Doppler-shift compensation in the Taiwanese leaf-nosed bat (*Hipposideros terasensis*) recorded with a telemetry microphone system during flight

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Biosonar behavior was examined in Taiwanese leaf-nosed bats (*Hipposideros terasensis*; CF-FM bats) during flight. Echolocation sounds were recorded using a telemetry microphone mounted on the bat's head. Flight speed and three-dimensional trajectory of the bat were reconstructed from images taken with a dual high-speed video camera system. Bats were observed to change the intensity and emission rate of pulses depending on the distance from the landing site. Frequencies of the dominant second harmonic constant frequency component (CF_2) of calls estimated from the bats' flight speed agreed strongly with observed values. Taiwanese leaf-nosed bats changed CF_2 frequencies depending on flight speed, which caused the CF_2 frequencies of the Doppler-shifted echoes to remain constant. Pulse frequencies were also estimated using echoes returning directly ahead of the bat and from its sides for two different flight conditions: landing and U-turn. Bats in flight may periodically alter their attended angles from the front to the side when emitting echolocation pulses. © *2005 Acoustical Society of America.* [DOI: 10.1121/1.2130940]

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I. INTRODUCTION

Echolocating bats have a highly developed biosonar system. By comparing emitted pulses with returning echoes, bats are capable of instantaneously recognizing the physical attributes of their environment. This enables them to catch insects or to avoid obstacles. Bats have evolved efficient echolocation techniques and are capable of adjusting the acoustical parameters of their calls to different echolocation requirements such as different target-background relationships (Novick and Vaisnys, 1964; Henson *et al.*, 1987; Lancaster *et al.*, 1992; Tian and Schnitzler, 1997; Moss and Surlykke, 2001; Ghose and Moss, 2003). Only the more recent studies have begun to quantify the acoustic parameters of bat calls and the corresponding echo signals while relating them to the spatio-temporal conditions under which the call-echo pairs were produced. Understanding these different echolocation strategies and their acoustical basis is particularly important for bat biosonar systems to serve as model systems for technological applications.

Hipposiderid (*Rhinolophus* spp.) and mustache bats (*Pteronotus parnellii*) produce echolocation calls in a very narrow frequency band (constant-frequency component, CF). During flight, the frequency of the CF component shifts due to Doppler effects. Horseshoe and mustache bats compensate for these Doppler shifts by adjusting their call frequency accordingly, thus maintaining the echo frequency within the narrow frequency range that the bats can hear best (Doppler-shift compensation, DSC) (Schnitzler, 1968; Schuller *et al.*, 1974; Simmons, 1974; Trappe and Schnitzler, 1982; Henson *et al.*, 1987; Gaioni *et al.*, 1990; Lancaster *et al.*, 1992; Keating *et al.*, 1994). In Hipposiderids, Gustafson and Schnitzler (1979) have first demonstrated that the bats in flight compensated for Doppler shifts caused by their own flight movement.

We examined changes in the dominant second harmonic CF component (CF_2) of echolocation calls emitted by Taiwanese leaf-nosed bats (*Hipposideros terasensis*) during different flight maneuvers in the laboratory (Riquimaroux and Watanabe, 2002). The echolocation sounds were recorded using a telemetry microphone (Telemike) mounted on the bat's head using previously reported radio telemetry techniques (Henson *et al.*, 1987; Lancaster *et al.*, 1992). Analysis of call frequency in response to the echo information the bat did hear enabled us to determine which target the bat paid attention to (e.g., target wall versus side walls). We estimated the position of the target listened to by the bat during flight

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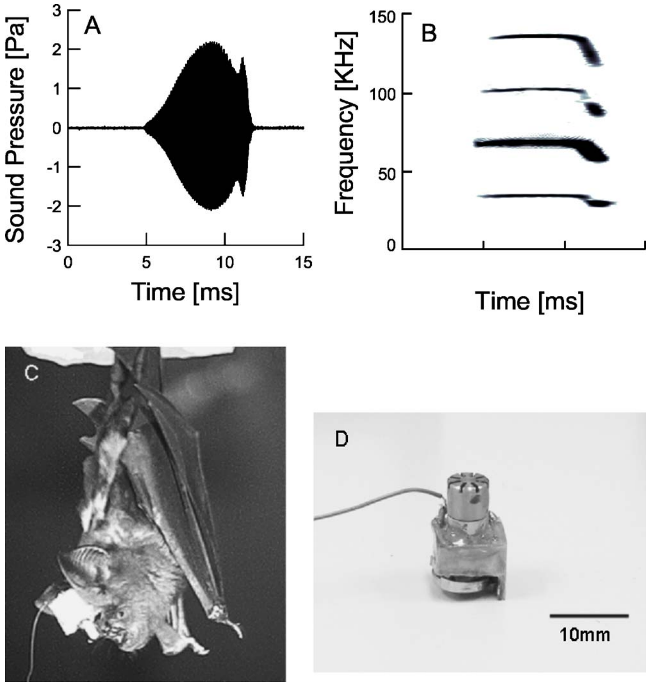

FIG. 1. Typical echolocation pulse in the Taiwanese leaf-nosed bat (*Hipposideros terasensis*) recorded from a Telemike mounted on the bat's head: (a) envelope and (b) sonagram. Calls usually contained four harmonics, with the second being dominant. Each call consisted of a long constant-frequency (CF) component followed by a short downward frequency-modulated (FM) component. Photographs of the Telemike: (c) stationary *Hipposideros terasensis* with the Telemike mounted on its head and (d) frontal view of the Telemike. Telemike consisted of a $\frac{1}{4}$-in. condenser microphone, transmitter, battery, and transmitting wire antenna.

by evaluating call parameters such as their CF_2 frequency and the interemission interval (IEI). By comparing these data with the three-dimensional coordinates of the flight path, we also checked whether bats altered the direction of attention during direct approaches to the target wall. The attended angle was the angle of this direction of attention relative to the flight path. This parameter provided important insights into the bat biosonar behavior, especially the direction towards which the bat directed its sonar beam. This then allowed us to study how the bat scanned the spatial characteristics of surrounding multiple targets while approaching its destination.

II. MATERIALS AND METHODS

A. Subjects

Three adult Taiwanese leaf-nosed bats (*Hipposideros terasensis*) were used in this study. The animals were captured in Taiwan and housed in a temperature- and humidity-controlled facility at Doshisha University, Japan. Body mass of the bats ranged from 50 to 60 g. Figure 1 shows the envelope (a) and sonagram (b) of a typical echolocation call. Taiwanese leaf-nosed bats use a compound signal consisting of an approximately 5-ms CF component followed by a short, 1-ms, downward frequency-modulated (FM) component. The frequency of the dominant second harmonic CF component of calls emitted at rest (resting frequency) is about 70 kHz. This frequency is emitted when the bat is not flying and experiencing flight-induced Doppler shifts.

B. Recording procedures

The experiments were conducted in a flight chamber 8 m(L) × 3 m(W) × 2 m(H). The chamber was made of steel plates painted black to avoid optical effects and minimize interference from external electromagnetic waves. The bats were released at one end of the chamber and allowed to fly freely to the opposite end of the flight chamber 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. Flight behaviors were recorded as the flying bat approached the target wall and either landed on the net or returned to the starting point without landing. Echolocation sounds were recorded by a custom-made telemetry microphone (Telemike; Dia-medical, Tokyo, Japan) mounted on the head of the bat [Figs. 1(c) and 1(d)]. The Telemike was a $\frac{1}{4}$-in. electrets condenser microphone (RION, SCM-204E, Tokyo, Japan), a small custom-designed FM transmitter unit, a battery, and a transmitting antenna. The plastic surface of the FM transmitter unit was glued to the scalp of the bat. Since the Telemike weighed less than 3 g, it was light enough to be carried by the animals, and the bats did not exhibit any fatigue during the experiments. Experiment sessions were less than an hour. The Telemike was easily removed from the bat's head after each experiment using a parting agent without irritating the scalp. The Telemike transmitted signals with a carrier frequency between 90 and 100 MHz to a wire antenna attached to the ceiling of the flight chamber. Received signals were demodulated using a custom-made FM receiver, high-pass filtered (NF Corporation, model 3625, Yokohama, Japan), and then digitally recorded on a 16-bit, 384-kHz DAT recorder (SONY, SIR-1000W, Tokyo, Japan). The acoustical parameters of the echolocation pulses, such as frequency and interemission interval (IEI), were analyzed from the sonagram using a custom program of Matlab on a personal computer. Each pulse was extracted on the displayed sonagram, and then a fast Fourier transform (FFT) was performed over 4096 points from the onset of the pulse so that the frequency of the CF_2 component was determined with the resolution of ±46.9 Hz. Prior to the recording session, CF_2 frequency for each bat at rest was measured with the Telemike mounted on the bat's head for at least 20 s. A mean of the 30 pulses that were randomly selected was determined as the resting frequency. The resting frequency showed no particular change over the observation during the experiment limited less than several flights for each bat per day. In this study, IEI was defined as the time from the beginning of one call to the beginning of the subsequent call. Since echolocation sounds were recorded directly by the microphone on the head of the flying bat, the acoustic parameters could be precisely measured without interference from the movement of the bat's head or Doppler-induced errors.

Flight behaviors of the bats were recorded using a dual digital high-speed video camera system (NIPPON ROPER Co., Ltd., CR Imager model 2000s, Chiba, Japan). Cameras were positioned along the edge of the flight chamber and did not interfere with the bat flight path. Video cameras recorded at 125 frames per second. Three-dimensional coordinates of the flying bats were reconstructed from these video images using commercial motion analysis software (DITECT, Dipp-Motion 2D version 2.1). Prior to recording, a reference frame with known coordinates was positioned in the center of the flight chamber, and then filmed by two cameras. The analysis software calibrated the reconstruction system from the coordinate data of the reference frame. Based on direct linear transformation technique, the positions of the flying bat or other objects were reconstructed from 2-D coordinate data in the video images. The signal triggering the video cameras was digitally recorded using a DAT recorder so that flight coordinates could be synchronized with sound data. Using coordinate data, the flight trajectory, flight speed, and distance from the target wall (target distance) were calculated. The flight speed was determined along the flight path of the bat using three-dimensional coordinate data.

We confirmed that echo frequencies directly measured by the Telemike are usually about several tens of Hertz higher than the resting frequency. This suggests that the reference frequency of *H. terasensis* is estimated to be approximately several tens of Hertz higher than the resting frequency. For calculation presented here, we used the resting frequency instead of the reference frequency since the reference frequency of *H. terasensis* was not physiologically determined and, in addition, it was still difficult to observe echoes with enough amplitude by Telemike.

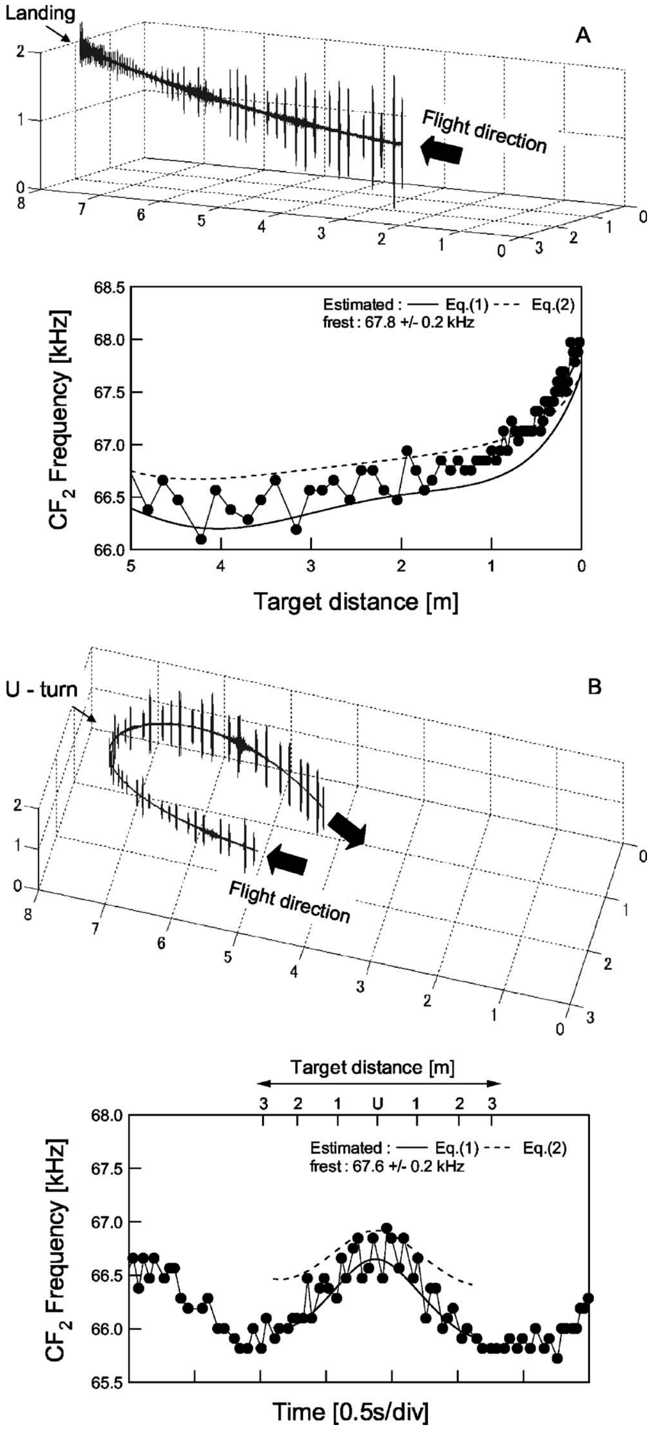

FIG. 2. Three-dimensional spatio-temporal reconstruction and changes in the call frequencies of *Hipposideros terasensis* echolocation behavior for two different flight scenarios: (a) landing and (b) U-turn. Upper graphs: Coordinate grids (1 m^2) show the dimensions of the flight chamber ($8\times3\times2$ m^3). Echolocation pulses recorded by a Telemike are placed alongside the flight trajectory. Lower graphs: Solid circles indicate call frequencies. Solid and dashed lines indicate estimated call frequencies calculated with Eqs. (1) and (2) (described in text), respectively.

III. RESULTS

A. Echolocation pulses of bats during flight

The echolocation behavior of bats was examined for two different flight tasks. The first was a direct approach to the target wall followed by landing on the mesh of the target wall. The second scenario consisted of an initial approach of the target wall followed by a U-turn. Figure 2 shows representative echolocation pulses recorded with the Telemike and the flight trajectory in two scenarios for indicating spatio-temporal aspects of the echolocation behavior. When the bats flew in the middle of the flight chamber in the landing scenario, the maximum call intensity was as much as 120 dB SPL peak-to-peak. The bats started to gradually decrease pulse intensity at 3–4 m from the target wall. At the same time, the pulse emission rate increased from 20–30 pulses/s to 70–80 pulses/s. This suggested that the emission pattern for *H. terasensis* intending to land showed three flight phases, search, approach and terminal, as in other Hipposiderids (Gustafson and Schnitzler, 1979). After landing, the bats suddenly increased call intensity and decreased pulse emission rate as they appeared to familiarize themselves with their immediate surroundings.

In the U-turn scenario, pulse emission rate remained almost constant at 20–30 pulses/s. The animals seemed to fly using only the surveillance phase to assess their surroundings while making U-turns. The differences in pulse trains observed during these two different flight scenarios indicated that the bats used different echolocation strategies for different echolocation tasks as reported in earlier publications.

B. Doppler-shift compensation

When analyzing the CF_2 frequency of the calls, we found that in the landing scenario, *H. terasensis* systematically changed call frequencies as a function of distance to the target wall [solid circles in Fig. 2(a)]. In the center of the flight chamber, where the target distance was about 4 m, the CF_2 frequencies of the bat calls were almost 2 kHz below resting frequency. Such frequency changes were likely due to Doppler-shift compensation and dependent on flight speed. Therefore, we determined the relationship between amount of call frequency changes and flight speed using the 3D coordinate data taken from the high-speed video cameras. Equation (1) was used to estimate the compensated frequencies of the pulse CF_2.

$$f_{\text{pulse}} = \frac{c - V}{c + V} f_{\text{rest}} \tag{1}$$

where V is bat flight speed, c is sound velocity in air (344 m/s), and f_{rest} is resting frequency. The f_{pulse} indicates the compensated frequency of the call CF_2. This keeps the frequency of the returning echo constant at resting frequency. The reference frequency is thought of as slightly above resting frequency (Schuller *et al.*, 1974; Henson, *et al.*, 1982; Riquimaroux *et al.*, 1992; Keating *et al.*, 1994). However, we used values for the resting frequency instead of the reference frequency for calculations presented here because the reference frequency of *H. terasensis* was not determined. The compensated pulse frequency estimated by Eq. (1) is indicated by the solid line in Fig. 2(a). We found that frequency of call CF_2 agreed well with the estimated values. This strongly suggested that the bats did indeed perform DSC in the landing scenario. When we estimated the call frequencies in the U-turn scenario with Eq. (1), we found that they agreed well with the call frequencies measured by the Telemike [Fig. 2(b)]. These results are similar to these from other CF-FM bats such as *Asellia tridens* (Gustafson and Schnitzler, 1979), *Pteronotus parnellii* (Gaioni *et al.*, 1990; Lancaster *et al.*, 1992), and *Rhinolophus ferrumequinum* (Schnitzler, 1968; Simmons, 1974; Schuller *et al.*, 1974). *Hipposideros terasensis* compensated for flight-induced frequency shifts in the returning echo signal by exhibiting DSC behavior.

C. Changes in call frequency and interemission interval (IEI)

A closer examination of the call frequencies emitted in both scenarios (Fig. 2) revealed that the bats, in addition to performing DSC, typically switched between slightly higher and lower call frequencies. Although the difference was small and measured only a few hundred Hz, this pattern of frequency alterations prompted us to examine temporal call parameters in more detail. Figure 3 depicts the typical relationship between the call frequency and interemission intervals (IEI) for the three bats in the landing scenario. We found that the alternating pattern seen in the call frequencies was also reflected in IEIs. *Hipposideros terasensis* calls clearly switched between long and short IEIs. Lower call frequencies [see arrows in Fig. 3(a)] were usually emitted after longer IEIs [asterisks in Fig. 3(a)]. These vocalization patterns were most often observed in the search and approach phases in the landing scenario.

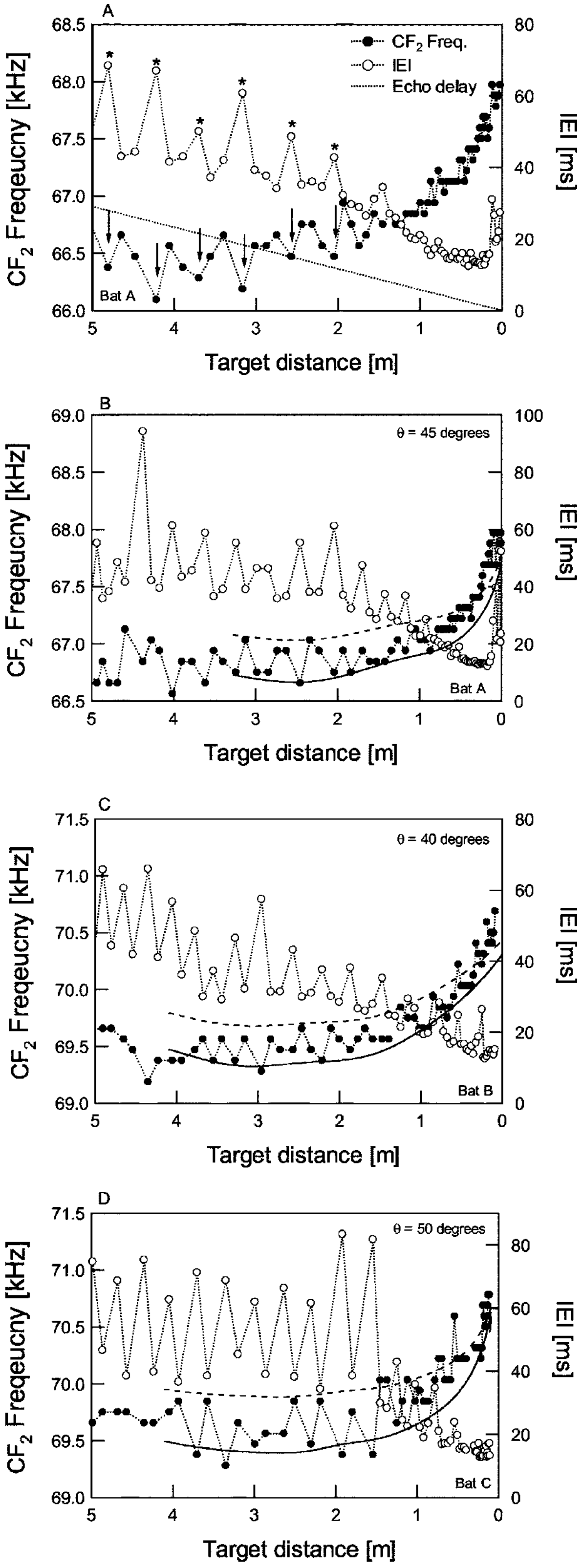

FIG. 3. Relationship between interemission intervals and call frequencies as a function of target distance for calls emitted by landing for three bats. Interemission interval is the time interval between the beginning of the pulse preceding the interval and the beginning of the current pulse. The dashed line in (a) indicates the echo delay from the target wall. Lower call frequencies (arrows) were usually emitted after long interemission interval (asterisks). Solid and dashed lines in (b)–(d) indicate estimated call frequencies calculated with Eqs. (1) and (2) (described in text), respectively. θ is estimated attended angle. (a) and (b) indicate the results of one individual for different flight sessions.

IV. DISCUSSIONS

A. Estimation of the attended angle from the call frequency

When comparing call frequencies estimated from Eq. (1) with those the bats actually emitted (Fig. 2), it becomes apparent that the call frequencies were somewhat underestimated; many calls were produced at frequencies above the estimated values. The values differed by as much as 500 Hz with a certain periodicity. The difference was three times larger than the standard deviation of the resting frequency. It also changed with the target distance, being greater for longer distances. In the U-turn scenario [Fig. 2(b)], the difference between estimated and measured call frequencies appeared to increase as the bats made the U-turn. Because these differences were larger than the standard deviations of the measured frequencies, the variations may have been intentional.

The frequencies estimated by Eq. (1) were assumed to be echoes from a target directly ahead of the bat. The bats flying in our flight chamber, however, were also likely to receive echoes from surrounding walls. If a bat emitted its call frequency based upon the echo reflected from an angle other than straight ahead, the different frequency of this echo might explain the periodic alterations observed in the call frequencies. This assumes that the bats switched their attention between the target wall and sidewalls. As a result, the angles at which the side wall echoes reached the bats' ears (attended angle) changed between call emissions. This would affect the amount of Doppler shift in the attended echo. Bats always adjusted their call frequency's response to previously heard echoes. Here we defined the angle between the direction of the attended echo and bat flight direction as attended angle. This angle can be estimated using the deviation observed in the call frequency. This deviation carried information about the direction of the previously attended echo. Equation (2) is based on Eq. (1) and includes the attended angle. The call frequency for a bat compensating for a Doppler-shifted sideways echo returning at an attended angle θ is

$$f_{\mathrm{pulse}} = \frac{c - V\cos\theta}{c + V\cos\theta} f_{\mathrm{rest}}. \tag{2}$$

The maximum attended angle is the angle where the upper values of the observed pulse frequency correspond to f_{pulse} estimated by Eq. (2). We used several values for the attended angles to estimate the maximum of the attended angle for the scenarios shown in Fig. 2. We found that f_{pulse} for an attended angle of 45° best fit the upper values of actually measured call frequencies for both landing and U-turn scenarios of this bat. Because the lower values of the measured call frequencies best matched the estimated call frequencies emitted in response to echoes returning at 0° [equivalent to Eq. (1)], we concluded that this bat switched between an attended angle of 0° and one of 45° based on periodic variations in call frequencies. Maximum attended angle for the three bats ranged from 40° to 50° (Fig. 3).

The alterations in attended angles were particularly obvious in the U-turn scenario [Fig. 2(b)]. The periodic frequency changes began at a target distance of about 2 m. This corresponded to where the U-turn began. The frequency changes continued throughout flight, presumably to avoid colliding with surrounding walls. Our data suggest that bats in flight were capable of perceiving the spatio-temporal structure of their surroundings by periodically adjusting the attended angle. In this study, the adjustments were between forward and sideways directions. We suggest that degree and rate of alterations in call frequency reflected the complexity of the echolocation task. Estimates for attended angles from measured pulse trains could indicate the way bats scan their surroundings.

When compensating for the highest occurring Doppler shift from straight ahead of the bat, echo frequencies from the side wall may occasionally fall into the tuning region below the resting frequency. This suggests that the bat may compensate for the negative frequency shift. Although further discussion should take into account the auditory abilities of this bat's species, DSC for negative shift has been demonstrated in other species (Metzner *et al.*, 2002). In addition, if a small negative shift never leads to compensation, echo frequencies even from slightly to the side will be out of the best auditory tuning of the bat during flight. We suppose that DSC for a small negative shift may be considered for a flying bat.

B. Relation between alterations in call frequency and IEI

How do alterations in call frequency, which presumably reflect changes in the attended angle, relate to the alterations in IEIs (see Fig. 3)? Figure 4 (left) schematically illustrates the conditions under which echo signals return to the bat at attended angles of 0° (E_{front} from the target wall) and 45° (E_{side} from the side walls). The echoes from the side walls, which we found to elicit higher call frequencies (Fig. 2), had shorter travel distances than the echoes returning from the target wall, which elicited lower call frequencies. This was especially clear during the early phases of DSC when the bat was still far from the target wall. Long travel distances of attended echoes would require the bat to wait longer before emitting the next call to avoid call-echo mismatches. Conversely, the bat called earlier if the echo returned sooner to maximize information gathered by call-echo pairs. Because bats always adjust call frequencies in response to echoes that corresponds to the previously emitted calls, lower calls frequencies are produced after longer IEIs (in response to E_{front}) and higher call frequencies after shorter IEIs (in response to E_{side}). This would explain the alterations of IEIs and call frequencies depicted in Fig. 3.

This interpretation of our results is schematically summarized in Fig. 4 (right). This figure shows how a bat would switch from short IEIs and less DSC [i.e., call frequencies higher than estimated by Eq. (1)] to longer IEIs and more DSC [corresponding to the frequencies estimated by Eq. (1)]. Based upon the spatial dimensions of our flight chamber, we suggest that the delays for E_{front} are longer than those for E_{side}, especially during early phases of DSC. Based on Eq. (2), the Doppler-shift experienced by the bat was larger for E_{front} than for E_{side}. Both echoes, E_{front} and E_{side}, were always

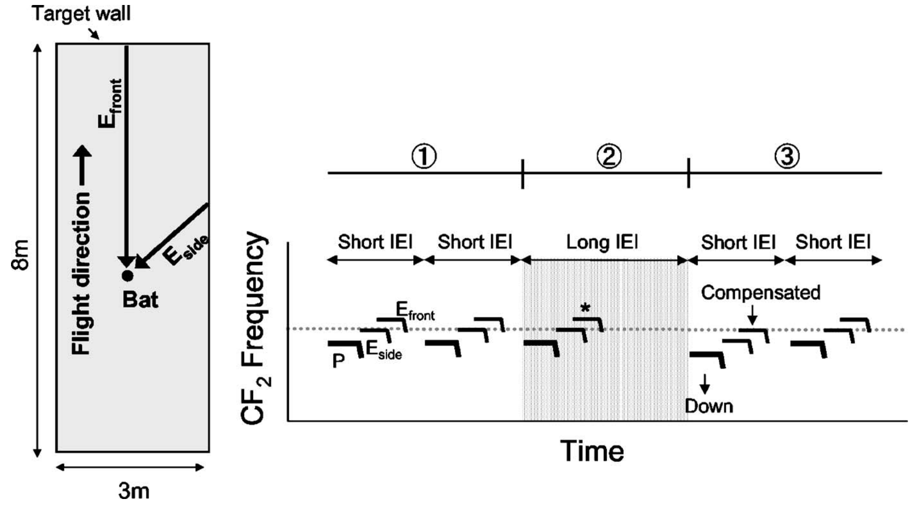

FIG. 4. Schematic diagram of *Hipposideros terasensis* calls and echoes. Left: The top view of the flight chamber indicating the directions and echoes from target wall (E_{front}) and side wall (E_{side}). The closed circle indicates the point at which the flying bat emitted the call producing the two echo signals shown here. Right: A sonagram of pulse-echo pairs for echoes returning from the front target and side walls. The dotted line indicates reference frequency. *P* indicates bat call and *E* indicates retuning echo. Numbered gray areas indicate the time period during which the bat shifts attention from side walls (1) to target wall (2) and back to side walls (3). The call marked "Down" is a low-frequency call emitted by the bat to ensure a return echo at reference frequency.

present. Since the bat switched its attention between the two echoes, it used different Doppler-shift information to adjust the frequency of the subsequent call. When the bat attended to echoes from the side walls (area "1" in Fig. 4), it lowered its call frequencies enough to make the E_{side} echo return at the reference frequency. The echo from the target wall had a longer delay and carried a larger Doppler shift. So, when the bat switched its attention to this echo (see E_{front} labeled by asterisk in gray area "2"), it emitted its next call after a longer IEI and a much lower frequency (see call marked "Down") to ensure the next echo returned at the reference frequency (see echo marked "Compensated"). This echolocation strategy might allow flying bats to perceive the spatial structure of their surroundings without constantly changing the direction of their flight path. In a detailed preliminary analysis of our video recordings, we found that *H. terasensis* exhibited intricate pinna movements closely timed to pulse emission. This phenomenon is common to hipposiderid and rhinolophoid bats. We did not, however, observe head turns. Pinna movements may be important for changing attended angle.

The long IEIs observed here and in other studies are thought to be related to bat respiratory rates and wing beat cycles (Suthers *et al.*, 1972; Schnitzler *et al.*, 1987; Lancaster *et al.*, 1992, 1995). For *H. terasensis*, our video analysis confirmed that wing beat cycle and changes in IEI are synchronized (unpublished observations). In the present study, therefore, we propose that bats may alternate between long and short IEIs when changing the attended angle from flight path target to targets on the side, synchronizing with wing beat cycles. This would be thought of as an effective maneuver for both flight and echolocation. Further investigation is be needed to confirm our hypothesis.

C. Call-echo overlap during DSC

In *Rhinolophus ferrumequinum*, the echo signal overlapped its outgoing pulse due to the long pulse duration (Tian and Schnitzler, 1997). Such call-echo overlap is considered a prerequisite for DSC (Schuller, 1974, 1977). When comparing IEI and echo travel time, however, we found that *H. terasensis* did not experience call-echo overlaps during flight because its call duration is so much shorter than in *Rhinolophus*. Nevertheless, *H. terasensis* compensated for flight-induced frequency shifts in the echo, suggesting that call-echo overlap was not a prerequisite to DSC. It also assumed a difference in signal processing mechanism for DSC between these two CF-FM bats. This difference probably depended on the acoustical characteristics of each species distinct calls.

In conclusion, the alterations in IEIs and amount of DSC observed in our flight scenarios suggested that the bats might use a series of short IEIs to investigate their immediate surroundings (presumably to avoid collisions with the side walls) and checked for distant targets ahead of the bat using longer IEIs. These alterations were caused by a change in the attended angle. By periodically focusing on different echoes (times sharing information), the bats were able to simultaneously perceive several targets. Such systematic variations in the attended angle may have important applications in the examination of other biosonar systems.

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