Echo-intensity compensation in echolocating bats (*Pipistrellus abramus*) during flight measured by a telemetry microphone

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An onboard microphone (Telemike) was developed to examine changes in the basic characteristics of echolocation sounds of small frequency-modulated echolocating bats, *Pipistrellus abramus*. Using a dual high-speed video camera system, spatiotemporal observations of echolocation characteristics were conducted on bats during a landing flight task in the laboratory. The Telemike allowed us to observe emitted pulses and returning echoes to which the flying bats listened during flight, and the acoustic parameters could be precisely measured without traditional problems such as the directional properties of the recording microphone and the emitted pulse, or traveling loss of the sound in the air. Pulse intensity in bats intending to land exhibited a marked decrease by 30 dB within 2 m of the target wall, and the reduction rate was approximately 6.5 dB per halving of distance. The intensity of echoes returning from the target wall indicated a nearly constant intensity (−42.6±5.5 dB weaker than the pulse emitted in search phase) within a target distance of 2 m. These findings provide direct evidence that bats adjust pulse intensity to compensate for changes in echo intensity to maintain a constant intensity of the echo returned from the approaching target at an optimal range. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2431337]

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I. INTRODUCTION

Bats (Microchiroptera) possess a highly developed sonar system. As biosonar animals, they are capable of echolocation that recognizes the physical attributes of their environment with great accuracy by comparing emitted pulses to returning echoes (Griffin, 1958). Echolocation pulses can differ markedly in structure, consisting of either only short downward frequency-modulated (FM) pulses or long constant-frequency (CF) pulses followed by a short FM component. Such variation in the structure of echolocation pulses is thought to reflect the adaptations of different species to the constraints imposed by their foraging behavior (Simmons and Stein, 1980; Neuweiler, 1984).

Rhinolophids, Hipposiderids, and a Mormoopid (the mustached bat, *Pteronotus parnellii*) all use a compound CF-FM pulse. As a bat approaches a target, the frequency of the returning echo is Doppler-shifted depending on the velocity of the bat in relation to the target. These bats compensate for the Doppler shifts by changing their pulse frequencies so that the echo frequencies remain constant and are precisely analyzed within the narrowly tuned frequency range in which the bats can hear best. This behavior is termed “Doppler-shift compensation” (DSC) and is an important behavioral adaptation for echolocation in CF-FM bats (Schnitzler, 1968; Schuller et al., 1974; Simmons, 1974; Gustafson and Schnitzler, 1979; Trappe and Schnitzler, 1982; Gaioni et al., 1990; Lancaster et al., 1992; Keating et al., 1994).

During flight, bats decrease the intensity of their emitted pulses when they approach a prey item or an obstacle (e.g., Griffin, 1958; Jen and Kamada, 1982; Vogler and Neuweiler, 1983; Kick and Simmons, 1984; Hartley et al., 1989; Tian and Schnitzler, 1997; Boonman and Jones, 2002). Kobler and colleagues (1985) have shown that a bat attached to a pendulum and swung toward a large fixed target decreases the intensity of its emitted pulse during the forward swing and increases the intensity during the backward swing. This behavior indicates the possibility of another compensation mechanism, in which pulse intensity is adjusted in relation to the distance to a target, resulting in maintenance of echo intensity within the optimal sensitivity range (echo-intensity compensation). Subsequently, reduction of pulse intensity has been quantitatively investigated in bats given a flight task (Hartley et al., 1989; Waters and Jones, 1995; Tian and Schnitzler, 1997; Boonman and Jones, 2002) and using a
pendulum device or a moving-target apparatus to elicit and measure changes in pulse intensity (Gaioni et al., 1990; Hartley, 1992b). Adjustment of pulse intensity by bats has been discussed in a number of studies as being related to echo-intensity compensation (e.g., Kick and Simmons, 1984; Hartley et al., 1989; Hartley, 1992a; b; Simmons et al., 1992; Waters and Jones, 1995; Tian and Schnitzler, 1997; Boonman and Jones, 2002). Recently, Au and Benoit-Bird (2003) demonstrated that free-ranging dolphins in the wild changed the amplitude of emitted echolocation signals depending on the range of the target to compensate for propagating loss in sound. Therefore, echo-intensity compensation may be effective in the biosonar systems of both bats and dolphins. However, accurate measurement of the intensity of directional pulses emitted by biosonar animals is still considered difficult using the traditional microphone system. For quantitative analysis of the pulse intensity which the flying bats actually emitted, recorded pulses required several corrections for compensating the directional properties of the recording microphone and the emitted pulse, and also traveling loss of sound in the air depending on the distance between the bat and the microphone (e.g., Hartley et al., 1989; Tian and Schnitzler, 1997; Boonman and Jones, 2002). Given these constraints, the pulse intensity measured by the traditional microphone potentially confounded interpretation of a bat's adjustment of pulse intensity in relation to its spatiotemporal behavior during echolocation. Furthermore, measuring the intensity of echoes as well as emitted pulses is necessary to reveal any echo-intensity compensation behavior employed by the animals. However, the relationship between the pulse and returning echo intensities has not been experimentally investigated in detail for bats during flight.

In this study, we examined echolocation behavior in Japanese house bats (Pipistrellus abramus, an FM bat) given a flight landing task in a laboratory. Echolocation sounds were recorded by a telemetry microphone (Telemike) mounted on the head of the bat (Henson et al., 1987; Lancaster et al., 1992; Riquimaroux and Watanabe, 2000; Hiryu et al., 2005). Since well-studied FM bat species are small (e.g., P. abramus weighs 5–8 g) in relation to the weight of telemetry microphones, sound recording using telemetry microphones has never been used to investigate echolocation in flying FM bats. We developed a small Telemike that was light enough to be carried by the animals, and combined the Telemike with a high-speed video camera system in order to examine the relationship between the echolocation sounds and the spatiotemporal behavior of bats during flight.

Bats are assumed to adjust their call parameters by feedback control in response to the attended returning echoes. Therefore, it is particularly important to investigate the behavioral response (call parameters) of bats associated with their corresponding acoustic stimuli (echoes) under the spatiotemporal conditions in which the pulse-echo pairs were produced. Since P. abramus emit short downward FM pulses with a mean duration of approximately 1 ms, the echoes arriving from targets could be recorded by the microphone above the head without overlapping with the outgoing pulses. We analyzed the signal characteristics of pulse-echo pairs to which the flying bats actually listened, and investigated adjustments of call parameters in the context of echo-intensity compensation.

II. MATERIALS AND METHODS

A. Subjects

Three adult Japanese house bats (P. abramus) were used in this study. The animals were captured from a large colony roosting in bridge girders near the campus of Doshisha University, Japan. Pipistrellus abramus is a member of the Vespertilionidae and is commonly found in Japan. Although closely related pipistrelle bats such as P. pipistrellus and P. kuhli have been studied extensively (e.g., Schnitzler et al., 1987; Kalko, 1995; Waters and Jones, 1995; Holderied and Helversen, 2003), the echolocation characteristics of P. abramus are not well known. The body mass of P. abramus ranges from 5 to 8 g, and the wingspan measures approximately 10 cm. Echolocation pulses are emitted through the mouth. The bats were kept in a rearing cage of 0.9 m in length lighting with red filters (>650 nm) to avoid optical effects (Hope and Bhatnagar, 1979; Ghose and Moss, 2003). The chamber was made of steel plates to minimize interference from external electromagnetic waves. All internal walls were painted in black. The bats were released at one end of the flight chamber and allowed to fly freely to the opposite end where a landing mesh [1 m (W) × 0.7 m (H)] was attached to the wall 1.8 m above the floor. This wall is referred to as the target wall during the landing flight task. Flight behavior was recorded as a flying bat approached the target wall for landing. Recording was conducted for three flight sessions of each bat (a total of nine flight sessions).

B. General experimental procedure

All experiments were conducted in a flight chamber measuring 8 m (L) × 3 m (W) × 2 m (H) under long wavelength lighting with red filters (>650 nm) to avoid optical effects (Hope and Bhatnagar, 1979; Ghose and Moss, 2003). The chamber was made of steel plates to minimize interference from external electromagnetic waves. All internal walls were painted in black. The bats were released at one end of the flight chamber and allowed to fly freely to the opposite end where a landing mesh [1 m (W) × 0.7 m (H)] was attached to the wall 1.8 m above the floor. This wall is referred to as the target wall during the landing flight task. Flight behavior was recorded as a flying bat approached the target wall for landing. Recording was conducted for three flight sessions of each bat (a total of nine flight sessions).

C. Telemike system

Echolocation sounds were recorded by a custom-made telemetry microphone (Telemike) mounted on the back of the bat (Fig. 1). The Telemike consists of a 1/8-inch omnidirectional condenser microphone (Knowles, FG-3329, Illinois, USA), an FM transmitter unit, a hearing aid battery of 1.5 V (Sony, SR421SW, Tokyo, Japan), and a transmitting antenna. The Telemike was attached to the back of a bat with a piece of double-sided glue tape, with the microphone positioned approximately 1 cm above the mouth. Because the Telemike weighed less than 0.6 g, including the battery, it was light enough to be carried by bats weighing about 5 g. The bats did not exhibit any fatigue during the experiments. Removal of the Telemike from the back of a bat after each experiment was facilitated by use of a parting agent to avoid skin irritation.
The Telemike transmitted signals with a carrier frequency between 100–105 MHz to a wire antenna attached to the ceiling of the flight chamber. Received signals were demodulated using a custom-made FM receiver. The signals were then high-pass filtered at 20 kHz (NF Corporation, model 3625, Yokohama, Japan), digitized by a 16-bit, 384 kHz DAT recorder (SONY, SIR-1000W, Tokyo, Japan), and stored on a hard disk of a personal computer. Prior to recording, the output of the Telemike system was calibrated using a loudspeaker (Pioneer, PT-R7, Tokyo, Japan) and Brüel and Kajer 1/8-in. microphone. The total frequency response of the Telemike system was within ±4 dB flat between 20 and 100 kHz. Since echolocation sounds were recorded directly by the microphone above the head of the flying bat, acoustic parameters such as amplitude could be measured precisely without interference from traveling loss of sound in the air or directional properties of the emitted pulse.

D. Three-dimensional reconstruction of spatiotemporal echolocation behavior

The flight behavior was recorded using a dual digital high-speed video camera system (NIPPON ROPER Co., Ltd., CR Imager model 2000s, Chiba, Japan). Cameras were placed at a corner of the flight chamber and did not interfere with the bats’ flight path. The frame rate was 125 per second. Three-dimensional coordinates of the flying bats were reconstructed from these video images using a commercial motion analysis software (DITECT, Dipp-Motion 2D ver. 2.1). Prior to recording bat flights, a reference frame with known coordinates was positioned in the center of the flight chamber, then recorded by two video cameras. The analysis software calibrated the reconstruction system with the coordinate data of the reference frame. Based on a direct linear transformation technique, the position of the flying bat or other object was reconstructed from two-dimensional coordinate data in the video images. The signal triggering the video cameras was digitally stored using a DAT recorder so that flight coordinates could be synchronized with sound data. Using three-dimensional coordinate data, the flight trajectory of the bat and the distance from the target wall (target distance) or other objects could be determined. The echo delay \( t \) was calculated from the distance between the flying bat and an object \( d \) using the formula \( t = 2d/c \), where \( c \) is the sound velocity in the air.

E. Sound analysis

The acoustical characteristics of echolocation sounds were analyzed from the sonogram using a custom program of Matlab on a personal computer. Figure 2(A) shows sonograms of typical pulse-echo pairs recorded by the Telemike...
when the flying bat approached the target wall. Near the center of the chamber (4 m from the target wall), a number of echoes (referred to as an echo train) were usually observed with different echo delays (the time difference between each pulse-echo pair) and intensities following an emitted pulse. The second and higher harmonic components of the returning echo were most often attenuated beyond 3–4 m from the target wall. On the other hand, when the bat was within a target distance of 1 and 2 m, the number of echoes reaching the flying bat decreased. The echoes were clearly separated from each other, and the second harmonic component appeared in the sonogram. In this study, only the fundamental component of the pulse-echo pair was analyzed. Each pulse or echo was extracted from the sonogram, and the echo delay was measured for all echoes observed by the Telemike. The sound pressure level of the pulse was calculated from the peak-to-peak amplitude voltage of the observed pulse in the time domain. Simultaneously, the sonogram exhibited a peak in energy at around 50–60 kHz in each sound of P. abramus during flight. Therefore, the spectral energy at the peak energy portion of each pulse and echo was measured in the displayed sonogram using the custom program of Matlab so that changes in intensity of a weak echo could be quantitatively evaluated in relation to the pulse intensity. The maximum magnitude of the spectral energy in each sound is referred to as the sound intensity in this study.

Typical changes in the echo delay determined from sound data are shown in Fig. 2(B) as a function of target distance during landing as the bat approached the target wall. The size of the solid circles indicates the relative variation in echo intensity where bigger circles designate sounds of greater intensity relative to smaller circles. In this flight experiment, the Telemike allowed us to observe echoes with an echo delay in the range of approximately 0.5–30 ms, corresponding to targets 0.1–5 m away from the bat. The three lines shown in Fig. 2(B) represent echo delays between the flying bat and three different objects—the target wall, floor, and ceiling of the chamber—calculated from the three-dimensional coordinate data of the flying bat. By comparing the echo delays shown in sound data (solid circles), the echoes from each surrounding wall of the flight chamber could be identified in the observed sonogram. For example, the arrows in Fig. 2(A) indicate echoes from the target wall. Echoes from the floor and ceiling of the chamber consistently showed intense sound pressure, as well as echoes from the target wall directly in the flight path of the bat.

Prior to flight recording, pulses of the bat in a stationary position were recorded using the Telemike for quantitative analysis. The acoustical parameters of the echolocation pulses were analyzed using the custom program of Matlab described above. Signal bandwidth and duration were determined from the sonogram at −25 dB relative to the peak intensity of the pulse.

## III. RESULTS

### A. General echolocation behavior of P. abramus

Pipistrellus abramus emits a short downward FM pulse with maximum energy at the fundamental component. The mean duration at rest is 1.22±0.34 ms (n=300), and the fundamental frequency was modulated from approximately 83 to 44 kHz by the three bats (Table I). The sound pressure level (SPL) of an emitted pulse at rest ranged from approximately 100 to 120 dB peak-to-peak (re 20 μPa), with an average of 111 dB at the microphone above the bat’s head. The sonogram exhibited a peak in energy at 56.0±8.12 kHz, which was 11–14 kHz higher than the terminal frequency.

For the landing experiment, a total of nine flight sessions were recorded for three bats. In flight, the pulse duration was elongated to 3–4 ms, and then decreased to 0.5 ms before landing the target wall. Figure 3 shows the envelope and frequency structure of a typical echolocation pulse emitted by a P. abramus in flight, recorded by the Telemike at a target distance of 3 m. The frequency of the fundamental component was modulated exponentially from 100 to 40 kHz, and the bandwidth of the emitted pulse was extended when in flight. A prominent CF-like portion (a shallow sweep portion at the end of the pulse; see Fig. 3) was

![FIG. 3. Typical echolocation pulse emitted by P. abramus during the landing flight, recorded by the Telemike. Data were taken from sound recorded at a distance of 3 m from the target wall. Echolocation pulses usually contained several harmonics, with the first being dominant.](image-url)
observed beyond a target distance of approximately 2 m.

Flight trajectories for the three bats during landing approaches are illustrated in three-dimensional images in Fig. 4. The echolocation pulses recorded with the Telemike are superimposed on the flight trajectory to indicate the spatiotemporal characteristics of echolocation behavior. The maximum flight speed for a direct approach to the target wall was approximately 4 m/s at 3–4 m from the target wall. Several common features were observed in the behavior of the three bats, including a marked decrease in interpulse interval and pulse amplitude as bats approached the target wall (approach phase), which usually started at a target distance of between 1 and 2 m. The pulse emission rate increased from 10–20 pulses per second at 3–4 m from the target wall to 130–140 pulses per second immediately prior to landing. The SPL of each pulse was calculated from the peak-to-peak amplitude voltage of the observed pulse in the time domain by the Telemike. The maximum SPL (peak-to-peak) at the microphone above the bat’s head was approximately 130 dB during flight, which was almost 20 dB higher than when the bat was at rest. Before the bats started the approach phase, the sound pressure level of emitted pulse was almost constant at 130 dB peak-to-peak (search phase).

B. Changes in sound intensity of the pulse-echo pair

Figure 5(A) shows changes in intensity in the peak energy portions of the pulse and echo as a function of target distance for the three bats, normalized to the average of the pulse intensity during the search phase. Data were taken from three flight sessions of each bat. Intensities of all echoes that could be extracted from the displayed sonograms are cumulatively plotted with open circles in Fig. 5(A).

The pulse intensity in bats intending to land started to decrease at a distance of between 1 and 2 m, and the reduction was approximately 30 dB before landing. On the other hand, the observed echo intensities were mainly between 40 to 50 dB weaker than the pulse but remained almost constant as the target distance decreased (open circles in Fig. 5(A)). The three bats decreased the intensity of their emitted pulses logarithmically with target distance [Fig. 5(B)]. The reduction rate within 2 m of the target distance was 5.6–7.5 dB per halving of the target distance for the three bats. On average, the reduction rate of pulse intensity was 6.5 dB (21.6 dB decrease per decade of the target distance).

Figure 5(C) shows the distribution of all observed echo intensities relative to the average of the pulse intensity during the search phase for nine total flight sessions of three bats. The distribution showed a single peak, with a mean of $-42.6 \pm 5.5$ dB, which corresponds to approximately 80–90 dB SPL (peak-to-peak). Variation in observed echo intensity may have been due to variation in the distance or direction of the object from which the echo returned, and/or the direction of the emitted pulse.

The change in intensity of a pulse-echo pair for one flight session by a bat is shown in Fig. 6. The intensity of the echo returning from the target wall to the bat (asterisks in
IV. DISCUSSION

A. Echo-intensity compensation during flight

Bats are thought to adjust their pulse intensity in response to the intensity of the returning echoes that they attend to during echolocation. In this experiment, bats were expected to attend to the echo from the target wall. The echo intensity from the target wall (asterisks in Fig. 6) recorded directly by the Telemike was maintained at a constant level within a target distance of 2 m, whereas the pulse intensity considerably decreased. This indicates that the bat adjusted its pulse intensity depending on target distance such that the intensity of the echo returning from its destination was constant. In other words, this finding suggests that the echo from the target (destination) could be a prominent stimulus to adjustment of pulse intensity by bats and that a bat could rec-
ognize an echo from its target (the target wall) among a number of echoes reaching it [e.g., Fig. 2(A)].

A number of studies have attempted to measure pulse intensity for bats during flight (e.g., Griffin, 1958; Jen and Kamada, 1982; Vogler and Neuwieder, 1983; Kick and Simmons, 1984; Hartley et al., 1989; Waters and Jones, 1995; Tian and Schnitzler, 1997; Boonman and Jones, 2002; Hold­eried and Helversen, 2003). These studies reported a decrease in pulse intensity as a bat approached its target, using traditional fixed microphones that did not interfere with the flight path of the bat. In several studies, the reduction rate of pulse intensity as a function of distance to the target has been quantitatively estimated (e.g., Hartley et al., 1989; Waters and Jones, 1995; Tian and Schnitzler, 1997; Boonman and Jones, 2002). For example, Tian and Schnitzler (1997) estimated the intensity of emitted pulses in Rhinolophus ferrumequinum during a landing approach, applying careful corrections to directional sounds recorded by the fixed microphone. Similarly, Noctilio leporinus decreased its pulse intensity while capturing a small target (mealworm) at a rate of about 6 dB on halving the target distance (Hartley, 1989). Although the reduction of emitted pulses by flying bats approaching a target varied slightly among the studies (e.g., Hartley et al., 1989; Waters and Jones, 1995; Boonman and Jones, 2002), these studies suggest that the bats are supposed to adjust their pulse intensity in response to the intensity of returning echoes.

We found that P. abramus decreased their pulse intensity at a rate of 6.5 dB on halving the target distance and exhibited nearly constant echo intensity from the target wall, which should be attended to by a bat on its landing flight. This finding provides direct evidence of echo-intensity compensation by echolocating bats during flight to maintain the intensity of the resulting echo within the range necessary for optimal signal processing. The leaf-nosed bat Hipposideros terasensis, which emits a CF-FM pulse, decreased its pulse intensity by approximately 6 dB on halving the target distance using the same landing flight task as used here (Hiryu, 2005). Recently, echo-intensity compensation was demonstrated for the echolocation system in dolphins (Au and Benoit-Bird, 2003). Free-ranging dolphins decreased the amplitude of their echolocation signals as they approached the target by 6 dB per halving of distance. These results suggest that adjusting pulse intensity may be a common strategy of biosonar animals approaching a target.

The systems employed to compensate for variation in intensity and frequency of echoes are unique to biosonar animals. Extant artificial sonar systems are generally designed to emit a pulse with a fixed frequency to measure the Doppler shift in the returning echo in order to detect the velocity of the target. In contrast, CF-FM bats adjust their call frequency to maintain an echo frequency within the range they can hear best (Schnitzler, 1968; Suga, 1984). Consequently, the auditory system in the mustached bats can detect a shift in echo frequency with a high degree of accuracy, as small as 50 Hz which corresponds to less than 0.1% of the CF2 frequency of the pulse emitted by the mustached bats (~61 kHz) (Suga, 1984; Riquimaroux et al., 1991). Echo-intensity compensation allows bats to receive echoes within a certain optimal intensity range, which may facilitate consistent and precise analysis of target information by the auditory system as seen in DSC (Kick and Simmons, 1984).

These compensation behaviors associated with adjustments of pulse frequency and intensity may be a fundamental strategy employed by the animals for streamlining their echolocations, and will contribute to inspire the design of future artificial sonar systems or echo-sensing devices.

B. Multiple echoes reaching a bat during flight

We observed that a number of echoes from surrounding targets reached the flying bats with different echo delays and different intensities after a pulse emission (Fig. 2). When a bat was flying, the frequency of echoes received was Doppler-shifted depending on flight speed. A frequency sweep was observed with a slight difference among echoes from different targets [Fig. 2(A)], which may be due to differences in the extent of the Doppler shift according to the direction or relative velocity of the targets in relation to the flight path of the bat. We suggest that the difference in the frequency slope between returning echoes may provide FM bats in flight with direction and velocity information on multiple targets.

What specific behavioral strategies do echolocating bats use for processing multiple echoes? Bats are supposed to adjust their call parameters by feedback control in response to information from previous echoes. Analysis of the emitted pulse frequency and interpulse interval shows that bats may change the focus of their attention between echoes during flight (Hiryu et al., 2005). By periodically focusing on different echoes, bats may process multiple auditory streams to perceive several targets in real time. In this flight experiment, the bats occasionally approached the wall attached with a landing mesh (referred to as the target wall in case of the landing scenario) and then returned to the starting point without landing. Interestingly, the bats during the U-turn did not decrease the intensity of emitted pulses as approached that wall, as seen when they were landing (Fig. 7). In addition, the observed intensity of echoes from that wall did not appear constant, showing a decrease of approximately 20 dB within a distance of 1 m before U-turn point [marked with U in Fig. 7(B)]. This suggests that the bats making a U-turn did not keep their attention on that wall as seen in case of landing scenario. It is likely that a bat may divert its attention to other targets depending on its flight direction in order to avoid colliding with surrounding walls while making a U-turn.

In this study, we focused on temporal changes in the sound intensity of pulse-echo pairs in the context of echo-intensity compensation. Further investigation of pulse-echo pairs to which a bat actually listens may lead to other adjustment mechanisms in echolocation systems for multiple targets in the immediate surroundings.

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FIG. 7. Three-dimensional spatiotemporal reconstruction for a U-turn flight (A), and sound intensity of the pulse (solid circles) and echo (open circles) as a function of the distance to the wall with a landing mesh (referred to as “target wall” in case of the landing flight) while a bat making U-turn (B). Asterisk indicates the echo from that wall. The bat made a U-turn at a distance of 0.2 m (marked U) from that wall. The bat during the U-turn did not decrease the intensity of emitted pulses as approached that wall, as seen when they were landing.

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Griffin, D. R. (1958). Listening in the Dark (Yale University, New Haven, CT).


Suga, N. (1984). “The extent to which biosonar information is represented in the bat auditory cortex,” in Dynamic aspects of neocortical function,


