ULTRASONIC ECHOLOCATION BEHAVIOR OF A FLYING BAT MEASURED BY A TELEMETRY SYSTEM AND A HIGH-SPEED VIDEO SYSTEM

PACS: 43.64.Tk, 43.66.Gf, 43.80.Ka, 43.80.Lb

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ABSTRACT

The present study investigated consistency of the constant frequency (CF) portion of biosonar pulses emitted by CF-FM bats and relationship between the pulse emission and wing motion. Here, pulse CF2 frequency at rest, closely related to the reference frequency, was measured for several months. Besides, Doppler-shift compensation was investigated on different days by a telemetry-microphone (Telemike) on the head to examine daily consistency of the reference frequency during flight. Data indicated that neither the pulse CF2 frequency at rest or the reference frequency during flight was fixed. Video images revealed that pulses are emitted during upstrokes of wing motion.

INTRODUCTION

Ultrasonic echolocation pulses that a CF-FM bat emits consisted of a long CF (constant frequency) part preceded and followed by a short FM (frequency modulated) part. Each pulse and echo are harmonically structured where the second harmonic is usually the most intense (**Fig. 1**). The CF-FM bats listen to the echo CF2 frequency and adjust the pulse CF2 frequency so that the echo CF2 frequency falls in the sharply tuned its own frequency range, called Doppler-shift compensation [Gaioni et al., 1990; Henson et al., 1982; Riquimaroux et al., 2000]. The frequency to which the bat adjusts its echo CF2 frequency is called the reference frequency. Doppler-shift compensation has been studied by an artificial device, e. g., a pendulum. So, bats never flew by themselves. Ablation of a particular area in the auditory cortex disrupted the acuity of Doppler-shift compensation [Riquimaroux et al., 1991]. Analog telemetry system was introduced but not systematically with precise digital equipment [Henson et al., 1987; Lancaster et al., 1992] because high-speed digital sampling of ultrasound was quite difficult. We succeeded digital recording pulses and echoes of a flying bat by an on-board telemetry microphone (Telemike) system [Riquimaroux and Watanabe, 2000]. The first purpose of the study is to analyze consistency of CF2 frequency over months. The second purpose of the study is to measure Doppler-shift compensation with a microphone on the flying bat's head for the first time. Here, we check consistency of the reference frequency. Thirdly, we try to record flying motion of bats by high-speed digital video cameras to analyze relationships between their vocalization and flying behavior, including the wing motion. It has been believed that the reference frequency for Doppler-shift compensation is an ID for each individual. So, each bat has its own reference frequency, which should be slightly different from each other. The auditory system of each bat has an extremely sharp filter tuned to its own reference frequency. Therefore, if the filter is based on hardware, the reference frequency has to be fixed without shifting day by day for precise and stable signal processing. Our preliminary experiment revealed that the pulse CF2 frequency at rest shifted a few kHz for a long period of time [Yamazaki et al., 1999]. The reference frequency to which Doppler-shifted echo CF2 frequency should be adjusted might also shift in accordance with the pulse CF2 frequency at rest.

METHODS

Subjects

Adult Taiwanese leaf-nosed bats (*Hipposideros terasensis*) were used. They are one of CF-FM bats. The fundamental frequency of CF is about 35 kHz and the second harmonic, about 70 kHz, is the most intense (**Fig. 1**). The weight is about 65g, the length is about 15 cm and the wing span is about 50 cm.

Recording Chamber

All measurements were done in a steel-walled chamber (8 m long, 3 m wide and 2 m high). Inside the chamber was painted in black.

Measurement of Pulses at Rest

Pulses at rest were recorded every other day before feeding. During recordings no other bats or humans were in the chamber. The bat roosted on the ceiling in the middle of the chamber during the measurement. A 1/4-inch condenser microphone (B & K, Type 4135) was placed right below the bat. The signal from the microphone was amplified.B & K, Type 5935L., passed through a 20 kHz high-pass filter (NF-5935) and digitally recorded by a DAT (SONY SIR-1000W). The sampling frequency was 384 kHz while the resolution was 16 bit.

Measurement of Pulses and Echoes during Flight

For measurement of pulses and echoes, Telemike composed of a small radio-transmitter and a 1/4-inch titanium condenser microphone (Custom made) was mounted on the head. The weight was about 3 g. Another condenser microphone (B & K, Type 4135), which was used for the measurement of pulses at rest, was placed closed to the target wall. The signals from Telemike was sent to an FM receiver (DIA medical, DTT-1000) and digitally recorded by a 2 channel DAT (SONY SIR-1000W). The procedure used was the same as that used for the measurement of pulses at rest. Both pulses and echoes were analyzed fo-

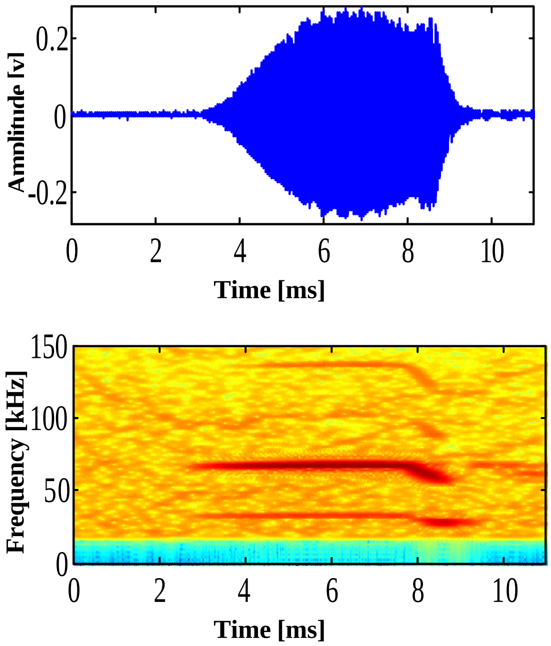

Fig. 1 Temporal structure of a biosonar pulse emitted by a leaf-nosed bat (*Hipposideros terasensis*). Top: Temporal amplitude envelope. Bottom: Temporal frequency change shown as a sound spectrogram.

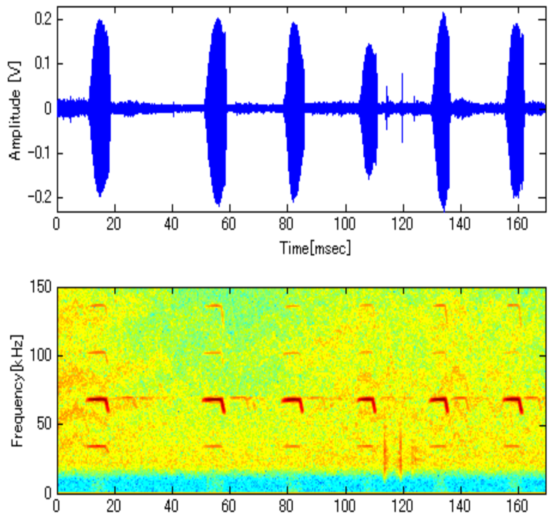

Fig. 2 Temporal structure of biosonar pulses and echoes of a flying leaf-nosed bat (*Hipposideros terasensis*) measured on the head by a telemetry microphone. Top: temporal amplitude envelope. Bottom: Temporal frequency change shown as a sound spectrogram.

cusing on CF2 frequencies (**Fig. 2**).

Recordings of Flying Motion

A pair of high-speed digital video cameras (Kodak, Model 2000) were used with 500 frames/sec to record flying motion of bats.

RESULTS

Pulse CF2 frequency at rest

A typical pulse emitted by a Taiwanese leaf-nosed bat when roosting is shown in **Fig. 1**. Previously found daily changes in pulse CF2 frequency at rest are illustrated in **Figs. 3** and **4**. **Fig. 3** represents data from Japanese leaf-nosed bat (Hipposideros turpis), which appears to be a close species of Taiwanese leaf-nosed bat, demonstrated CF2 frequency shift larger than 1 kHz [Okatake et al., 1999; Yamazaki et al., 1999]. Similarly, Taiwanese leaf-nosed bats revealed shifts in CF2 frequency as much as 1.6 kHz for one day (**Fig. 4**; Riquimaroux and Yamasumi, 2001). The present experiment proved that pulse CF2 frequency of the same bat may change more than 2 kHz (**Fig. 5**).

CF2 Frequency of Pulses and Echoes during Flight

Temporal structures of amplitude and frequency of pulses and echoes monitored at the head during flight are illustrated in Fig. 2. The harmonic structure can be confirmed where the second harmonic, 70 kHz component, is the strongest. Two representative examples recorded on different days are shown in **Fig. 6**. Both demonstrated that Doppler-shifted echo CF2 frequencies were stabilized at one frequency range, showing Doppler-shift compensation. The pulse CF2 frequency at rest for the left figure was about 70.3 kHz while it was about 70.8 kHz for the right figure (broken lines). The difference in pulse CF2 frequency was about 500 Hz. The pulse CF2 frequency during flight indicated the same tendency, the right figure showed higher than the left (triangles). The echo CF2 frequency at the head was about 60.7 kHz for the left and about 79.2 kHz for the right on average with 500 Hz difference.

Relationship between Pulse Emission and Wing Motion

Simultaneous recordings of bat's vocalization by microphone and wing motion by video camera with a common time marker could verified the temporal relationship between pulse emission and wing motion. A time pattern of pulse emission is illustrated in **Fig. 7**. The bat vocalized during upstroke of the wing motion, corresponding to exhale phase. We could find a train of 3 to 5 pulses for one upstroke motion with a short inhaling interval during downstroke motion when the bat U-turned at the wall (**Fig. 8a**). However, the bat appeared to vocalize without breathing when landed at the wall (**Fig. 8b**).

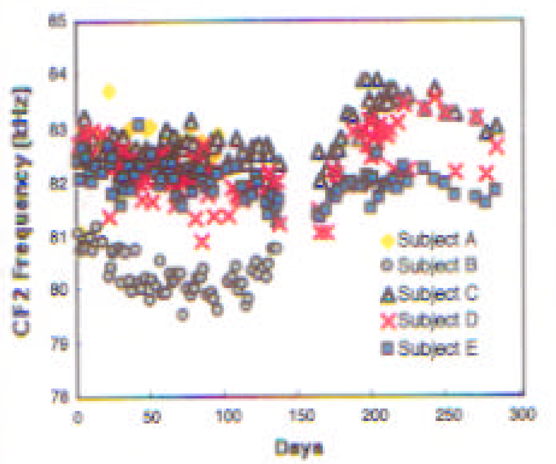

Fig. 3 Daily changes in pulse CF2 frequencies when bats are roosting. Data were taken from Japanese leaf-nosed bats (*Hipposideros turpis*).

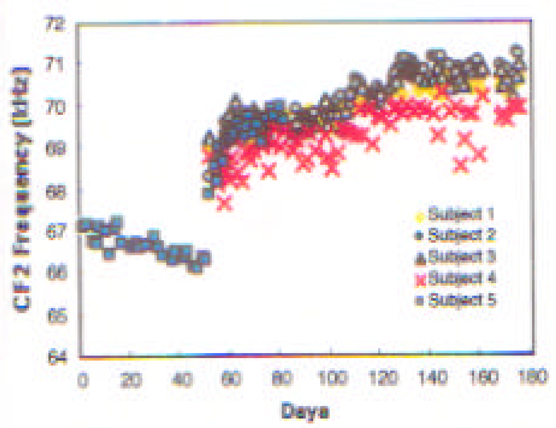

Fig. 4 Daily changes in pulse CF2 frequencies when bats are roosting. Data were taken from Taiwanese leaf-nosed bats (*Hipposideros terasensis*).

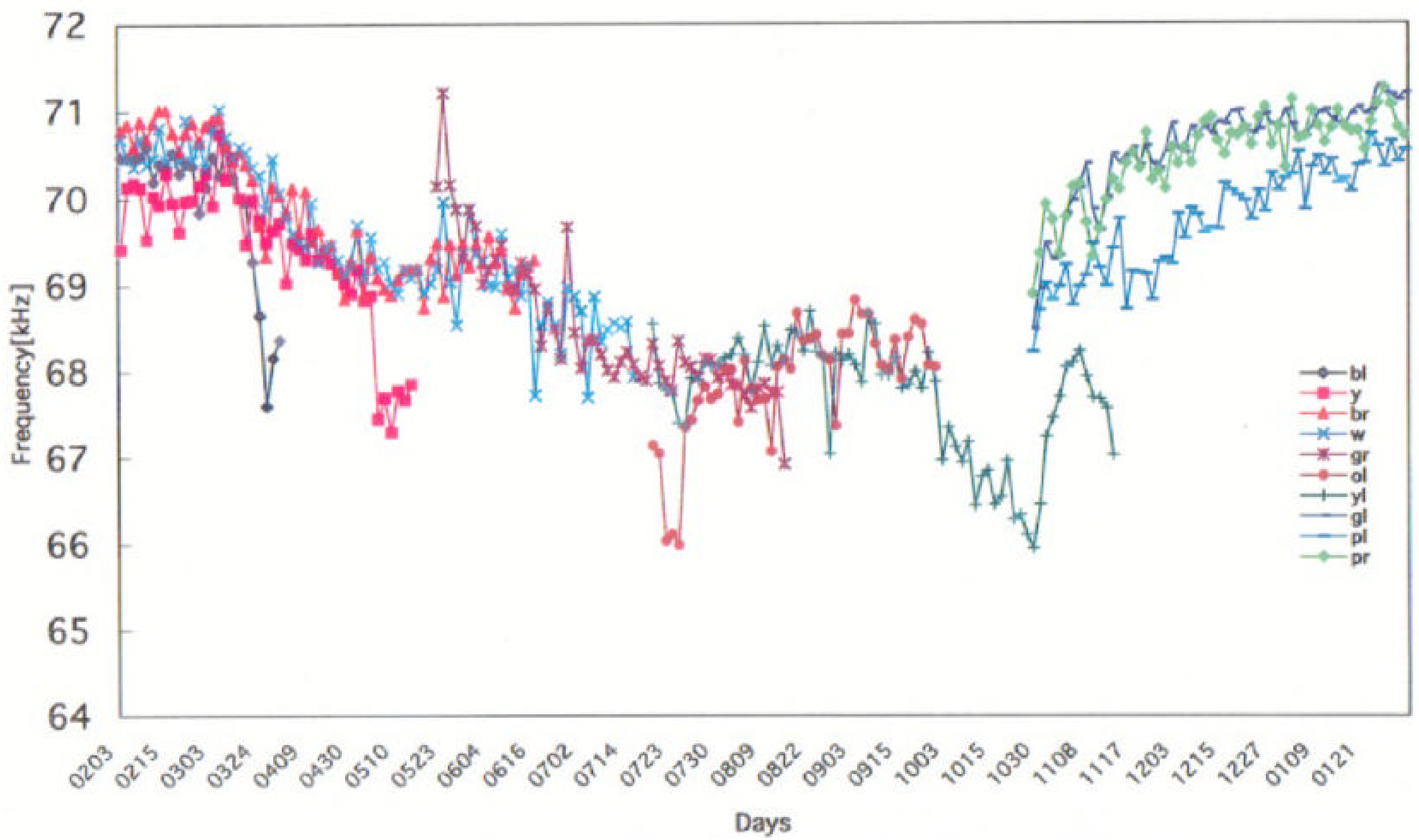

Fig. 5 Daily changes in pulse CF2 frequencies when bats are roosting. Data were taken from Taiwanese leaf-nosed bats (*Hipposideros terasensis*) for about a year. Different symbpls represent different bats.

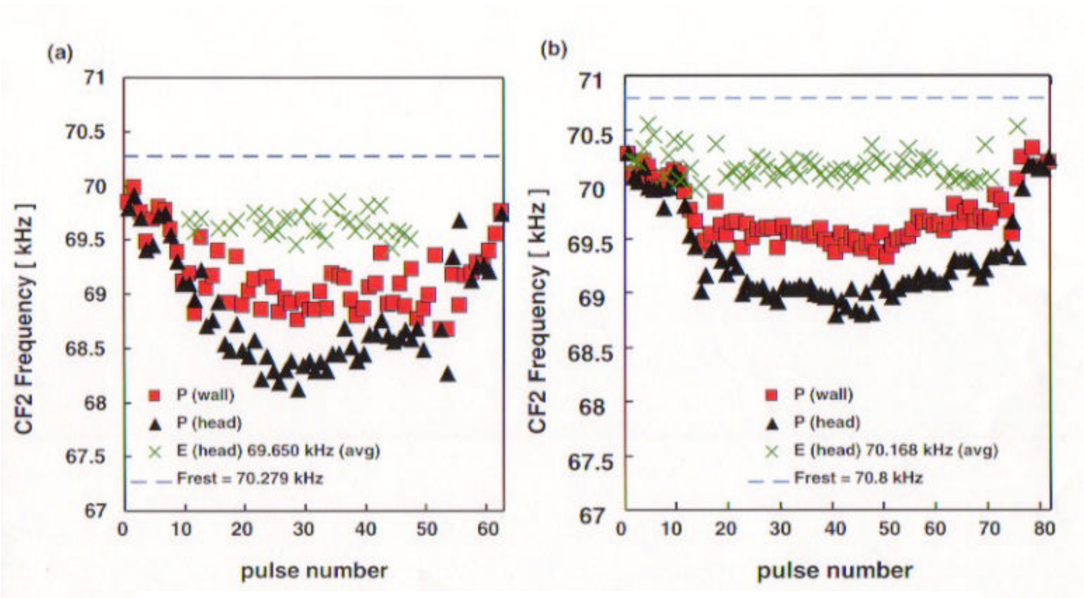

Fig. 6 Pulses and echoes of a flying bat measured on different days. CF2 frequency shift is observed. The bat landed at the end.

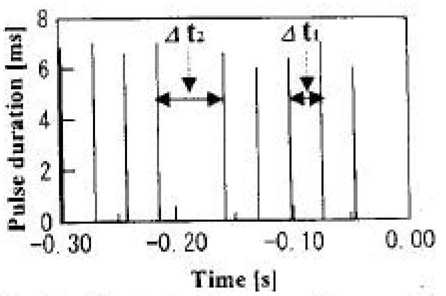

Fig. 7 Typical time pattern of emitted pulses. Δt1: inter-pulse interval within a train. Δt2: interval between succeeding trains.

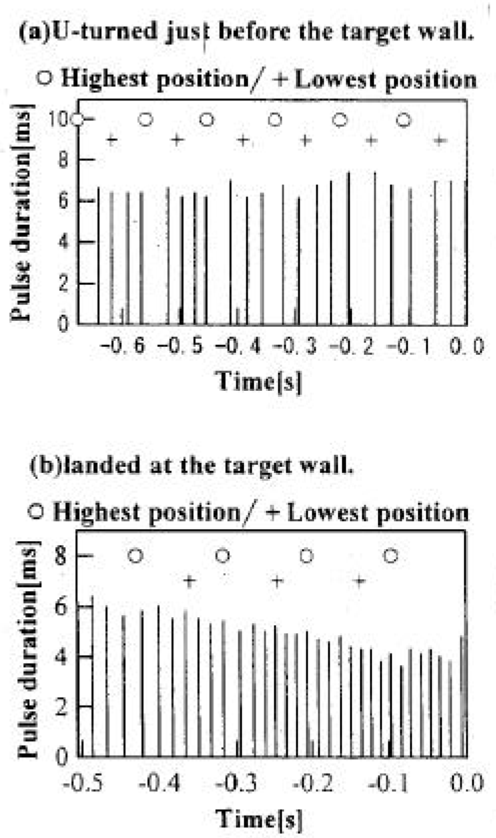

Fig. 8 Relationship between wing motion and pulse emission. Circles: highest posiion. Pluses: lowest position. a: U-turned before the wall. b: landed at the wall.

DISCUSSION AND SUMMARY

We have found that pulse CF2 frequency at rest is not consistent for a long period but varies much shown in Fig. 5. The cause of the variation is not yet confirmed. Possible candidates could be annual hormonal change and/or influence of vocalization from other individuals. Thus far, the pulse CF2 frequency at rest has been believed to be an ID of each individual [Suga, 1984]. However, the present experiment was the first long-term recording of the pulse CF2 frequency of the same individuals. The present study verified Doppler-shift compensation at the microphone on the head of a flying bat. More, CF2 frequency of pulses and echoes during flight demonstrated a tendency to shift in accordance with a shift in the pulse CF2 frequency at rest. In other words, although the echo CF2 frequency appeared to be stabilized at one frequency (Doppler-shift compensation), the reference frequency at which the echo CF2 frequency should be stabilized might not be fixed for each individual but could be changed in cooperation with the environment. The reference frequency may not be an absolute reference but a relative reference. The system with relative reference frequency could more flexibly cooperate with sudden change in the environment than the system with a fixed reference frequency. The dynamic central nervous system that can produce stable and precise measurement should be investigated.

ACKNOWLEDGEMENTS

The authors show a great appreciation to those students who cooperated with experiments and those who helped us to collect bats. This work was partly supported by Grant-in-Aid for Scientific Research (B)(1) 09450172 by the Ministry of Education, Special Research Grants for the Development of Characteristic Education from the Promotion and Mutual Aid Corporation for Private Schools Japan, Doshisha University's Research Promotion Fund and a grant to RCAST at Doshisha University from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

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