which has been used by humans to intercept moving objects (Chohan et al., 2006; Cutting et al., 1995; Lenoir et al., 1999; Wei, 2007; Wei et al., 2008). When an animal uses the CB strategy, the pursuer predicts an optimal bearing to intercept the pursuee in the near future and maintains this bearing angle until it meets with the pursuee. Prediction of the optimal bearing to intercept the pursuee is difficult, especially when the pursuee's movement is erratic. Therefore, we propose an IOB instead of a CB strategy to examine conspecific pursuit behavior in big brown bats. The IOB strategy calculates an optimal bearing but the pursuer continuously updates this optimal bearing as it pursues the target.

Ghose et al. (2006) demonstrated that the big brown bat employs a CATD strategy, which is nearly time-optimal, to intercept its prey. When the pursuit is in the CATD state, the lines jointing the pursuer and pursuee are parallel at any time, and the angle between the target and the horizon is constant (Justh and Krishnaprasad, 2006). This strategy is mathematically identical to the motion camouflage strategy, which are used by visual animals to conceal the pursuer's presence from the pursuee (Anderson and McOwan, 2003; Srinivasan and Davey, 1995; Mizutani et al., 2003). By moving in parallel and only changing the distance between pursuer and pursuee, the pursuer can move closer to the pursuee without been detected. An animal uses motion camouflage to prevent visual detection by other animals. Echolocating bats are auditory-guided animals and their sonar pulses expose their presence to others; therefore, bats may use this strategy to pursue insect prey for efficiency rather than camouflage (Ghose et al., 2006). Besides, the CATD strategy is also identical to the IOB strategy when two animals maintain an exact CATD/IOB state. The only difference is that the pursuer controls its heading to make it match an optimal bearing when using IOB strategy and it controls the baseline, which connects the pursuer and pursuee, to be parallel by using CATD strategy as it pursues another individual. The detailed proof of this will be shown below in Material and Methods section.

The purpose of the present study was to quantify the flight behavior and the interaction between two echolocating bats when they flew in a large flight room and competed for a single prey item. Then we examined which strategies one bat used to pursue another bat. Finally, the prey capture success rate was used to evaluate performance of the leader/follower and to relate prey capture performance with the flight behavior of the two bats.

5.2 Materials and Methods

5.2.1 Animals

Big brown bats, *Eptesicus fuscus*, are a most common bat species in North America. Bats used in this experiment were collected in Maryland, USA and maintained in captivity in University of Maryland, College Park. All experiments were conducted from late spring to early fall, which is the most active time period during a year for this species. The light/dark cycle in the animal housing facility was reversed to ensure that animals were active during the times when experiments were run (8-11 a.m.). Experimental procedures and animal care were approved by the Institutional Animal Care and Use Committee (IACUC) in University of Maryland.

5.2.2 Experimental setup and data recordings

All bats were first trained to intercept a tethered mealworm alone in a large flight room (7 x 6 x 2.5 m). After the bat learned the task and reached an 80% success capture rate, it was paired with different individuals to compete for a single tethered mealworm. Each trial ended when one bat in a pair captured the worm. The presence of a prey item encouraged the two bats to fly and interact in the flight room. Preliminary experiments on flight behavior of multiple bats showed that big brown bats stopped flying when there was no worm in the room.

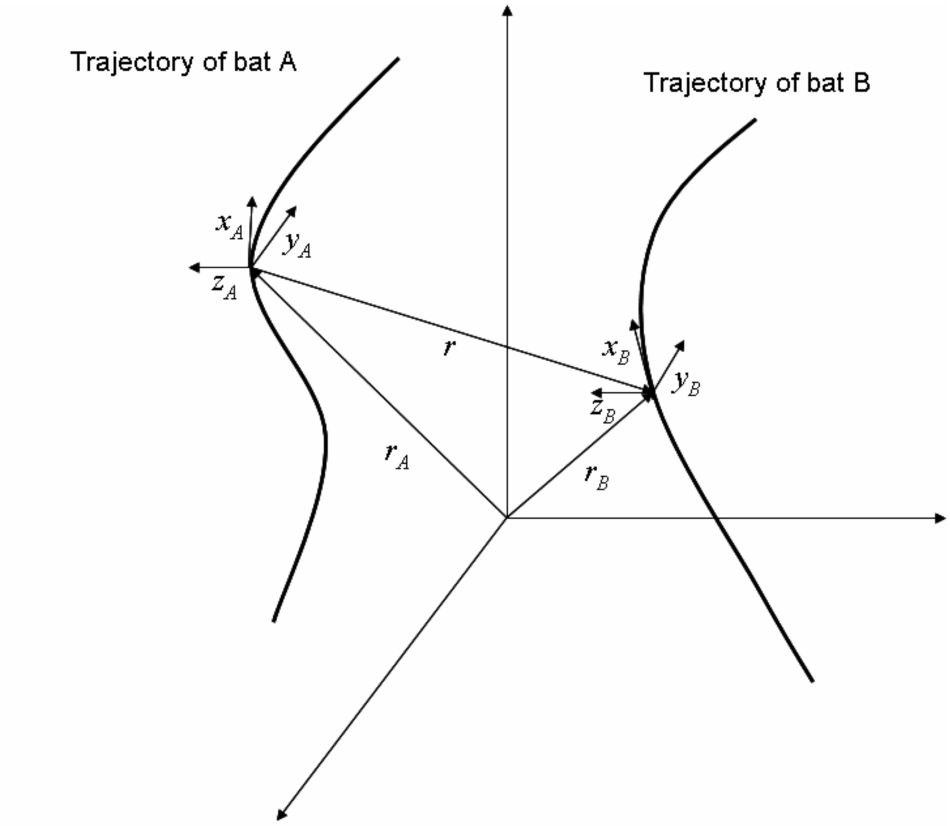


Figure 5.1 Schematic of flight trajectories of each bat in a pair. The bat in the front is the pursuee and the bat in the rear is the pursuer. The unit tangent vector x_A (x_B) is along the velocity of bat A (bat B), and y_A (y_B), z_A (z_B) span the normal plane to x_A (x_B). The vector r_A (r_B) points from the origin of the coordinate system to the position of bat A(or B) and baseline r is the vector points from pursuer to pursuee (if bat A was pursuing bat B, then $r = r_A - r_B$ and if bat A was pursuing bat B, then $r = r_B - r_A$). The bat that flies in the front is the pursuee and the one in the rear is the pursuer.

The recording of flight behavior was carried out with two high-speed cameras (Kodak MotionCorder Analyzer, Model 1000, 240 frames per second), mounted in two adjacent corners of the flight room. Data were recorded over eight seconds before the trial ended, which occurred when one bat captured the worm. Video recordings were further analyzed off-line with a custom MATLAB program to reconstruct the 3-D flight trajectory of each bat.

5.2.3 Data analysis

Cost function

Most data analysis in this section followed the equations and algorithms in Justh and Krishnaprasad (2005); Reddy et al. (2006, 2008); Reddy (2007) and Wei (2007). We defined the bat that flew in the front is a pursuee (leading) bat and the bat that flew behind it is a pursuer (following) bat. These roles were defined strictly by their flight behavior and could be reversed at any time in the trial. Each bat in a pair can be viewed as a point particle in 3-D space and it moves along certain trajectory (Figure 5.1). The unit tangent vector x_A (x_B) is along the velocity of bat A (bat B), and y_A (y_B), z_A (z_B) spans the normal plane to x_A (x_B). The vector r_A (r_B) points from the origin of the coordinate system to the position of bat A (or B), and baseline r is the vector that points from pursuer to pursuee (if bat A was pursuing bat B, then $r = r_A - r_B$ and if bat A was pursuing bat B, then $r = r_B - r_A$).

The CP strategy, which means the following bat is flying toward the leading bat, holds when the pursuer's velocity is pointing toward the pursuee. This suggests a cost function of the form

$$\Lambda = \frac{r}{|r|} \cdot x_p$$

When Λ = -1, the pursuer is in the CP state. If bat A (B) is the pursuer, then $x_p = x_A$ (x_B).

The IOB strategy means that the following bat maintain an optimal angle to pursuit the leading bat. When the bat uses IOB strategy to pursue the other bat, the angle between its heading direction and baseline r should be equal to the optimal bearing. This suggests a cost function defined by

$$\Phi = \frac{r}{|r|} \cdot \left(R(\theta) x_p \right)$$

where $R(\theta)$ is a rotation matrix

$$R(\theta) = \begin{pmatrix} \cos\theta & -\sin\theta & 0 \\ \sin\theta & \cos\theta & 0 \\ 0 & 0 & 1 \end{pmatrix}$$

and θ is the optimal bearing which can be calculated by the following equation

$$\theta = \sin^{-1}\left(\frac{v_e \sin\beta}{v_p} \right)$$

where v_e (pursuee) and v_p (pursuer) are the speed of each bat, β is the angle between baseline and the pursuee's velocity (Ghose et al., 2006)(Figure 2A). When Φ = -1, the pursuer is using the IOB strategy.

The CATD strategy indicates that the following bat keeps an absolute target angle when pursuing the leading bat. This strategy holds when the baselines are parallel and an appropriate cost function can be defined as

$$\Gamma = \frac{r}{|r|} \cdot \frac{\dot{r}}{|\dot{r}|}$$

when Γ = -1, the pursuer is in the CATD state.

IOB and CATD strategies

The optimal bearing used in the cost function of IOB strategy is θ, which is

$$\theta = \sin^{-1}\left(\frac{v_e \sin\beta}{v_p}\right)$$

=>

$$v_p \sin\theta - v_e \sin\beta = 0$$

$$v_p y_p \cdot \frac{r}{|r|} = v_p \cos\left(\frac{\pi}{2} + \theta\right)$$

$$= -v_p \sin\theta$$

$$v_e y_e \cdot \frac{r}{|r|} = v_e \cos\left(\frac{\pi}{2} + \beta\right)$$

$$= -v_e \sin\beta$$

$$v_p \sin\theta - v_e \sin\beta = 0$$

=>

$$\left(-v_e y_e + v_p y_p\right) \cdot \frac{r}{|r|} = 0$$

=>

$$\left(v_p x_p - v_e y_e\right)^{\perp} \cdot \frac{r}{|r|} = 0$$

Because

$$\dot{r} = v_p x_p - v_e x_e$$

$$\dot{r}^{\perp} \cdot \frac{r}{|r|} = 0 \Leftrightarrow \frac{\dot{r}}{|\dot{r}|} \cdot \frac{r}{|r|} = \Gamma = \pm 1$$

Therefore, IOB = CATD when $\Gamma = \pm 1$.

The exact state of CATD is identical to the exact state of IOB. However, the pursuer uses different strategy to achieve the exact state of CATD by keeping the heading as close as optimal bearing (θ_p, which is the angle between pursuee and velocity, is close to θ in Figure 5.2A) or by maintaining the baseline as parallel as possible (δ is close to 0° in Figure 5.2B).

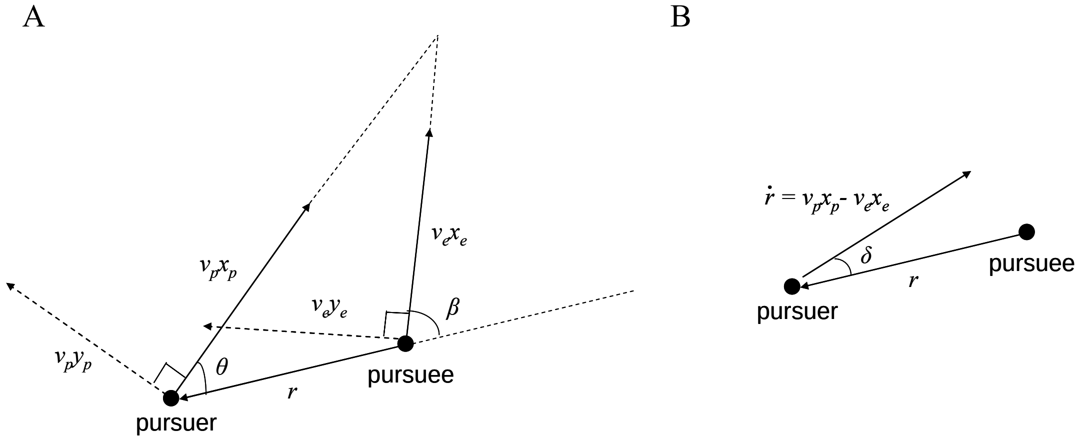


Figure 5.2 Schematics of flight trajectories by using instantaneous optimal bearing (IOB) and constant absolute target direction (CATD) strategies. (a) IOB strategy: The angle θ is the optimal bearing. The speed of each bat is v_p and v_e, respectively. The pursuer tried to keep its bearing close to optimal bearing by using IOB strategy. (b) CATD strategy: The angle δ is the angle between two baselines, r and $\dot{r}$, and the pursuer tries to bring δ to 0° as close as possible by using CATD strategy.

5.3 Results

5.3.1 General flight behavior

Four pairs of big brown bats were used in this experiment, including two male-male, one female-male and one female-female pairs. Figure 5.3A-F shows two examples of paired bats' flight trajectories when competing for a single mealworm. Two bats in the first example flew in tandem and one was following the other's flight path tightly (Figure 5.3A: 3-D view; Figure 5.3B: top view; Figure 5.3C: side view). The trailing bat in the second example did not follow the leading bat's flight trajectory closely (Figure 5.3D: 3-D view; Figure 5.3F: side view) but these two bats were both flying in similar circuits from the top view (Figure 5.3E: top view).

The leader-follower behavior as in the examples above is commonly observed in the flight trajectories of bats in pairs. The flight behaviors of paired bats can be categorized into three groups, converging, diverging and following flights, according to their bearing (θ_e: pursuee, and θ_p: pursuer) and inter-bat heading angle (α) (Table 5.1, Figure 5.4). The bearing of bat is the angle between the other bat and its heading direction and the inter-bat heading angle is the angle between heading directions of each bat.

$$\theta_e = \cos^{-1}\left(\frac{r \cdot x_e}{|r||x_e|}\right)$$

$$\theta_p = \cos^{-1}\left(-\frac{r \cdot x_p}{|r||x_p|}\right)$$

$$\alpha = \cos^{-1}\left(\frac{x_p \cdot x_e}{|x_p||x_e|}\right)$$

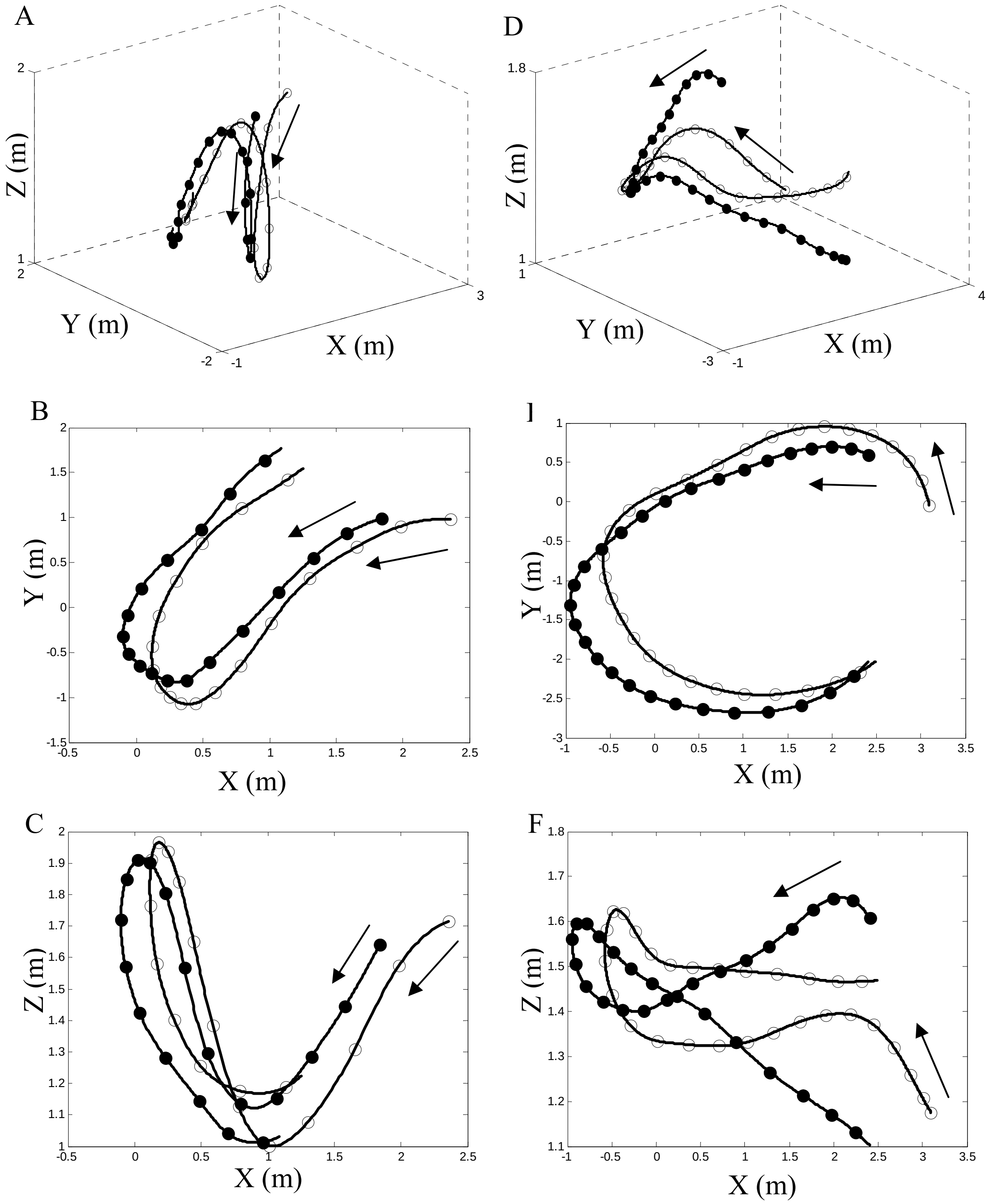
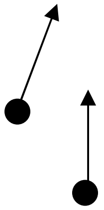
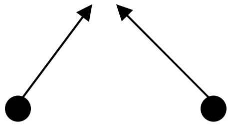
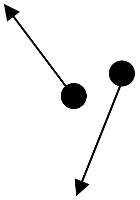
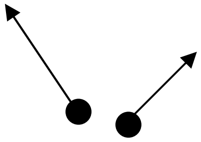


Figure 5.3 Flight trajectories of each bat from two selected trials. Open circles represent one bat and closed circles mean the other bat. The interval between two successive circles is 100 ms and each arrow along the trajectory marks the flight direction. (A) Trial #1: 3-D view; (B) Trial #1: top view; (C) Trial #1: side view; (D) Trial #2: 3-D view; (E) Trial #2: top view; (F) Trial #2: side view.

Referring to Table 5.1, the following flight describes the flight behavior when one bat was behind the other bat and flew toward a similar direction. During converging flight both bats flew toward each other, and during diverging flight both bats flew away from each other. The proportion of following flight is significantly larger than the other two flight behaviors (Figure 5.5, one-way ANOVA, $p < 0.05$, post-hoc: Scheffé test). On average, 75% of the time one bat followed the other bat, another 16 % of the time they flew away from each other, and the remaining 9% of the time they flew toward each other.

Table 5.1 Definitions and examples of three different flight behaviors, following, converging and diverging.

Flight Behavior	Bearing (θ_p and θ_e)	Inter-bat angle (α)	Example
Following	$\theta_e \geq 90°$ and $\theta_p < 90°$	$\alpha < 90°$	
Converging	$\theta_e < 90°$ and $\theta_p < 90°$	$0° \leq \alpha \leq 180°$	
Diverging I	$\theta_e \geq 90°$ and $\theta_p < 90°$	$\alpha \geq 90°$	
Diverging II	$\theta_e \geq 90°$ and $\theta_p \geq 90°$	$0° \leq \alpha \leq 180°$	

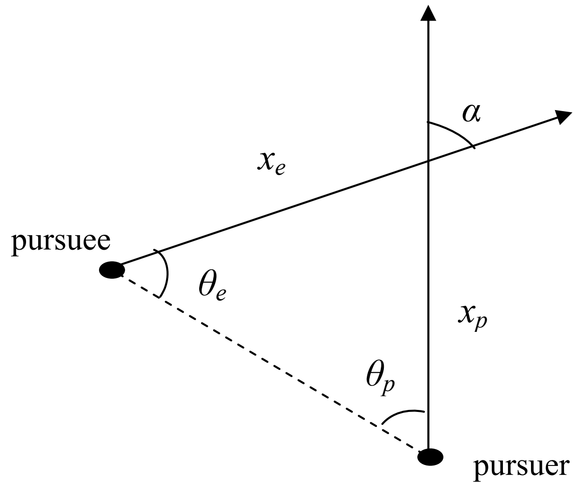


Figure 5.4 Schematic of relative position of pursuer and pursuee. The bearing of pursuer is θ_p and the bearing of pursuee is θ_e. The inter-bat angle is α. Vectors x_p and x_e are the unit tangent vectors which are along the velocity of pursuer and pursuee, respectively.

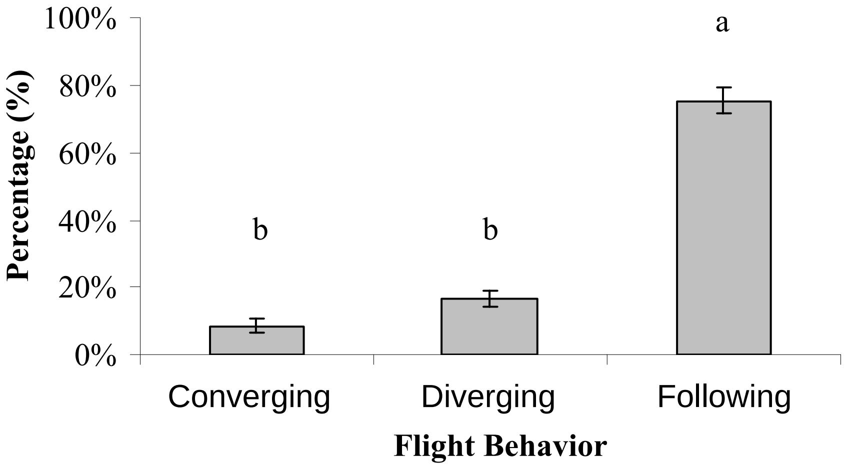


Figure 5.5 Proportion of different flight behaviors. One-way ANOVA was applied to analyze if the percentage of each flight is significantly different than others. Post-hoc Scheffé test shows that the following flight is significantly more common than the other two flight behaviors. Same letter above the bar represents no significantly difference between two flights and different letters means there is significantly different between them.

The flight room is 7 m long, 6 m wide and 2.5 m high, so the longest distance across the diagonal of the room is about 9 m. However, the inter-bat distance in this study was rarely longer than 3 m, and the longest inter-bat distance was 4.18 m. A histogram of inter-bat distance is shown in Figure 5.6A, and most of the time the inter-bat separation is less than 2 m. Two bats kept a distance shorter than 1 m over half of the time (60%), 30% of the time between 1 to 2 m and the rest of the time (9%) more than 2 m (Figure 5.6A). Paired bats not only maintained relatively short spacing but also small angular separation. Figure 5.6B shows the polar plot of inter-bat angle histogram, and paired bats tended to maintain a small angular separation. Almost half of the time (48%), the angle between two bats' heading directions was between 0° and 30°, 25% of the time between 30° and 60°, 11% of the time between 60° and 90°, and 16% of the time was over 90°.

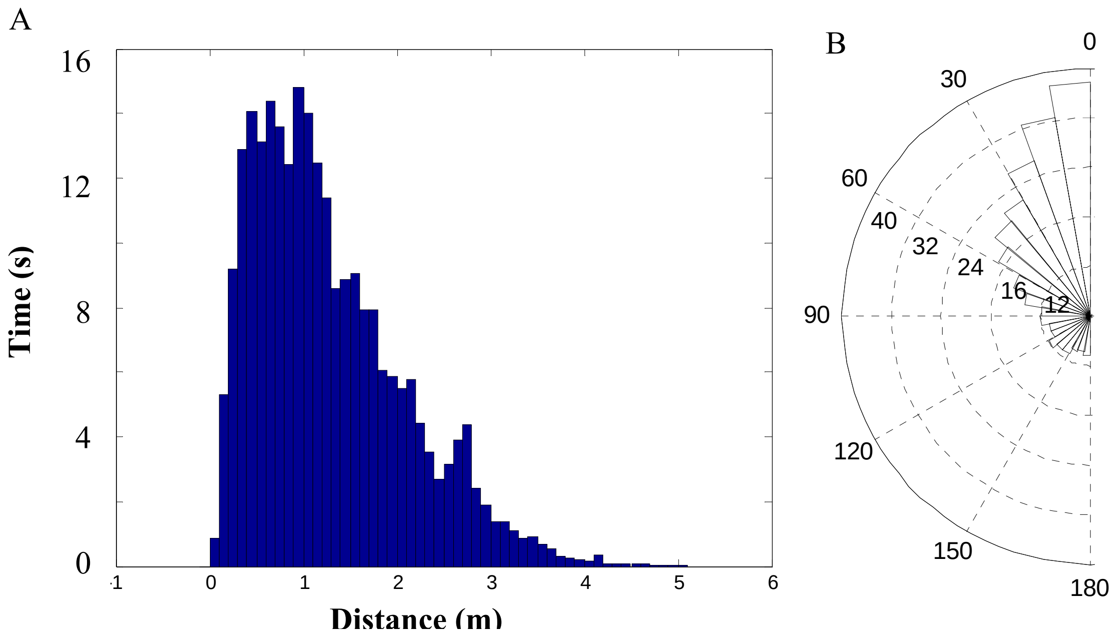


Figure 5.6 The relative position of paired bats. (A) The histogram of inter-bat distance. Most of the time the inter-bat distance is shorter than 2 m. (B) The polar plot that shows the angle histogram of angular separation between bats. The number around the semi-circle refers to inter-bat angle and the number along the radius is time. Most of the time the inter-bat angle is smaller than 90°.

5.3.2 Prey capture performance

Since there was only one tethered mealworm in the room in each trial, both bats needed to compete to gain access to the worm, and only one of them would capture it. Whether one bat could capture the worm successfully or not depended on the individual animal it competed with. One bat might capture the worm most of the time when paired with a given bat, but failed to fly close to the worm when paired with a different competitor. Five individuals (M1, M2, M3, F1, F2) were used in this study and two (M3, F2) of them were paired with more than one individual (Figure 5.7). The prey capture performance of one male bat, M3, was 86% when paired with the male bat, M1 (in M1-M3 pair), but it only caught the mealworm 41% of the time when paired with the male bat, M2 (in M2-M3 pair). The female bat, F2, successfully captured the worm 68% of the time when paired with the female, F1 (in F1-F2 pair), but only caught the prey 23% of the time when paired with the male bat, M3 (in F2-M3 pair). Application of a chi-squared test reveals that one bat's performance in prey capture was significantly better than the other in all bat pairs, except M2-M3. The bat with a significantly larger percentage of capture rate implies that it was more successfully in accessing the worm than its competitor.

Other than changes in prey capture performance, the flight behavior of an individual bat may also be influenced by the presence of another bat. The following section reports the flight behavior data from different pairs.

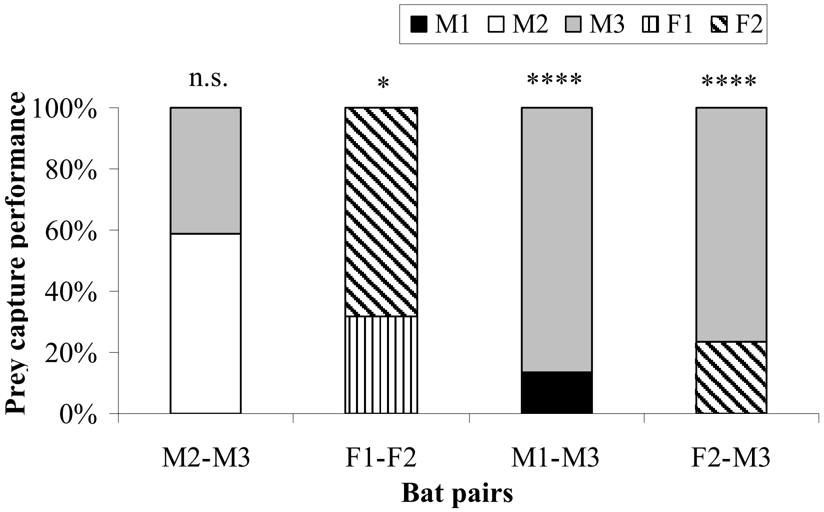


Figure 5.7 The prey capture performance of each bat in pairs. Prey capture performance is the percentage of catch trials by total trials. Chi-squared test was applied to examine if the performance is significantly different between two bats. *: $p < 0.05$; ****: $p < 0.0001$; n.s.: no significant difference

5.3.3 Male-male pair

Three male bats were paired into two male-male pairs, M1-M3 and M2-M3, in this study. These two bat pairs showed differences in both their prey capture performance and flight behavior (Figure 5.7, Figure 5.8A, B). Bat M1 usually led bat M3 and maintained acute inter-bat heading angles (α) (Figure 5.8A, left and middle). About 75% of the time bat M3 trailed bat M1, and the other 8% of the time their positions were reversed. For 17% of the time these two bats did not follow each other (Figure 5.8A, right). Another male-male pair, M2-M3, shows different flight behavior from the M1-M3 pair (Figure 5.8B). The majority of bearing measurements was acute angle for bat M2 and obtuse for bat M3 (Figure 5.8B, left). Although a notable amount of time the inter-bat heading angle was smaller than 90° (Figure 5.8B, middle), the distribution was not as concentrated as that in the M1-M3 pair. The pie chart in Figure 5.8B (right) shows that almost half of the time M2 was following M3, 24% of the time M3 was following M2 and 31% of the time their flight behavior did not belong to following flight. Bat M2 spent much time following bat M2, but there was also about one-third of the time bat pair M2-M3 did not follow each other.

Paired bats were always released at the same time from the investigator's hands and unless the inter-bat distance was long, bats seldom approached the tethered worm immediately. Each bat was allowed to interact with the other bat freely before capturing the worm. Physical contact and landing behavior were commonly observed in male-male interactions. Bat M3 was tested in two different male-male pairs, and its flight behavior changed according to the bat it was paired with. When paired with M1, bat M3 spent most of the time following bat M1 and captured the tethered mealworms significantly more times than bat M1. After several trials, bat M1 began to land on the wall and stayed there until the trial ended, while bat M3 captured the worm without any interference from M1 (4/37 trials). In another bat pair, M2-M3, bat M3 did not often follow M2, and it did not intercept the mealworm significantly more time than the other bat either. Rarely (1/41 trials), bat M3 landed on the wall but took off immediately to join the other bat for the prey capture competition.

5.3.4 Female-male pair

Bat M3 was paired with bat F2 to examine the interaction between male and female bats. Because bat M3 was also paired with other male bats, its flight behavior in male-male pairs can be compared with the behavior it showed when paired with the female. The male bat spent nearly half the time trailing the female bat, and most of the time the inter-bat angle was smaller than 90° (Figure 5.8C). The time the male bat followed the female bat was almost double the time the female bat followed the male bat. In the trials when bat M3 was paired with other male bats, it followed bat M1 and was followed by bat M2. In this female-male pair, bat M3 followed the female bat and gained access to the worm in significantly more trials than the female bat. In addition, the female bat landed on the wall and stopped pursuing the tethered worm in 3 out of 43 trials, while the male bat did not show this same landing behavior.

5.3.5 Female-female pair

When female bat F2 was paired with male bat M3, it usually flew in front of the male bat and caught significantly fewer worms than the male. However, when paired with another female bat, F1, it captured significantly more worms than bat F1 and spent almost half of the time following bat F1 (Figure 5.8D). About 36% of the time the female-female pair did not follow each other and this percentage is the highest among all bat pairs. This pair is also the only pair that did not have any landings on the wall during trials.

5.3.6 Individual differences in flight behavior

Two bats that were paired with different individuals showed different prey capture performance and flight behavior, depending on the individual it was paired with. The bat that spent more time as a follower had better prey capture performance. In addition, the individual that showed wall-landing behavior usually caught fewer worms than the one which did not show such behavior. The majority of flight behavior was following flight across all pairs. Bat pairs M1-M3 and F2-M3 showed more following flight, while M2-M3 and F1-F2 exhibited less following flight.

Most of the time the inter-bat heading angle α was smaller than 90°, which indicates that they tended to fly in a similar direction. For some pairs of bats, the histogram of inter-bat angle was concentrated at a small acute angle (smaller than 30°), which means that their heading directions were almost parallel. The bat captured the worm when the other bat was, on average, 1.38 m away (SE=0.08). The minimum inter-bat distance during target interception was 0.24 and the maximum was longer than 2.70 m (one bat landed on the wall and was out of camera view so the inter-bat distance during this target interception could not be determined).

Table 5.2 shows the speed (m/s) of each bat in the pairs and the absolute difference in speed between paired bats. Paired *t*-test was applied to examine the speed difference at each sampling point, and the results show that there were significant differences in paired bats' speed for every pair. Dividing the faster bat's average speed by the slower bat's average speed yields the speed ratio. Two male-male pairs had larger speed ratios than female-female and female-male pairs. Bats in the female-female pair were the slowest flyers across all bat pairs, and the female bat F2, who was also paired with another male bat M3, flew significantly faster when paired with M3 than F1 (independent sample t-test, $t = -28$, $p < 0.0001$). The male bat M3, who was paired with three other bats, M1, M2 and F2, maintained the same speed when paired with M2 and F2 but significantly increased its speed when paired with M1 (one-way ANOVA, $F = 99$, $p < 0.0001$, post-hoc: Scheffé test). The same bat did not always have the same flight speed but the individual who followed the other bat usually flew at the faster speed.

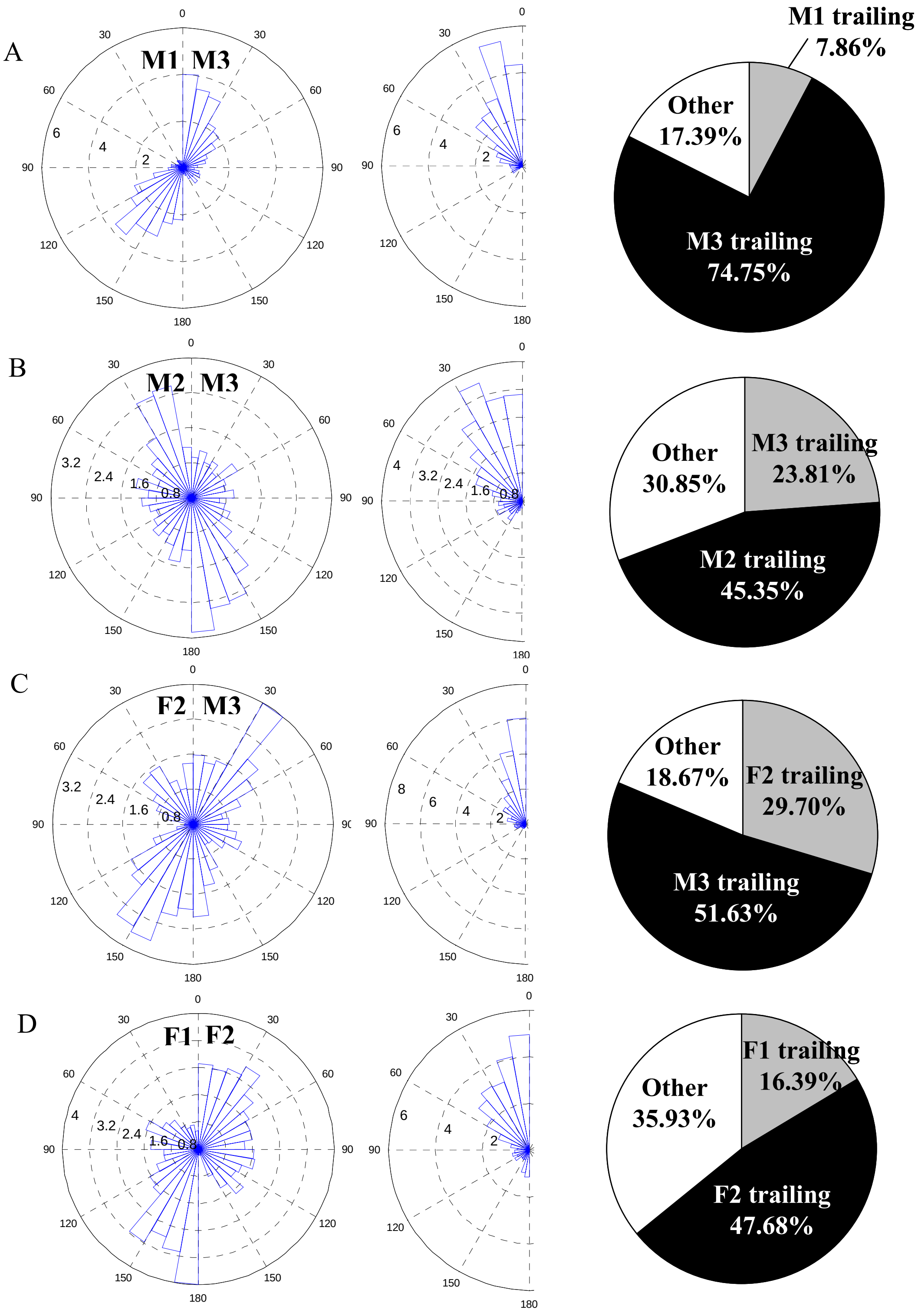


Figure 5.8 The relative position of each bat in each pair. Left panels are polar plots that show the bearing of each bat in pairs. Middle polar plots show the inter-bat angle in each pair. Right panels are the pie chart illustrating the proportion of flight behavior. (A) M1-M3 pair; (B) M2-M3 pair; (C) F2-M3 pair; (D) F1-F2 pair.

Table 5.2 Speed (mean ± SE) of each bat in pairs. The difference between each bat's speed is the absolute difference (mean ± SE) and the speed ratio is ratio of the faster bat's flight speed to the slower bat's flight speed. Paired *t* test examined if the speed of each bat was different and **** means $p < 0.0001$.

Bat A-B	Bat A	Bat B	Paired *t*-test	Difference	Speed ratio
M1-M3	3.23 ± 0.01	3.70 ± 0.01	****	0.47 ± 0.02	1.15
M2-M3	3.94 ± 0.02	3.45 ± 0.02	****	0.49 ± 0.02	1.14
F2-M3	3.26 ± 0.01	3.40 ± 0.02	****	0.14 ± 0.02	1.04
F1-F2	2.55 ± 0.01	2.72 ± 0.01	****	0.17 ± 0.01	1.07

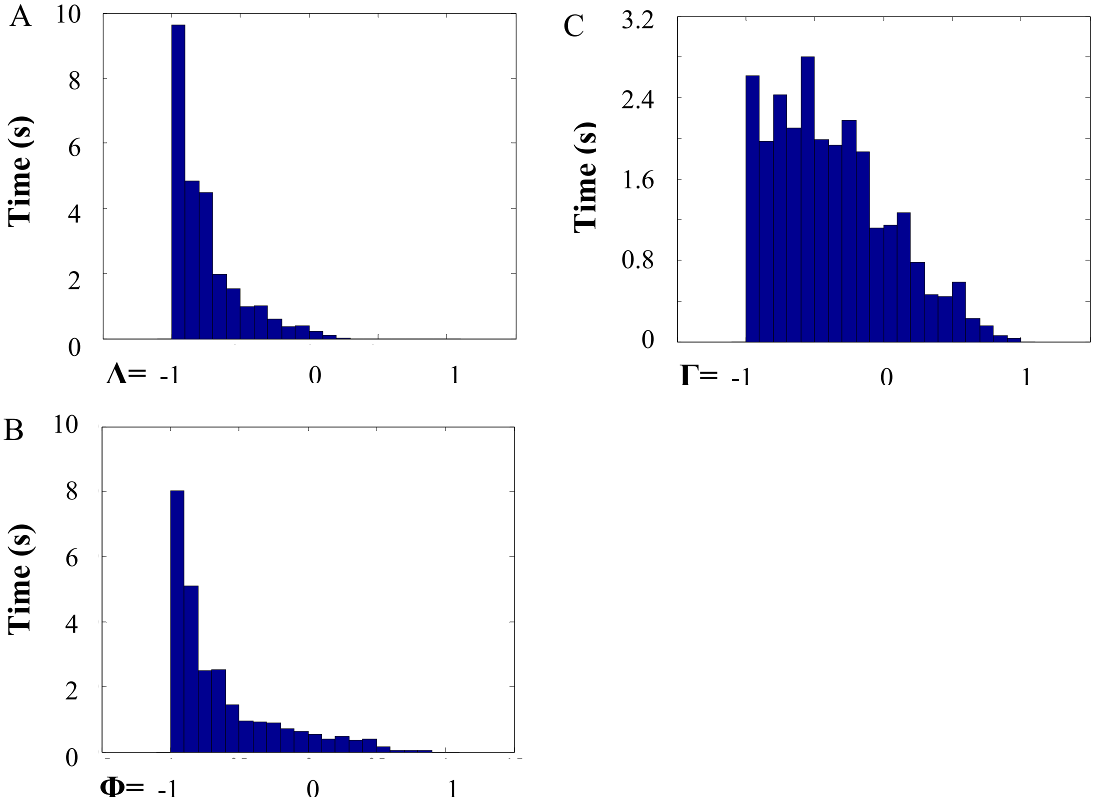


Figure 5.9 Distribution of the cost function of three pursuit strategies: (A) classical pursuit (CP), cost function Λ; (B instantaneous optimal bearing (IOB), cost function Φ; and (C) constant absolute target direction (CATD), cost function Γ.

5.3.7 Pursuit strategy

Four criteria were used to select trial segments for analysis: (1) Trial time: The trial segment should be longer than one second; (2) Feeding buzz: Feeding buzz, which is produced by the bat when approaching prey items, is a series of sonar pulses with short pulse intervals (< 9 ms). The trial segment should not include the feeding buzz to exclude the influence of pursuing another target (mealworm); (3) Following flight: The bat should follow the other bat; (4) Distance: The spatial separation between paired bats should be decreasing or remain shorter than one meter.

The reasons for choosing these four criteria are explained here. Although the data collection of each trial lasted eight seconds, sometimes one or both bats flew out of camera view, which made some data sets fragmented. Therefore, only those trial segments that are longer than one continuous second were included in this analysis. When the bat attempted to take the tethered worm, the worm position affected the bat's flight trajectory. So position data during the buzz were excluded in this analysis as well. The reason for choosing following flight for analysis is that it is the most common and continuous flight behavior in this study. Other flight behaviors, such as converging and diverging flights, were either not observed in our data often enough or were usually fragmented. As for the distance, it is unlikely two bats tried to pursue each other or were able to complete a successful pursuit when the inter-bat distance was increasing.

The cost function for CP (classical pursuit), IOB (instantaneous optimal bearing) and CATD (constant absolute target direction) is Λ, Φ and Γ, respectively. Histograms of Λ, Φ and Γ are shown in Figure 5.9A-C. The trailing bat uses a CP strategy to pursue the bat in front of it when $\Lambda = -1$, and it uses a CATD pursuit strategy when $\Phi = -1$ or $\Gamma = -1$. The closer the cost function is to -1, the more close the bat uses that pursuit strategy. Each bat in a pair in this study relied mostly on the CP or IOB strategy to pursue the other bat, because there were more values of Λ or Φ were close to -1 than values of Γ were close to -1 (Figure 5.9A-C). Although values of $\Gamma = -1$ were not as many as $\Lambda = -1$, the peak of Γ distribution was still close to -1. In addition, the bat often used IOB strategy (Φ was close to -1) to achieve an exact CATD state. Therefore, the trailing bat sometimes used the CATD strategy to pursue the other bat, too. The closer the cost function was to -1, the closer the paired bats were to the state of CP, IOB or CATD. The cost function value between -0.8 and -1 was selected to determine the pursuit strategy of bats, and the duration a bat pair remained in the state of CP and IOB was significantly longer than the state of CATD (CP = 50.54 ± 0.07, IOB= 52.26 ± 0.08, CATD = 22.42 ± 0.03, Mann-Whitney test, $p < 0.001$). The pursuer bat tried to reach CP or CATD state when pursuing the other bat, but it reached the CATD state by maintaining angle between its heading and the other bat as close as the optimal bearing.

5.4 Discussion

Three different flight behaviors, following, converging and diverging, were identified in this study according to the inter-bat heading angle and bearing of each bat. Following flight was the most common flight pattern among them. Flight behavior and prey capture performance changed as the bat was paired with different individuals. Although sample size for studying sex difference in flight behavior was not large enough to draw a conclusion, male bats tended to be more aggressive than female bats. The section below will consider the purpose of following flight and individual differences in echolocating bats' and other animals' flight behavior. In addition, the possible strategy the bat used to pursue the other bat is discussed below.

5.4.1 Function of following flight

Around 85% of the time the inter-bat angle was smaller than 90° and 60% of the time the distance between paired bats was shorter than 1 m. Small angular and spatial separation suggests the possibility of mutual influence in paired bats' flight behavior. Both bats followed similar trajectories in the selected examples presented in Figure 5.3, demonstrating the close relationship between flight trajectories of the two bats. Nearly 76% of the time one bat was following behind the other bat and maintained an inter-bat angle smaller than 90°. Given the close relationship between flight trajectories of paired bats, we conclude that the following flight in this study is likely to be a conspecific chasing behavior.

Chasing behavior can be initiated by a potential predator or mate and the final contact with targets implies chasing behavior in animals, *e.g.* if a male housefly follows a female housefly and then mates. The purpose of chasing and capturing the female housefly is to make physical contact. For the predator-prey condition, the predator's purpose is to intercept and eat the prey. No copulation behavior was observed in this experiment, so the bat was not considered to be chasing another bat to seek out its mate. The predator-prey relationship did not hold for paired bats, as *E. fuscus* is insectivorous and no cannibalistic behavior has been reported in this bat species. Conspecific chases have been reported in several bat species, such as *E. fuscus* (Simmons et al., 2001) and *Lasiurus borealis* (Hickey and Fenton, 1990), but the purpose of this chasing behavior is still not well understood. The most likely purpose for the conspecific chasing behavior in this study is to defend a food source, because only one prey item was provided at a time. By chasing, physically and vocally attacking another individual, the bat gained access to the food frequently by causing the other bat to land on the wall.

5.4.2 Individual differences in flight behavior

Although males tended to show agonistic behavior when flying with conspecifics, it is not conclusive that whether there are gender differences in flight behavior due to small sample size. The female-female pair also showed less frequent following flight, compared to other pairs. Although one male-male pair, M2-M3, showed less following flight than the other male-male pair, the flight speeds of both male bats were greater than the female-female pair. The flight speed of female bat, F2, increased from 2.72 to 3.26 m/s when paired with female F1 and male M3, respectively. This indicates that female bats are capable of flying as fast as male bats, but they did not do so when paired with other females. The speed ratio of two male-male pairs is 1.15 and 1.14, and the speed ratio of the female-male and female-female pairs is 1.04 and 1.07. The individual that spent more time trailing the other bat usually flew faster, and the speed ratio is larger in two male-male pairs than in other pairs. A higher speed ratio could mean more intense following (*i.e.* chasing) than a lower speed ratio.

Flight behavior is also influenced by the individual a bat paired with. Both female bat F2 and male bat M3 modified their flight behavior when paired with different individuals. The female bat F2 often flew behind the other bat and caught significantly more worms when paired with F1. Its prey capture performance decreased when paired with male M3, and it changed its position from trailing to leading. Bat M3 caught significantly more worms than its competitor when paired with M1 and F2, but did not show a significantly higher prey capture performance when paired with M2. Its relative position to the other bat also changed along with the individual it was paired with.

Previous studies have reported that female houseflies show different flight behavior than male houseflies (Wehrhahn, 1979; Wehrhahn et al., 1982; Zeil, 1986). Male houseflies usually defend their territory by chasing other males away, and they also chase other females for mating purpose. The turning angle and the turning speed of the male correlated with the error angle (bearing) between the chasing fly and chased fly. The same relationship was not observed in female houseflies when they flew behind another male or female. Wehrhahn et al. (1982) concluded that female tracking is less efficient than male chasing. Female flies do not pursue male flies for mating purpose and a lack of chasing purpose may be also the reason that female houseflies did not use efficient tracking or chasing strategy.

5.4.3 Pursuit strategy

We examined three pursuit strategies here and concluded that the bat stayed in nearly CP and IOB states more often than in the nearly CATD state. When Λ, Φ or Γ is between -0.8 and -1, the bat is considered to use CP, IOB or CATD strategy. According to the definition of Λ and Φ, the optimal bearing is 0° when Λ = Φ. For most of the range Λ= -0.8 ~ -1, Φ was also between -0.8 and -1, although Λ was rarely equal to Φ. The resemblance between the histograms of Λ and Φ may be due to the likelihood that the optimal bearing of the pursuer is close to 0°. Since bats in this study did not fly in a straight line and they did not fly at constant speed, using IOB as a strategy implies the need to update the optimal bearing continuously. However, it is still a question as to whether the bat can continuously update the optimal bearing quickly enough to use IOB, so the bats in this study may use CP rather than IOB to pursue the other bat of a pair.

Past research in big brown bats has reported that they use a CATD strategy to pursue insect prey (Ghose et al., 2006; Reddy, 2007; Reddy et al., 2008). The strategy CATD is also considered to be a more efficient means to pursue the target than the CP strategy (Glendinning, 2004). However, this study shows that the bat used CP strategy to pursue its conspecific. The use of different strategies may be due to the difference in the nature of predatory-prey chase and conspecifics chase. First, the prey is often slower than the predator, but bats of the same species have similar flight speeds. Second, the bat's attention may not always be on the other bat, because the goal of its flight is to capture the tethered mealworm. Although the portions of flight trajectories during the feeding buzz were excluded in this study, the bat might still turn its attention to the worm occasionally. Third, the bat's goal is not to intercept and capture the other bat, but to overtake it and reach the worm first. Differences in chasing purposes may influence the choice of pursuit strategies.

5.4.4 Pursuit-evasion game

The flight behavior in this study can be regarded as illustrating a symmetric pursuit-evasion contest, which means that both pursuer and pursuee are interested in the same resource, such as food or mates, and the pursuer and pursuee roles can be switched between two animals. Two big brown bats competing for the same prey item in the flight room serves as an example of symmetric pursuit-evasion contest. Although one bat tended to be pursuer in most trials, their roles as the pursuer and the pursuee were sometimes reversed. The predator-prey pursuit-evasion setting is an example of an asymmetric contest, because the roles of pursuer and pursuee are fixed and their target is not the same.

The comparison between predatory-prey and bat-bat pursuit may not be the most appropriate one, because of the speed and final goals. A better comparison may be the game of tag, in which one person chases another and taps that person. The role of pursuer and pursuee is reversed once the pursuer successfully tags the pursuee. Reynolds (1994) simulated the game of tag by using two simulated vehicles and discovered that it is also easier and faster for a pursuer to accomplish the task by running faster than the pursuee. This simulation is similar to the observation of bat-bat interactions in this study. In a male-male pair example, the flight behavior of one male bat, such as chasing the other male and forcing it to fly off-track by physical contact, are comparable to the game of tag.

In the work of Wei et al. (2008), an evolutionary game theoretical approach is discussed, to explore the observed prevalence of CATD strategy in bat prey-capture behavior. The behavior of paired bats in the present study can provide another interesting scenario for a game theory study. One strategy that is commonly used by male bats is that the bat chases the other bat around, produces screech calls which may serve as threat, and hits the other bat to throw it off balance. Two possible results ensue from this aggressive behavior: one is that the pursued bat lands on the wall and does not take off again until after the pursuer has taken the prey item and the trial ends; a second possible outcome is that the pursuee ignores the aggressive move made by the pursuer and tries to gain access to the worm. In examples of the first situation, the pursuer caught the prey most of the time (*e.g.* M1-M3 pair) and in examples of the second situation, the pursuer and pursuee captured similar number of worms, and their roles sometimes reversed (*e.g.* M2-M3 pair).

The successful bat captured the worm when its competitor was, on the average, 1.38 m away. This suggests that the bat may have tried to elongate the distance between itself and the competitor, before it engaged in the prey capture process (lock on prey and attack). If the second bat was too close to the first bat when it was nearing the worm, the competitor may have tried to interfere with the capture attempt. The advantage of being the leading bat is that if the distance between itself and the trailing bat is long enough, the leading bat has the advantage of accessing the worm first. Some preliminary trials (not included in the analysis reported here) showed that when the investigator accidentally released one bat significantly earlier than the other bat, the bat that took off earlier and captured the worm immediately. However, two bats spent more time interacting with each other before one of them captured the worm if both bats were released simultaneously. The disadvantage of being the leading bat is that it is more likely to be chased by the trailing bat, and it is also more difficult for the leading bat to localize its competitor from behind. On the other hand, the advantage of being the trailing bat is that it can potentially engage in pursuit and force the leading bat to land on the wall. In addition, it can accurately localize the leading bat and devise a strategy to capture the worm. The results of this study show that the trailing bat had a higher capture rate than the leading bat.

5.5 Conclusion

Echolocating bats showed different flight behaviors when paired with different conspecifics. The prey capture performance was also affected by the individual the bat was paired with. Individual differences seem to have larger effect on flight behavior than gender differences. If the bat ignored the aggressive behavior from its competitor, it had a better chance of accessing the tethered mealworm. Flying behind and chasing away the other bat seem to be a successful strategy to capture more prey items. The bat often used classical pursuit (CP) strategy, which means that the bat's heading direction is toward the position of the other bat during pursuit.

Chapter 6: Conclusion and future directions

6.1 General conclusion

Echolocating big brown bats adapt to alterations of sound localization cues and the presence of conspecifics by modifying their flight behavior and/or echolocation behavior. Bats in this study adjusted only flight behavior when approaching the mealworm in the ear manipulation experiment, while they modified both their echolocation calls and flight behavior in the acoustic interference experiment. The prey capture performance, which was the percentage of trials the bat caught the worm, was used to evaluate how each experimental condition affected the bat's behavior and how fast it adapted to the new situation. The performance of tragus-deflected bats dropped right after the external ear manipulation, but the bat adapted quickly after a few trials. Conspecific presence decreased the success rate of prey capture for both bats in a pair, and the performance remained low for some individuals.

Many previous studies have already shown that echolocating bats have the ability to modify their echolocation calls under a rapidly changing environment (see Chapter 1: Introduction). However, few studies have focused on adaptation in flight behavior and the bat's behavior when flying with conspecifics. This thesis discovered two major findings on the echolocating bat's adaptive behavior, which have not been previously reported. The first finding is that big brown bats are able to adjust their flight trajectories to adapt to altered sound localization cues. Scientists have demonstrated similar motor behavior adjustments in human who wore prism goggles that distorted visual input (Shratton 1896; 1897a; 1897b). Vision to the human is like audition to the echolocating bat in guiding spatial orientation. Thus, it is reasonable to infer that altered acoustic input may lead to adaptive behaviors in the echolocating bat, similar to reported adaptive motor adjustments in humans in response to altered visual input. Such adjustments in bat behavior were demonstrated in this thesis. Another major finding is that echolocating bats used silence as a strategy to avoid signal jamming from conspecifics.

Studying the echolocation behavior of more than one bat has been difficult, because methods to sort and analyze calls from multiple bats have been limited. However, this thesis provides a method to analyze this kind of data and could be possibly expanded to a limited number of bat individuals. Vocal adjustment is a commonly reported strategy in echolocating bat's adaptive behavior to avoid signal jamming. Silence, an unexpected but logical strategy, has been overlooked by scientists who study the jamming avoidance response in bats. In fact, engineers have developed passive radar/sonar as a way to conceal one's presence and multi-static radar/sonar in order to cooperatively detect targets within a larger area than single radar/sonar can do. Both these findings have opened new directions in bat echolocation research and many follow-up experiments can be conducted to pursue questions raised by this thesis. The following sections will introduce some ideas about new experiments inspired by this thesis.

6.2 Sound localization experiments

Deflecting the tragus of the big brown bat did not produce a large effect on the bat's prey capture performance, which suggests that the bat can still roughly localize the prey position following the external ear manipulation. It is believed that tragus plays an important role in vertical sound localization in echolocating bats. This experiment demonstrates that the tragus is related to vertical sound localization, but other parts of the external ear may also play roles in localizing sound sources in the vertical plane. Furthermore, the spectral cues created by the structure of the external ear may not carry the only information contributing to the bat's vertical sound localization.

Previous studies on sound localization in echolocating bats were conducted on animals sitting on a platform. The research presented in this thesis took a step forward by studying the role of the tragus on vertical localization and adaptive flight behavior in the echolocating bat. Further experiments can be designed based on the results of this study, to improve our understanding of the vertical sound localization by the bat.

Sonar beam analysis, especially in the vertical plane, should be included in future studies of vertical sound localization in free-flying bats. The direction of the bat's sonar beam reveals information about where the bat "looks" when approaching a target. If sonar beam measurements in the tragus-manipulated bat show that it is slightly above or below the target in the vertical plane, it can provide additional evidence that this ear manipulation alters the bat's perception along the vertical axis. More densely positioned microphones in the array are required to record complete sonar beam aim data of free-flying bats.

New research can also focus on the adaptive flight behavior in echolocating bats, since they adjusted their flight behavior, such as approaching angle and elevation, in response to the manipulation of the external ear. Larger changes in flight behavior can be induced by more dramatic ear manipulations, such as blocking one ear canal or adding an ear mold to change the bat's original ear shape. The bat is expected to adapt to the manipulation after some practice trials, unless the modification abolishes the bat's sound localization in both the vertical and horizontal planes. Observation of the bat's audio-motor adaptation helps us understand how the animal coordinates new auditory input and motor output.

6.3 Acoustic interference experiment

Experiments with two or more bats flying in the same room introduce challenges to data analysis because of the difficulty in telling which vocalization belongs to which bat. Research presented in this thesis describes an approach that permitted unambiguous assignment of signals to the vocalizing bat, which revealed interesting new findings that have not been reported before. Separation of call frequency is considered to be a common strategy for conspecific bats to avoid echolocation call interference. Individual bats in this study used different frequency ranges when flying in pairs, and these differences increased as the inter-bat separation decreased. Surprisingly, the bat sometimes used silence as a strategy to avoid jamming as well, and this silent period lasted from 0.2 to over 2 s, indicating that the silent bat flew without its own echolocation for 0.6 to over 6 m (assuming the bat's flight speed is 3 m/sec). The shorter the inter-bat separation, the more the bat showed silent behavior.

When two bats flew in a pair in the same room and competed for the same prey item, chasing behavior was frequently observed. In addition, male bats were in general more aggressive than females. Being a trailing bat and chasing the other bat seems to be a successful strategy to gain access to the worm.

6.3.1 Silence

Echolocating bats are generally believed to use echolocation continuously to guide their navigation, but bats in this study went silent to avoid signal jamming with conspecifics. This newly discovered strategy suggests new directions for bat echolocation research.

The first question is how the bat navigates without echolocation. The definition of silent behavior in this study is one or both bats stopped vocalizing for over 0.2 seconds. Therefore, the silent bat could still use the other bat's vocalizations for orientation when the other bat is echolocating. Passive listening in bats has not drawn as much research attention as echolocation behavior. A complex experimental space, such as placement of multiple obstacles in the room, can be introduced to raise the difficulty for the bat to navigate though this cluttered environment. If the bat still shows silent behavior under these cluttered conditions when paired with another bat, this can provide further evidence that the bat can use passive listening for a considerable amount of time to guide it through its surrounding.

More than two bats can be studied in the same room to investigate how a bat decides to vocalize or not and how many individuals are necessary to vocalize in a group. Bats often fly out of their roost in a large group at dusk and how they avoid interference with calls from many other bats remains unknown. This study proposes a possible strategy, silence, for the bat orienting in a large group of conspecifics. The number of vocalizing individuals has to be large enough to guide every other members of the group and also small enough to avoid signal jamming from other calling individuals. Such research can provide answers as to how the animals find balance between silence and vocalization.

Humans and other visual animals determine if their distance to an object is changing by binocular disparity cues and by comparing the image size changes on the retina. It is still an open question if echolocating animals can do the same by listening to echo delays and comparing intensity level changes of the sound source. Future experiments can be designed to investigate how auditory animals determining time-to-contact of a looming auditory object.

6.3.2 Vocal adjustment

The big brown bat adjusted its call frequency to avoid jamming, especially when paired with the conspecific whose call frequencies were similar to it. If differences between two bats' baseline (flying alone) call frequencies were large, they did not shift their call frequency much when flying together. However, it is unknown how much separation in frequency is sufficient for the bat to discriminate two different calls. A yes-no experiment can be designed to determine out the just noticeable difference (JND) in frequency for the echolocating bat. Two FM signals with different frequency ranges can be played to the bat, who needs to report if these two signals are different by crawling to one (yes) or the other (no) side of the Y-shape platform. By gradually decreasing the difference in frequency of these two signals, we can determine the JND in frequency for the bat. These two signals can be played with delay to determine the JND in temporal separation of two signals. The same design can be applied to find the JND in other parameters, such as duration, bandwidth, sweep rate and shapes of FM signals. The JND in each sound parameter determines the separation that is essential for the bat to tell the difference between two signals.

Most of big brown bats' echolocation calls are broadband FM sweeps, which means that each vocalization covers a wide frequency range. It is unknown which part of an echolocation call is critical for a bat to localize objects in space. The bat may be able to tolerate low frequency masking, high frequency masking or it may need the entire call to precisely localize objects (Paschal and Wong, 1994; Surlykke, 1992). Overall, human and other animals localize broadband better than narrowband signals (Bulter, 1986; Konishi, 2000). White noise with various frequencies can be broadcasted through omnidirectional loudspeakers while the bat flies in the room to capture prey or perform other behavioral tasks. The success rate for the bat to complete its task is related to the magnitude of interference by noise to the bat's echolocation. Besides, recordings of the bat's echolocation calls could show if it shifts call frequencies away from noise to prevent jamming. The bat can also be trained to determine the range of a phantom target by listening to the echo playbacks of its calls through a loudspeaker. The echo playback can be filtered by the investigator to broadcast only a limited band of the call to test if the bat can use a filtered echo to determine the range of the phantom target (Moss and Schnitzler, 1987).

The bat's ability to discriminate its calls from others has not been fully studied yet. The bat's ability to recognize its own vocalizations from others can be tested in a yes-no psychophysical experiment. A series of stimuli that includes a mixture of calls from other bats and the subject bat are played to the subject bat. It is trained to crawl toward one (yes) or the other (no) arm of the platform to report if these vocalizations include its own calls or not. It is important for a bat to recognize its own signals, because it needs to respond to echoes that return from the sonar pulses it produces in order to get an accurate representation of the object's 3-D position.

6.3.3 Flight behavior

The problem we encountered when analyzing the flight behavior of paired bats is the uncertainty of both bats' intention. Analysis of the sonar beam pattern can be used to clarify this. When the bat points its sonar beam toward the prey, this suggests that the bat is directing its attention to the prey to go after it. If the bat directs its sonar beam toward the other bat, this suggests that it is tracking its conspecifics. Auditory "gaze" of echolocating bats can be determined by measurement and analysis of their sonar beam patterns. Future work should focus on how the bat controls its sonar beam to track another bat and how the bat uses echolocation information it receives to control its flight.

Chasing behavior in echolocating bats has not received much research attention. In addition, the strict definition and purpose of this behavior is not yet clear.

Animals often chase each other for defending territory or pursuing mates. Bats in this study may chase each other to defend a food source, because there was only one prey item presented in each trial. More behavioral observations are necessary to determine the function of chasing behavior in bats. Some bats in this study seemed more aggressive than others in accessing the prey, suggestive of a dominance heirarchy. How the dominance between paired bats and how this social hierarchy extends to multiple bats warrant further study.

The two-bat prey capture experiment presented in this thesis can be expanded to multiple bats. Cooperation and competition among multiple animals can bring new perspectives on how every single bat in a group copes with a complex auditory scene and interacts with neighboring bats. A laboratory flight room setup is ideal for studying this topic, because 3-D video tracking, high quality of echolocation call recordings and the controlled experimental environment. Research findings can improve our knowledge about animal aggregate behaviors and collective intelligence.

6.4 Multiple-bat problem

Many animals in nature aggregate in large numbers and travel together with conspecifics, such as schools of fish, flocks of birds and swarms of insects, because of advantages in foraging and migrating with others (Parrish and Hamner 1997). Many echolocating bat species are gregarious and often form a large group when flying out of their roosts at dusk. For example, over one million Brazilian free-tailed bats (*Tadarida brasiliensis*) have been observed to emerge from the roost within two hours (Betke et al., 2008b). This remarkable group behavior raises many questions in bat research: How does an individual echolocating bat sort its vocalizations and echoes from those of conspecifics to orient among millions of others? How does a group of bats move coherently along the same direction? Does a bat in a group function individually or coordinate with other group members? A recent research finding from a laboratory study of free-flying big brown bats (*Eptesicus fuscus*) may shed a light on these questions (Chiu et al., 2008).

6.4.1 The Discovery of Silent Behavior in Echolocating Bats

We recently uncovered a surprising behavior in echolocating bats, namely silence, when the animals flew in pairs (Chiu et al., 2008). The prevalence of silent behavior depended on the spatial separation between the two bats and the similarity of their calls when they flew alone. When bats flew less than one meter apart, silent behavior occurred as much as 76% of the time (mean of 40% across seven pairs). This value dropped to about 20% when bats flew further than one meter apart. In addition, the more similar two bats' calls were during baseline recordings, the more silent behavior they exhibited when they were paired.

Silent behavior in echolocating bats was only recently documented, because of the technical challenge of assigning calls to the vocalizing individual when flying with others. Current devices used in recording bat vocalizations cannot discriminate each call and assign it to the vocalizing individual bat automatically, because a microphone placed within a few meters of two free-flying big brown bats will pick up a string of calls that could be produced by one bat, the other bat, or both. Our analysis method allowed us to assign echolocation calls to individual vocalizing bats when two individuals were paired in the same large flight room (Chiu et al., 2008). We used more than one microphone (spaced about 1-2 meters apart), and measured the arrival time of the bats' calls at each of the microphones, while we simultaneously tracked the 3-D position of the bats using video. When a call is accurately assigned to the bat that produced it, the travel time difference between two microphones, estimated from the 3-D position data, is equal to the actual difference measured from the signal arrival times at the spatially separated microphones.

6.4.2 Methodology to Study Vocal Behavior of Bats Flying in Groups

The method used to sort and assign calls to the vocalizing animal in the two-bat condition can be extended to a limited number of bats, but can hardly be applied to millions of bats. Instead, other techniques could be utilized to record echolocation and flight data in a situation with extremely large numbers of bats. Scientists have used thermal cameras to capture the emergence of bat groups from roosts and track the flight trajectory of individual bats (Betke et al., 2008a). Such thermal camera images would have to be synchronized to specialized microphone recordings taken from the flying bats. Telemetry microphones, a newly developed technology (Hiryu et al. 2007), could make it feasible to record echolocation calls generated by many individuals flying with millions of other bats.

6.4.3 Silent Behavior and Cooperative Sonar

Previous studies have shown that several echolocating bat species adjust their echolocation call frequencies to avoid signal jamming from conspecifics (Bates et al., 2008; Obrist, 1995; Ulanovsky et al., 2004). The newly discovered strategy, silence, reveals that the big brown bat sometimes stops its echolocation to avoid signal interference from others (Chiu et al., 2008). This jamming avoidance function of silent behavior is suggested by the observations that the bat showed more silent behavior when inter-bat spacing was short and when it was paired with an individual whose signals were similar to its own.

The discovery of silent behavior also implies the possibility that the bat may use another individual's echolocation to substitute the function of its own echolocation. Echolocating animals have been reported to use eavesdropping to track food sources, to discriminate objects or to orient in the environment. A silent bottlenose dolphin (*Tursiops truncatus*) recognizes various objects by listening to another dolphin's echolocation at a close distance (Xitco and Roitblat, 1996). A group of Hawaiian spinner dolphins (*Stenella longirostris*) passively listens to one or a few group members' echolocation signals to orient in the ocean (Lammers and Au, 2003). Wild rough-toothed dolphins (*Steno bredanensis*) that swim in synchronized formation tend to produce fewer echolocation calls than those that swim in asynchronous formation, which suggests that dolphins swimming in groups may use other individuals' echolocation signals for orientation (Gotz et al., 2006). In addition, an acoustic experiment has verified that a sonar receiver can use echo returns from another sonar transmitter (Kuc, 2002). This result suggests the possibility that a passively listening animal can localize objects from sonar echoes generated by a neighbor under two conditions: first, the sonar source and the listener are closely spaced; second, the listener and the sonar source keep a fixed formation.

Echolocating bats can listen to echolocation calls made by conspecifics and use them to track food sources or find an occupied roost (Barclay, 1982; Balcombe and Fenton, 1988; Jones, 2008). The term eavesdropping is often applied to describe a listener extracting information from others in a communication network, and most studies on this topic have been in non-echolocating animals, such as birds, frogs, etc (Janik, 2005). The silent behavior in big brown bats suggests the possible use of cooperative sonar and eavesdropping in echolocating bats (Kuc, 2002). Returning to the question posed above, "How does an echolocating bat sort its vocalizations and echoes from those of conspecifics to orient among millions of others?" the answer may be, "Silence." Perhaps only a few bats in a large group generate echolocation calls and other members remain silent to avoid severe signal interference. However, this question must be answered through empirical studies, which could also attempt to determine how many vocalizing individuals in a group are sufficient to support group orientation.

6.5 Sonar beam analysis

The sonar beam of echolocating bats is directional and the beam axis locks onto the target in the terminal phase of prey capture (Ghose and Moss, 2003). The beam axis, which indicates where the bat's attention is, can be used as an index to study the auditory gaze of echolocating bats.

It is difficult to tell what the bat's intention is by only investigating the spectrogram of bat echolocation calls when two bats are flying in the same room. The spectrogram tells us the time-frequency structure of calls but cannot provide information about where the bat points its sonar beam to. Moreover, because both food items and conspecifics were presented to the bat, it is important to know which objects the bat was “looking” at. Several questions can be studied by recording and analyzing sonar beam data of echolocating bats.

Does the following bat always direct its beam axis toward the leading bat? We found that the big brown bat followed another bat in the flight room most of the time but we did not fully understand the function of this following behavior. It is assumed in this study that one bat was pursuing another bat because some hostile behavior, such as physical contact or screech calls, of the follower was sometimes observed. If the follower always points its sonar beam toward the leader, we can be more confident to conclude that the follower really actively tracked the leader and tried to chase it.

Does the sonar beam axis of the leading bat always point toward the target? Two objects in the room may draw the bat’s attention, one is the tethered mealworm and the other is another flying conspecific. It seems difficult for the leading bat to “look” back toward the following bat because it is not an easy task to fly forward and turn the head backward all the time. However, the leading bat may occasionally direct its beam backward to keep track of another bat’s position since they need to compete for the same food item.

Is the bat responding to another bat’s existence and movement? We are almost certain from observation that paired bats both were aware of each other’s existence because some interaction, such as vocalizations made for social purposes, physical contact with another individual, etc. However, it is unknown that how long one bat paid attention to another bat. The bat may only gaze at another bat occasionally and move its sonar beam toward a more worthy target, which was the tethered mealworm in this study, or the bat could always direct its attention to another bat's movement in order to find an appropriate moment to access the worm.

Where does the bat point its sonar beam before and after it goes silent? A silence strategy was discovered in this thesis but it is unclear yet if bats "shared" their echolocation in some ways. A beam pattern analysis before and after the bat went silent may help us understand why the bat decided to shut off its echolocation. Moreover, the sonar beam pattern of the vocalizing bat may clarify the possibility for the silent bat to listen to another bat's vocalization for its own orientation purpose.

Where do paired bats direct their sonar beams in different flight configurations? Three major flight behaviors, which are following, converging and diverging, were described in this thesis. Paired bats may show different sonar beam directing behaviors in different flight configurations. For example, both bats may direct the sonar beam patterns away from each other in converging flight to avoid signal interference, which can be viewed as another newly discovered strategy to avoid signal jamming. Simmons et al. (1995) has hypothesized that bats can simply turn their sonar beam axes away from each other to avoid interference since the sonar beams of echolocation bats are highly directional.

Sonar beam analysis in echolocating bats provides a new perspective to study the auditory gaze and attention of bats. Analysis of sonar beam data can answer several research questions. Where does the bat really "look" when it flies with conspecifics? Can bats turn sonar beams away to avoid jamming? Does the bat constantly lock its beam on another bat or just check its movement occasionally? Future research should focus on sonar beam pattern analysis in order to obtain a clear picture of bat orientation and jamming avoidance in the presence of conspecifics.

6.6 Summary

This study reports on adaptive echolocation and flight behaviors of free flying big brown bats under different experimental conditions. Free-flying bats provide the chance to observe their nearly natural behavior, but stimuli in an environment is harder to control than experiments with the bat restrained in one place. Research findings from this study motivate further investigation. Psychoacoustic experiments are necessary to determine the bat's ability to discriminate different signals, determine the 3-D position of an object, recognize meaningful sounds from background noise, etc. Sonar beam analysis can serve to specify the direction of the bat's attention and how this auditory "gaze" guides the bat's flight control.

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