

## Adaptive echolocation behavior in bats for the analysis of auditory scenes

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### SUMMARY

**Echolocating bats emit sonar 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 a conspecific 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 call frequency differences, suggesting that bats actively change their sonar call structure if pre-existing differences in call design are small. Call design adjustments 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. We propose that dissimilarity between the time–frequency features of sonar calls produced by different bats aids each individual in segregating echoes of its own sonar vocalizations from the acoustic signals of neighboring bats.**

Key words: bats, echolocation, adaptive vocal behavior, flexibility, call design, auditory scene analysis, conspecifics.

### 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 process the acoustic signals, integrate meaningful segments and separate these sounds from background noise. The ability to analyze auditory scenes is exhibited by humans and other animal species, such as birds and frogs, which rely heavily on acoustic communication (Hulse, 2002).

Bregman 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 (Bregman, 1990). 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, 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; Fay, 2000). Separation in spectral features of vocalizations and call timing are crucial factors that affect acoustic

behavior 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 surroundings.

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 the presence of 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 lack records of the 3-D positions of the 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 trajectories in individual bats. We hypothesize that bats adjust features of their echolocation calls when flying in the same air space in order to analyze auditory scenes and avoid signal jamming. This leads us to predict that the amount of call modification may be related to the similarity in baseline call design of individual bats, the relative position between paired bats and the timing of successive vocalizations. We report here the first detailed study to address changes in sonar call design of identified free-flying echolocating bats in response to vocalizing conspecifics. Results of this study extend our understanding of the echolocating bat's active vocal control in the analysis of auditory scenes.

## MATERIALS AND METHODS

### Animals

We studied the vocal behavior of eight big brown bats, *Eptesicus fuscus* Beauvois, and data from seven pairs are reported in the present study. Bats were collected from different regions in Maryland (collection permit #SCO 42501) and kept in captivity at the University of Maryland, College Park, MD, 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 h to ensure that bats were at their most active periods during the behavioral experiment. The mass of each bat was between 14 and 16 g, 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, MD, USA.

### Experimental setup

All eight bats were first trained to fly and capture a tethered mealworm *Tenebrio molitor* Linnaeus in a large anechoic flight room (7×6×2.5 m) (L×W×H) equipped with synchronized audio and high-speed stereo 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 10–20 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. Paired bats were released simultaneously from the same spot in the flight room and the releasing spot was always the same in baseline and two-bat conditions. 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 for each bat. Fifteen trials per day over a minimum of three test days, yielding at least 45 two-bat trials per bat pair, were recorded in the two-bat condition after completely finishing collecting baseline data. Between 20 and 30 trials per individual/pair with high-quality audio and video recordings from each condition were selected for further analysis.

### Data recordings

Audio data were recorded with three ultrasound-sensitive microphones (UltraSound Advice, London, UK) on the floor, and video data were recorded with two high-speed digital video cameras (Kodak MotionCorder Analyzer, Model 1000, 240 frames s<sup>-1</sup>; San Diego, CA, USA) mounted in two adjacent corners of the flight room, permitting the 3-D reconstruction of the bat's flight path. The frequency response of all three microphones was flat within ±3 dB for frequencies between 20–90 kHz. The sensitivity dropped by 10 dB for frequencies between 90 and 100 kHz. 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 (Mathworks, Natick, MA, USA) (see below).

### Data analysis

A custom MATLAB program was used to analyze audio data, and five parameters were applied to characterize the call design of an 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<sup>-1</sup>), 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 the position of each bat and microphone and reconstructing the 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 ultrasound-sensitive microphones on the floor recorded the 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 (Fig. 1). Because the microphones were positioned at different locations in the room, a call that was produced by a bat would reach these microphones at different times. The actual audio delay of one call refers to the difference of the recorded signal's onset time between two microphones. The position of these two microphones and paired bats were already established by video data analysis. The estimated audio delay was computed by measuring the distance of each bat to the microphones and estimating the acoustic signal travel time differences of the calls at each of these microphones. When we assigned a given call to the vocalizing individual, we confirmed that the actual and estimated audio delays were the same. Therefore, by comparing the values of actual and estimated audio delay, we could unambiguously associate each echolocation call to the bat that vocalized. Detailed analysis methods are reported in Chiu et al. (Chiu et al., 2008).

## 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. In the present study we investigated possible factors driving call modifications, including

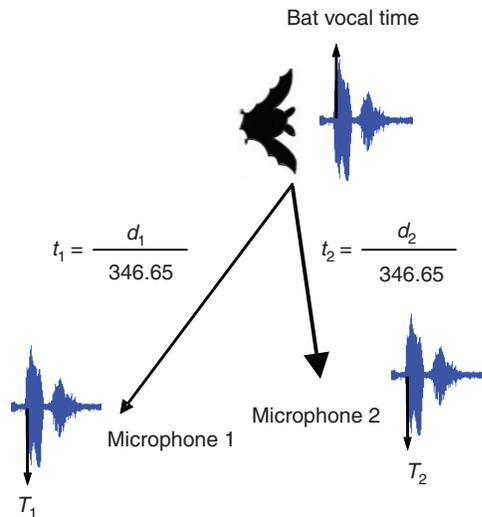


Fig. 1. Illustration of assignment of echolocation calls to individual bats. The sound speed is  $346.65 \text{ m s}^{-1}$ ;  $T_1$  and  $T_2$  is the onset time of recorded calls at microphone 1 and 2, respectively;  $t_1$  and  $t_2$  is the signal travel time from the bat to microphones 1 and 2, respectively, which are estimated from video recordings;  $d_1$  and  $d_2$  is the distance between bat and microphone 1 and 2, respectively. Actual audio delay is calculated from audio recordings and is equal to  $T_1 - T_2$ . Estimated audio delay is calculated from video recordings and is equal to  $t_1 - t_2$ . Values of *real audio delay* and estimated audio delay are the same if one call was correctly assigned to the vocalizing bat.

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 fly 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.

#### Analysis of sequential calls produced by paired bats

The most common flight behavior of paired bats in this study was following flight, which is defined as one bat flying behind the other bat and both bats heading toward a similar direction (the angle between paired bats' headings is acute). About 66% of the time in this study one bat followed the other one, 10% of the time two bats flew toward each other and another 24% of the time bats flew away from each other (Chiu et al., 2008). Individual bats usually showed differences in call design and these differences may be used to avoid call interference from neighboring conspecifics. Fig. 2 shows the flight trajectories, relative positions and call design measurements 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 (Fig. 2A,B). The separation in start frequency between the sonar calls of paired bats increased as the inter-bat distance decreased. Small separations were observed in their sonar call end frequencies, and changes in the inter-bat spacing did not appear related to these separations. These two bats maintained a small separation in call duration and sweep rate but the separation also did not change with inter-bat spacing. Bats in the second example were flying almost in parallel at the beginning of the

segment and subsequently one bat fell behind the other bat before their flight paths diverged (Fig. 2C,D). These two bats maintained a small amount of separation in call frequency as they flew in close proximity. Separation in call duration was similar to that in the first example but separations in call sweep rate were smaller than those in example No. 1. This example does not show any systematic increase in call design separation with decreasing inter-bat distance but all the data presented come from distances of less than 85 cm.

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. Fig. 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 from this analysis because the main focus here is to determine the differences in call design between paired bats in response to the other bat's calls. Therefore, the sequential call analysis example in Fig. 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  $346.65 \text{ m s}^{-1}$  at  $25^\circ\text{C}$ ). 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 related to the presence of prey rather than conspecifics.

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 Fig. 4. Nearly 90% of vocalizations exceeded the baseline separations in duration and sweep rate when two bats flew together whereas 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.

#### Similarity in baseline call design

Individual bats in this study showed different amounts of separation in their baseline call design, and the similarity between the call design of paired bats influenced how each bat adjusted 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 is calculated by subtracting the difference between the means of the baseline call features of paired bats from the difference between features of two sequential calls produced by different animals in the 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 separations. A negative correlation was found between the baseline separation of spectral call features and the magnitude of call design adjustment under paired conditions (Fig. 5A–C). Fig. 5A–C show that the bat pairs with the most similar baseline call frequencies (start/end) and bandwidth increased their

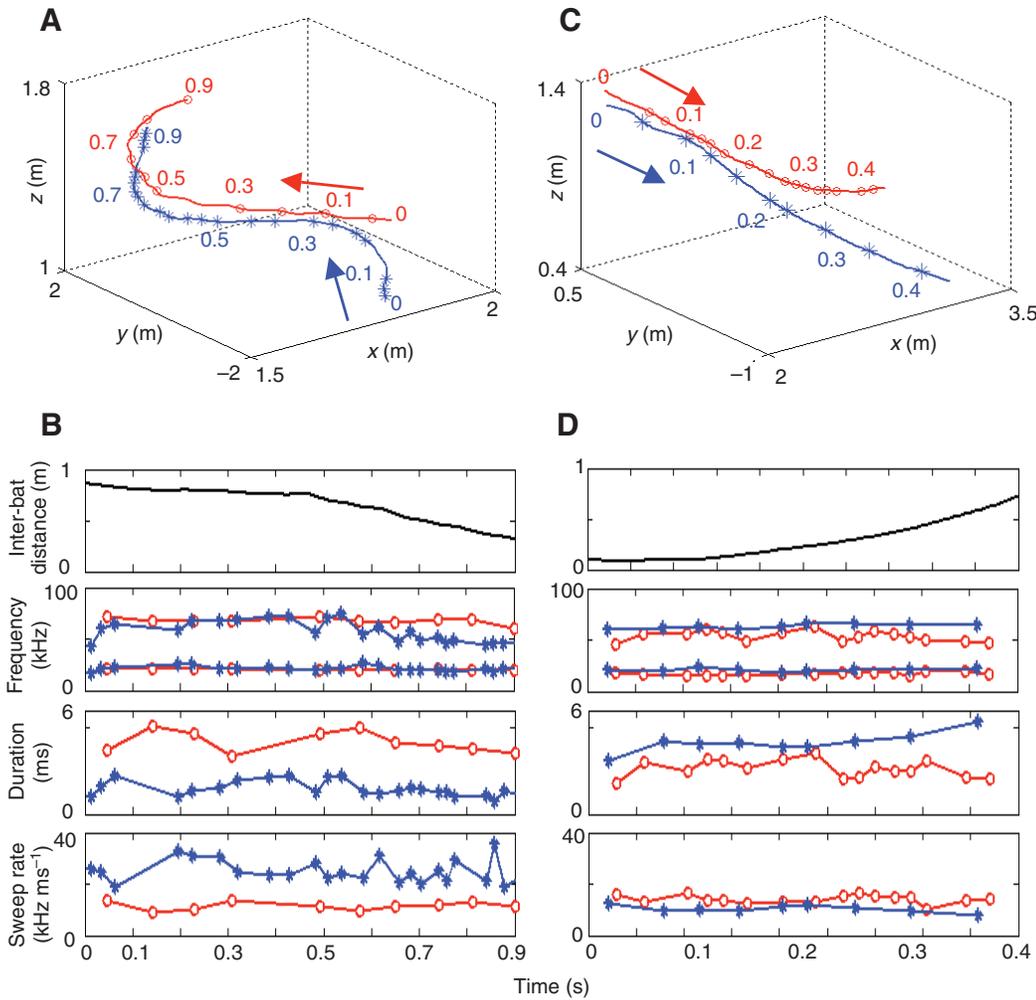


Fig. 2. Two examples show the relative position of paired bats and the design of their vocalizations. The 3-D flight paths of each bat in (A) example No. 1 and (B) example No. 2. Arrows in the starting points of each flight curve marked the flight direction of each bat. Flight trajectories of each bat were marked by different colors (blue and red). One bat flew behind the other bat and followed the leading bat's flight trajectory in example No. 1. Two bats flew almost parallel in the beginning of example No. 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 represents one vocalization from bat A (asterisks) and bat B (open circles). The inter-bat distance and call design of bat A and bat B are shown in (B) example No. 1 and (D) example No. 2. The asterisks represent vocalizations from bat A and the open circles represent vocalizations from bat B. From the upper to lower 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 and sweep rate.

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 two call parameters (Fig. 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 (Fig. 6). A positive correlation between these two measurements means that the individual with the higher start frequency maintained this higher frequency in the two-bat condition for those bat pairs with greater start frequency separations in the baseline 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 or not depended on baseline call frequency design.

#### Spatial separation

Call design differences of successive calls produced by different bats were significantly affected by the spatial separation of paired animals [one-way analysis of variance (ANOVA),  $P < 0.05$  for all five parameters]. The Scheffé test was used for *post-hoc* comparisons to determine which inter-bat spacing influenced vocal adjustment

of bats. The largest separations in start and end frequencies, duration and bandwidth occurred when the inter-bat distance was shorter than 0.5 m (Fig. 7). When the inter-bat distance was between 0.5 and 1 m,

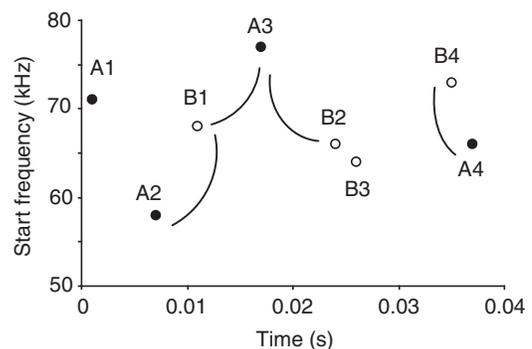


Fig. 3. Schematic representation of sequential call analysis. Each point represents the start frequency of one vocalization, and different letters mean calls made by different bats. For example, A1 is the first call bat A produced and B3 is the third call bat B generated. The x-axis is the time and y-axis is the start frequency of calls. Curves between two calls represent two consecutive vocalizations produced by different bats and absolute differences between these two sequential calls are used to represent separation in paired bats' call design. Two consecutive calls, which were not connected by curves, were not included in data analysis because they were produced by the same individual.

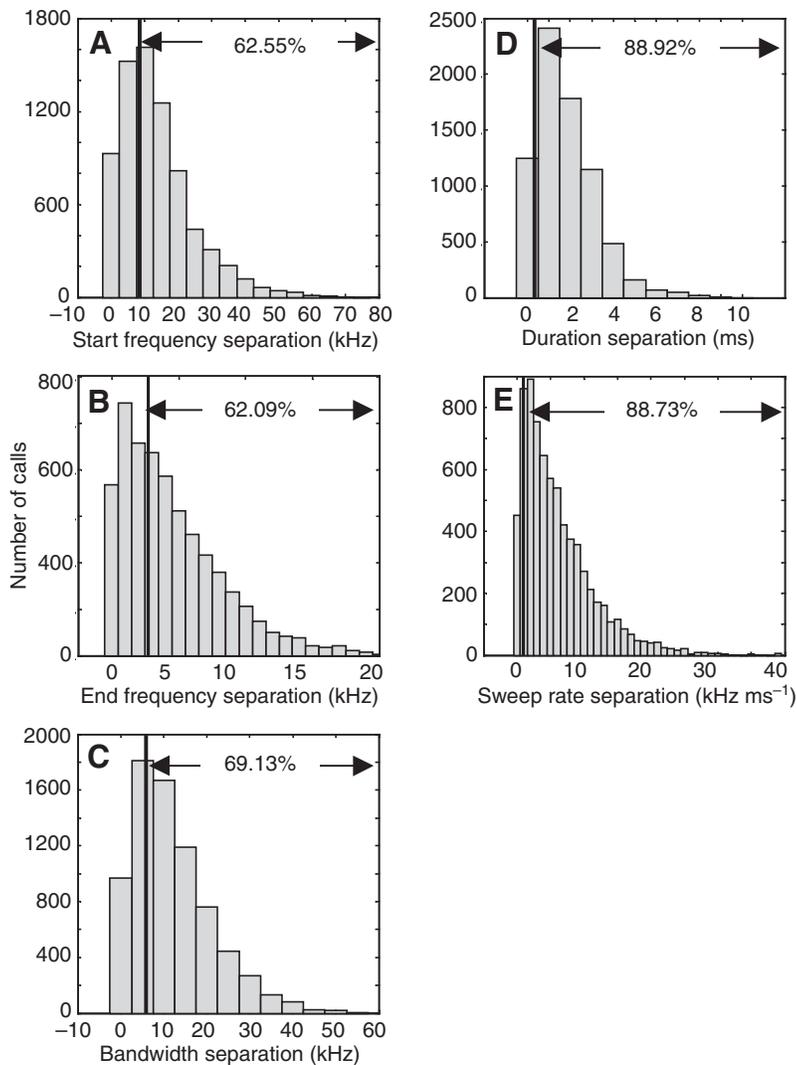


Fig. 4. Distribution of call design separation between two sequential calls produced by different bats when they flew together. The thick black line in each histogram indicates the baseline separation, which is the difference in call design between two bats when they each flew alone. The percentages mark the proportion 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.

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.

#### Temporal separation of successive calls

Temporal separation in sonar calls could also be a factor affecting the echolocation call design adjustments of paired bats. Bats dynamically varied the interval between successive calls and timed their sonar vocalizations to avoid overlap with the other bat's calls. In this study, only 9.41% of calls produced by paired bats overlapped for any portion of the signal duration. The effect of temporal separation between successive calls produced by different bats was examined by comparing the call design separation of paired bats as a function of the time window separating their calls. We divided successive calls into two groups; one with a short time window ( $\leq 5$  ms) separating the signals of the two bats and one with a longer time window ( $> 5$  ms) separating the signals of the two bats. As the relative position of the bats and microphones was recorded in this study, we were able to calculate each bat's vocalization time and the

time this call arrived at the other bat's ears. Therefore, the temporal separation of calls produced by two bats is defined here by the interval between the time when the call of one animal reached the ears of the other (listening) animal and the time when the listening animal produced its next call. We applied an independent sample *t*-test to examine whether the time window separating the sequential calls of the two bats influenced design adjustments in the features of calls. When the time window between the call received by one bat and its next sonar call was less than 5 ms, the magnitude of separation between call features was significantly greater than when this time window was greater than 5 ms (for all five parameters,  $P < 0.05$ ).

#### Analysis of global call adjustments by individual bats

Sequential call analysis reveals 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 the general pattern of call structure adjustments in individual bats.

#### Direction and magnitude of call feature adjustments across bat pairs

Call design in the two-bat condition minus that in the baseline condition represented the amounts of change from the baseline

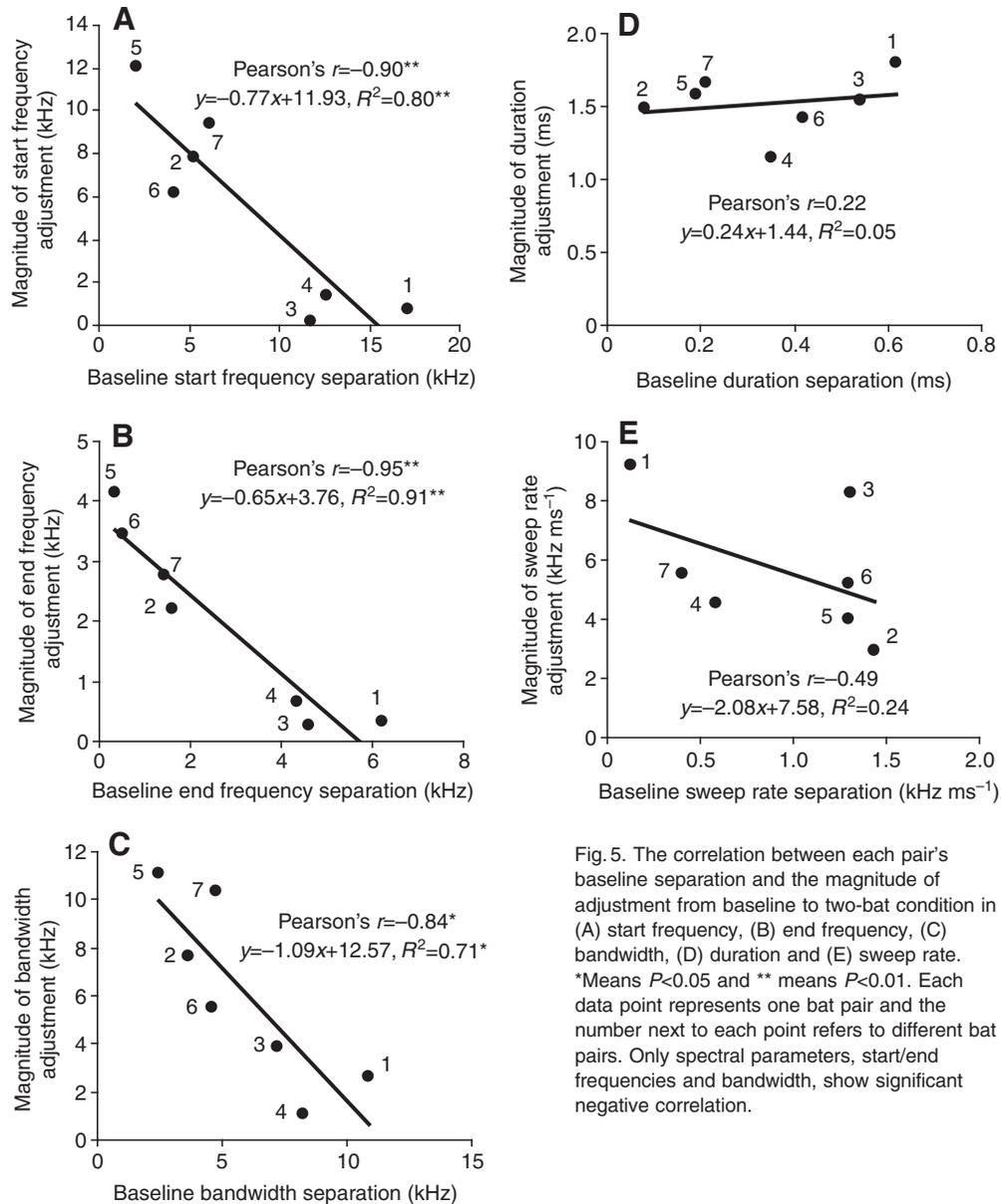


Fig. 5. The correlation between each pair's baseline separation and the magnitude of adjustment from baseline to two-bat condition in (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate. \*Means  $P < 0.05$  and \*\* means  $P < 0.01$ . Each data point represents one 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.

condition, and all bats modified at least one call parameter when paired with another bat (Fig. 8). Call design changes in different pairs analyzed 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 the other individual in pair 5 modified its start frequency, bandwidth and sweep rate. No consistent change pattern was observed in the direction of sonar call 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 always 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.

**Call adjustment depends on pulse interval**

Call design adjustment by an individual bat varied with the rate at which it produced sonar calls. The magnitude of call design adjustment refers to the absolute difference between each individual bat's call design in baseline and two-bat conditions and it is plotted as a function of pulse intervals in Fig. 9. Pulse intervals were divided into five time bins of 5 ms intervals. Pulse intervals below 10 ms were excluded from this analysis to eliminate feeding buzzes. Differences in magnitude of call adjustment were significantly influenced by pulse interval (one-way ANOVA,  $P < 0.05$  for all five parameters). The Scheffé test was used for *post-hoc* comparisons to determine whether call parameter adjustments differed across pulse interval bins. The magnitude of start/end frequencies, bandwidth and sweep rate adjustment decreased as pulse intervals increased, and the magnitude of duration adjustment showed the reversed trend. When pulse intervals were less than 30 ms, the magnitude of start frequency and bandwidth adjustment was the largest. Big brown bats showed the largest change in call sweep

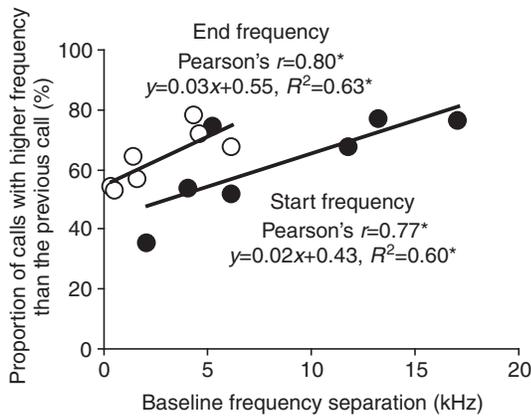


Fig. 6. The correlation between start/end frequencies separation and proportion of calls with higher start/end frequencies than the preceding call. The closed circles represent start frequency and the open circles represent end frequency in each bat pair. The bat with higher start frequency tended to keep a higher frequency than the other bat in the pair when the start frequency separation is large for this pair. End frequency shows a similar trend to start frequency.

rate from baseline producing sounds with intervals between 10 and 15 ms. The magnitude of sweep rate adjustment decreased for longer pulse intervals.

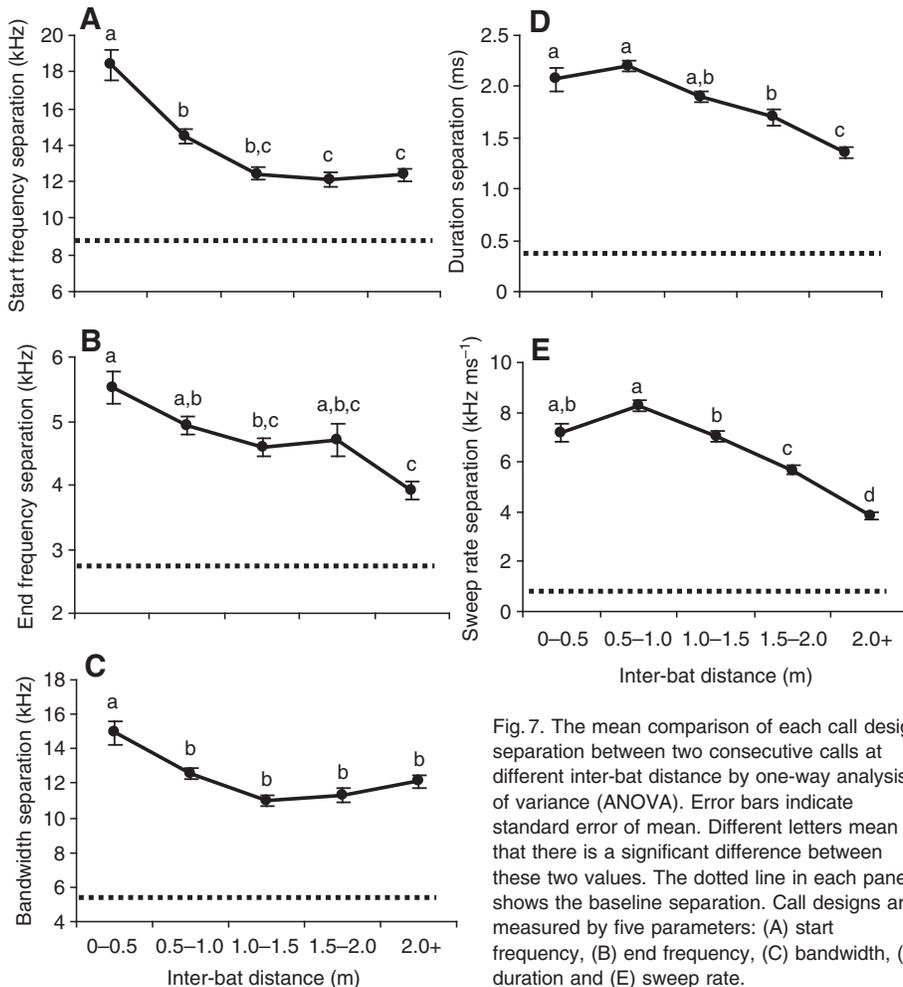


Fig. 7. The mean comparison of each call design separation between two consecutive calls at different inter-bat distance by one-way analysis of variance (ANOVA). Error bars indicate standard error of mean. Different letters mean that there is a significant difference between these two values. The dotted line in each panel shows the baseline separation. Call designs are measured by five parameters: (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate.

**DISCUSSION**

Humans and other animals can distinguish and make sense of auditory streams from complex acoustic scenes (Bregman, 1990; Hulse, 2002). 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 similarity in baseline call design of individual bats. Distinct spectral features or temporal patterns can help bats integrate and segregate auditory streams in a complex environment (Moss and Surlykke, 2001). The results of this study suggest possible acoustic cues, arising from call design differences, which could allow echolocating bats to segregate echoes from their own sonar vocalizations from the sonar signals of nearby conspecifics.

**Rule one for signal modification: 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 segregate their signals from those 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

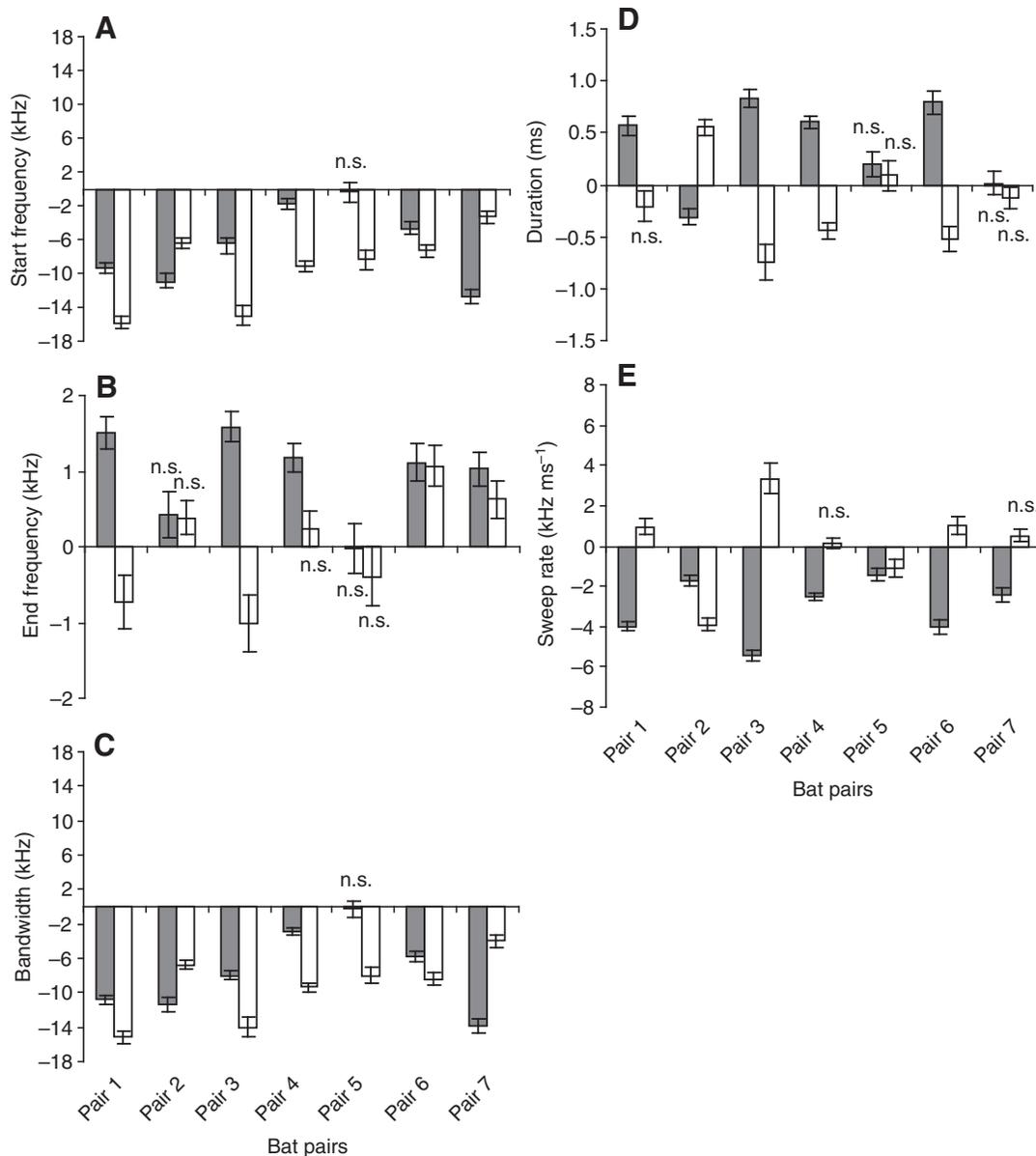


Fig. 8. The amount of deviation from baseline data in the two-bat condition for each bat in each pair. White and gray bars indicate data from different bats in a pair. Five call parameters were presented here: (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate. All 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 numbers correspond to those shown in Fig. 5. Error bars represent standard error of the mean.

and Westby, 1992). Adult female bats can identify their own pups 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 use individual-specific isolation calls to help identify their own offspring (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 so also do adult bats. Inter-individual differences in call design have been observed in several bat species (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 of this species 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* and *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 different acoustic sources. The correlation between the similarity in call features of bats flying alone

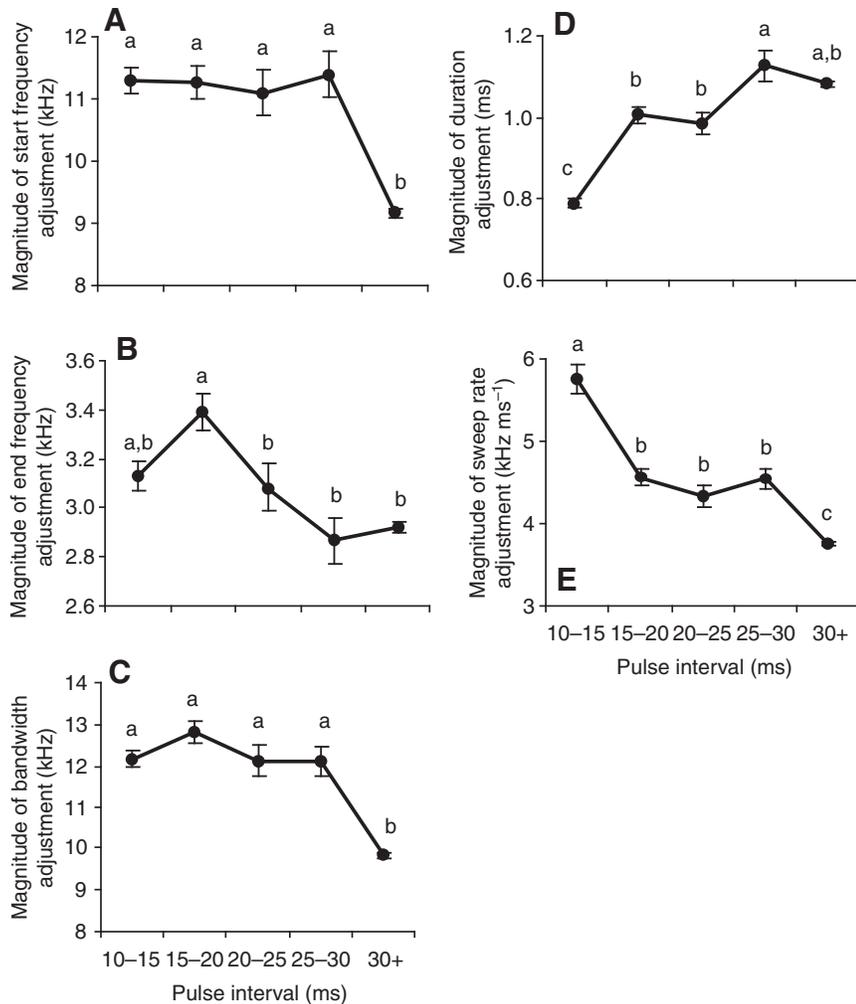


Fig. 9. The magnitude of call design adjustment from baseline to two-bat condition as a function of pulse intervals. Error bars indicate standard error of mean and different letters mean that there is a significant difference between these two values. The x-axis is the pulse interval of individual bats and the y-axis is the magnitude of adjustment for five call parameters: (A) start frequency, (B) end frequency, (C) bandwidth, (D) duration and (E) sweep rate.

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 calling frequencies or bandwidth if baseline vocalizations showed similar spectral features to the bat it was paired with. Paired bats, whose calls already showed considerable design feature 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 mean 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<sup>-1</sup> for sweep rate. These mean values provide an estimate of discriminable spectral and temporal feature separations in call design of paired big brown bats. Two pipistrelle bats, *Pipistrellus pipistrellus* and *Pipistrellus 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 previous 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 mean start frequency (13.51 kHz) and end frequency (4.62 kHz) separation in the present study. The constant frequency component of lesser mouse-tailed bat's (*Rhinopoma hardwickei*) echolocation calls tend to fall into one of three different frequency bands (30, 32.5, 35 kHz) when they fly in a group (Habersetzer, 1981). This result suggests that a 2.5–5 kHz separation in call frequency is enough for *R. hardwickei* to discriminate differences between its own echolocation call and the calls of conspecifics. These findings suggest a reference for conducting further psychoacoustic experiments on the bat's ability to discriminate signals with different time–frequency structures.

#### Rule two for signal modification: spatial separation

We analyzed in detail vocal changes the bat made in response to the presence of another 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, as one bat may enlarge differences between its calls and those of the other bat for a short period of time when call interference is large. We discovered that separation in call design is dependent on the inter-bat distance. Start/end frequencies, duration and bandwidth of the FM sweep showed the largest differences between paired bats when the inter-bat distance was shorter than

0.5 m. The magnitude of call interference became high when paired bats flew close to each other and one bat in a pair sometimes stopped vocalizing for more than 0.2 s, possibly to avoid signal jamming from conspecifics. Silence has been observed in paired echolocating bats competing for a single food item, and it has been hypothesized that silence is a strategy used by bats to avoid call interference (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 maintain spatial separation among individuals when communicating in complex acoustic environments, potentially to avoid call interference. For example, male frogs typically maintain a minimum distance in a chorus (Gerhardt and Huber, 2002).

### Rule three for call modification: temporal separation of successive calls

In this study, only occasionally did vocalizations of paired bats overlap in time. Instead, there were temporal gaps between the calls of individual bats, and the intervals between calls varied over the course of each trial. Two bird species, the red-eyed vireo (*Vireo olivaceus*) and the least flycatcher (*Empidonax minimus*), modify temporal patterns of their songs to avoid signal overlap (Ficken et al., 1974). Male singing nightingales (*Luscinia megarhynchos*) sing preferentially during the silent windows between heterospecific songs in order to transmit their songs more efficiently (Brumm, 2006). The cotton-top tamarins (*Saguinus oedipus*) can adjust their vocalizing time to fall into the silent windows between white noises (Egnor et al., 2007). The tropical frog, *Eleutherodactylus coqui*, also adjusts the timing of its mating calls to fall in gaps between the vocalizations of neighboring frogs (Narins, 1992; Zelick and Narins, 1983). The echolocating bat could apply the same principle by listening to the other bat's vocalizations to select its call timing, and when intervals between the calls of paired bats are short enough to create interference, this may drive further adjustments to sonar signal design. Support for this comes from our present finding that the largest call design separations occurred when one bat vocalized less than 5 ms after the other bat's vocalizations. The increases in call design differences for closely timed calls imply that the big brown bat actively controls timing and call features to avoid call interference from conspecifics. As elaborated below, behavioral studies of echo ranging by echolocation in bats have reported that interfering signals disrupt distance discrimination, and the acoustic feature and temporal separation between jamming signals and echoes affects the magnitude of interference (Masters and Raver 1996; Møhl and Surlykke 1989; Roverud, 1989; Roverud and Grinnell, 1985a; Roverud and Grinnell, 1985b).

### Global signal adjustments in the presence of conspecifics

Big brown bats changed features of their echolocation calls when flying with conspecifics. The question of whether the observed differences in call features are the result of active jamming avoidance or simply due to individual-specific call design can be resolved here by comparing calls in the two-bat condition with baseline vocalization data. In our study, most individuals flying in pairs showed significant changes in each call parameter compared with the calls produced in baseline recordings when each flew alone, suggesting that the presence of the conspecific elicited vocal adjustments. Call design separation was affected by the spatial distance between 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.

Several bat species, including *R. hardwickei*, *Balantiopteryx plicata*, *T. brasiliensis* and *Tadarida teniotis*, have been reported to adjust their call frequencies when flying in groups (Bartonička et al., 2007; Habersetzer, 1981; Ibáñez 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. (Ulanovsky et al. 2004) and Gillam et al. (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 the present study also showed call modification in end frequency, adjustments in start frequency were larger than end frequency. This finding is consistent with another study that reported a larger call frequency separation in start frequency than in end frequency in *E. fuscus* and *Lasiurus cinereus* but not in *Lasiurus borealis* and *Euderma maculatum* (Obrist, 1995). Previous and present research findings suggest that inter-specific 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 their EOD frequencies 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 reports on electric fish have described how two fish adjust their EODs to increase differences between their signals. For example, wave-type electric fish modify their EOD frequencies, 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 the 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; Ibáñez et al., 2004; Kössl et al., 1999; Miller and Degn, 1981; Ratcliffe et al., 2004; Surlykke and Moss, 2000). Gray sac-winged bats, *B. plicata*, shifted their peak frequencies slightly upward when flying in groups (Ibáñez et al., 2004) and *T. brasiliensis* shifted their end frequencies upward when playback bat calls were broadcast (Gillam et al., 2007). Bates et al. reported that the big brown bat, performing in a two-alternative forced-choice detection task, shifted calling frequencies upward when lower jamming frequencies were broadcast and shifted calls downward when higher jamming frequencies were broadcast (Bates et al., 2008). 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 big brown bats did not collide with each other or show any sign of disorientation demonstrates that this species employs successful strategies 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, as 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 of high frequency sounds (Lawrence and Simmons, 1982). Call intensity decrease due to the presence of conspecifics could be another vocal adjustment strategy the bat uses to avoid signal jamming. A calibrated measurement of the bat's call intensity is required in the future to confirm whether bats decrease their call intensity to avoid signal jamming.

Echolocating bats generate pulses with short intervals when attempting to capture their prey or approaching obstacles and produce sonar pulses with low repetition rate when searching for targets or orienting in space. It has been inferred that bats use high repetition rate calls to acquire precise information from targets and use low repetition rate calls when no target of interest is shown in the vicinity (Schnitzler and Kalko, 2001). Big brown bats in this study increased the magnitude of adjustment in start/end frequencies, bandwidth and sweep rate when pulse intervals decreased, which suggests that the bat modifies features of its sonar calls the most when it needs to stream detailed information from target echoes at short distance.

#### 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 suggests that the same principles can be applied to auditory scene analysis (Bregman, 1990). The principle of similarity enables the auditory system to segregate and integrate complex sound patterns. Echolocating bats may apply these principles to distinguish its own 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 provides 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 slope of its FM sweep to maximize differences from calls of conspecifics. Consistent with this suggestion are the results of psychophysical experiments on target ranging by echolocating bats. In one such experiment, the big brown bat's range discrimination performance deteriorated when a phantom target echo of the bat's own call was replaced by signals of other bats with different call designs (Master and Raver, 1996). In a follow-up study, they found that FM sweep curvature changes in sonar signals compromised the bat's ranging ability (Masters and Raver, 2000).

As noted above, interference signals can also affect sonar ranging by bats. Masters and Raver (Masters and Raver, 1996) report that

interference signals degraded target range discrimination performance of the big brown bat, and the magnitude of interference depended on the similarity between target echoes and interference signals. Another study in *P. 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, the big brown bat's range discrimination performance deteriorated only when the click of ruby tiger moth (*Phragmatobia fuliginosa*) was broadcast within 1.5 ms before the echo return (Miller, 1991), in a time window when the click may have served as a forward masker of the echo playback stimulus (Moss and Schnitzer, 1995). Results from these studies suggest that calls sharing similar time–frequency structure disrupt the bat's ranging ability the most. Therefore, minimizing the similarity in call design from conspecifics seems to be a successful strategy for the bat to avoid sonar jamming from the signals of nearby conspecifics.

#### Two jamming avoidance strategies: vocal adjustment and silence

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

An echolocating bat shows signs of disorientation when its hearing is disrupted (Griffin, 1958) but it avoids collisions with another flying animal when it goes silent (Chiu et al., 2008). A silent bat can still listen to environmental sounds, including the calls and echoes of conspecifics in the vicinity, and passive localization of these sound sources presumably guides its orientation in the environment. The listener needs to be close to the vocalizing animal in order to use the other's vocalization for orientation (Kuc, 2002; Xitco and Roitblat, 1996). As the vocalizing bat can fly unexpectedly out of 'ear shot' of the passively listening bat, an echolocating bat risks disorientation when it shuts off its echolocation. Many conditions would therefore favor a bat's vocal adjustment strategy over a silence strategy. However, the bat may encounter difficulties finding a transmission channel that is free from overlap with other individuals when employing a vocal adjustment strategy for jamming avoidance, particularly when it exits/enters its roost with many dozens of conspecifics. Under such conditions, vocal adjustment may prove of little use and other strategies would be needed. Silence is one potential strategy for a bat to employ when many conspecifics are flying in close proximity.

Detailing the factors that drive silent and vocal adjustment behaviors in echolocating bats is a subject for future research. As a starting hypothesis, we propose that silence is a strategy the big brown bat employs primarily to avoid potentially disabling interference under conditions when its localization accuracy requirements are not high, e.g. avoiding obstacles. In this context, it is important to note that the big brown bat always produces sonar calls as it prepares to intercept prey, when the timing of vocalizations and returning echoes is used for precise target localization (Chiu et al., 2008). Vocal adjustment, as reported in the present study, may be used when it is difficult for the bat to use the signals of a

conspicuous or localization accuracy requirements are high, e.g. during prey capture.

### Conclusions

The big brown bat (*E. fuscus*) encounters and interacts with conspecifics frequently in nature (Simmons et al., 2001). Flying with other bats does not disrupt the ability of *E. fuscus* to use echolocation for spatial orientation, indicating that this bat species must employ strategies to cope with possible signal interference from conspecifics. Results reported in this study show increases in sonar signal call design separation of *E. fuscus* flying in pairs, and the magnitude of signal changes depends on the baseline similarity between call features of individual bats flying alone. These data are consistent with the hypothesis that the big brown bat utilizes call design modifications to avoid call interference from neighboring conspecifics. We propose that dissimilarity in time–frequency signal structure enables the big brown bat to segregate auditory streams of its calls and echoes from those of neighboring conspecifics.

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