Response to Frequency Shifted Artificial Echoes in the Bat *Rhinolophus ferrumequinum**

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Summary. In 5 roosting bats the resting frequency, that is the mean frequency of the cf-portion of consecutive sounds, is kept constant with a standard deviation which varies between 30–120 Hz in different bats and at different days. In 15 bats the emitted sounds were electronically shifted in frequency and played back as artificial echoes. Upward frequency shifts were responded by a decrease of the emission frequency. This frequency compensation occurred at frequency shifts of up to 4400 Hz in all bats and up to 6000 Hz in a few bats. The frequency decrease in different bats over the whole compensation range was 50–300 Hz smaller than the frequency shifts in the echoes. The echoes, therefore, returned at a frequency, called the reference frequency, which was by this compensation offset higher than the resting frequency. The standard deviations of the emission frequency in compensating bats were only slightly larger than in roosting bats and the same in the whole compensation range. All bats started to compensate frequency shifts when they were slightly larger than the compensation offset. Downward frequency shifts were not responded by a change of the emission frequency, but the accuracy with which the emission frequency was kept decreased somewhat. From these results it is concluded that the Doppler shift compensation system of the Horseshoe bats compares the echo frequency with the reference frequency and compensates deviations of upward frequency shifts.

Introduction

In roosting bats the echoes from stationary targets have the same frequency as the emitted sounds. If, however, a bat or target is moving the echo frequency is changed due to Doppler shifts. The difference between the emission frequency and the echo frequency is a measure of the relative speed between bat and target. Horseshoe bats use orientation sounds with a long portion of nearly constant frequency (CF) preceeded and followed by short frequency modulated portions (FM). When flying towards a stationary target, they compensate for the Doppler shifts caused by the flight movement by lowering the frequency of the emitted sounds. The CF-component of the echoes is, therefore, kept constant within a small frequency band just above the resting

frequency of a roosting bat. The Doppler shift compensation is done by a feedback control system. This was demonstrated in one roosting bat echolocating a moving pendulum and by experiments with bats flying in a wind tunnel and in He-O_2-mixture (Schnitzler, 1968, 1973a). In the behavioural experiments of Schnitzler the Doppler shifts were caused by the flight movement of the bat or by a swinging reflector. Simmons (1973) confirmed the Doppler shift compensation in *Rhinolophus ferrumequinum* by playing back the orientation sounds raised 1 kHz by an electronic device.

We simulated the Doppler shifts with a different technique, which provided very good accuracy and frequency stability and allowed us to evaluate the compensation system in the whole frequency range.

Methods

Moving Target Simulator. An electronic device for simulating moving targets should shift the frequency of the emitted sounds by a controllable amount without affecting the intensity and frequency pattern. This can be done by the heterodyning technique:

Multiplication of the two signals

$$s_0(t) = a \cos 2 \pi f_0 t \quad \text{and} \quad s_1(t) = b \cos 2 \pi f_1 t$$

gives

$$x(t) = s_0(t) \cdot s_1(t) = (ab/2) \left[\cos 2 \pi (f_1 + f_0) t + \cos 2 \pi (f_1 - f_0) t\right];$$

$x(t)$ is the sum of two signals with frequencies $(f_1 + f_0)$ and $(f_1 - f_0)$. The echolocation sound $s(t)$ of a bat can be represented as a Fourier integral. Heterodyning $s(t)$ with $s_0(t)$ shifts every component by the same amount and therefore $s(t)$ is shifted in the whole frequency pattern by $+f_0$ and $-f_0$.

For f_0 near f_1 the two sidebands can easily be separated by filtering. For heterodyning we used the multiplier section (VCA-input) of a sinewave generator (Wavetek Model 136).

The echolocation sounds of *Rhinolophus ferrumequinum* with the emission frequency (f_t) were picked up with a Bruel & Kjaer microphone (Type 4135 and 2618), amplified (Bruel & Kjaer 2603) and heterodyned with a frequency $f_0 = 90$ kHz. The resulting sidebands $(f_t + f_0)$ and $(f_t - f_0)$ were separated by filtering with the low and high pass sections of a Krohnhite filter (model 3322). The high frequency sideband $(f_t + f_0)$ was again heterodyned with the frequency $(f_0 \pm \Delta f)$. The resulting upper sideband $(f_t + 2f_0 \pm \Delta f)$ was not used. The lower sideband $(f_t \pm \Delta f)$ constitutes the echolocation sound shifted in frequency by $\pm \Delta f$.

After an attenuator (HP 350 D) this signal was amplified with a HP 467 A amplifier and played back to the bat with a homemade ultrasonic condensor loudspeaker. The accuracy of the frequency shifts depends only on the stability of the sinewave generators used.

Frequency Measurement. The frequency of the emitted sounds was continuously monitored. Every cycle of the lower sideband signal $(f_t - f_0)$ after the first heterodyning stage triggered a square pulse of constant area (HP 8005 A), which was fed in a 500 Hz low pass filter (Krohnhite model 3321).

The output voltage of the low pass filter is proportional to the frequency of the pulses averaged during about 2 msec, and therefore proportional to the input frequency to the pulse generator. This apparatus allows one to measure f_t with a resolution of about 10 Hz at frequencies above 5 kHz.

This frequency dependent output voltage was recorded on a fast strip chart recorder and on magnetic tape. It was also sampled every 10 msecs after the onset of a sound by a PDP-12 computer which set up on-line frequency histograms. From these histograms the mean value of the frequency and the standard deviation were calculated.

Animals. During the experiment the animal was placed in a device which restrained the body but allowed head movements. The microphone and the loud-speaker were positioned 34 cm in front of the bat.

Results

Frequency of the CF-Component in Roosting Bats. In *Rhinolophus ferrumequinum* the CF-component extends for at least $^9/_{10}$ of the entire sound duration (10–60 msec). We analysed the CF-component from 5 msec after the beginning to 5 msec before the end of the orientation sound in order to be sure that the frequency measured was not influenced by the preceeding and the following FM-sweeps. Within the CF-component of an orientation sound the frequency changed within a narrow band. A total of 8 measurements of up to 172 consecutive sounds were made using three bats. Mean bandwidth between 30 Hz (standard deviation 20 Hz) and 100 Hz (standard deviation 60 Hz) were measured. The fine structure of the CF-portion could not be classified and showed variations between different bats and also within one bat during prolonged sound emission. If sound emission stopped for several respiratory cycles the CF-component in the first new sound was lower than in a continuously transmitting bat and swept upward up to 400 Hz. The mean values of the CF-components of consecutive sounds were determined with two methods: In one experiment the frequency patterns of up to 1140 orientation sounds were recorded on Oscilloscript paper film on several days in 3 bats.

The average frequency of the CF-component was visually evaluated for each sound and represented in a frequency histogram (Fig. 1). The mean value of these average frequencies, i.e. resting frequencies, and the standard deviations are given in Table 1. In all three bats the standard deviations of the resting frequency were between 30 and 50 Hz. At different days the resting frequency did not differ more than 90 Hz in one bat.

In a second experiment we measured on one day in two bats the frequencies of the CF-portion with the PDP-12 computer as described in the method section. In 33 measurements of groups with 250–700 succeeding sounds the standard deviation was between 50 and 120 Hz and the resting frequency varied up to 100 Hz in one bat. Playing back the emitted sounds at intensities of the artificial echo varying from 70 to 20 db of attenuation relative to the intensity of the emitted sound,
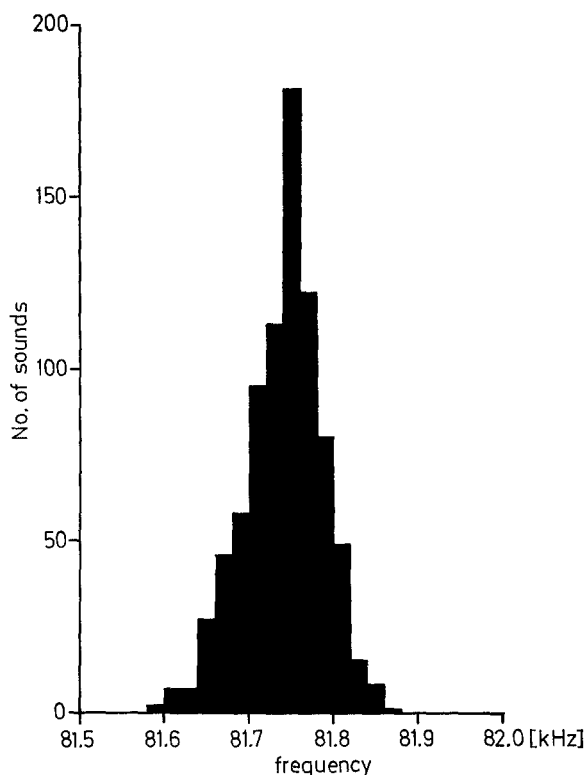
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Fig. 1. Frequency histogram for the constant frequency portions of 806 consecutive sounds in a roosting bat

without changing the frequency did not change the mean value and the standard deviation of the resting frequency.

The resting frequency is typical for each individual bat and was found to be between 81 and 84.2 kHz in all bats evaluated until now.

Increase of the Frequency in Artificial Echoes. When the frequency of the artificial echo was shifted upward by Δf Hz, the bats started to lower the emission frequency of the subsequent sounds. After a few sounds the bats continuously compensated the frequency shift and reached a new level of constant emission frequency. We measured the difference between the new emission frequency and the resting frequency, i.e. the compensation shift ($f_t - f_{rest}$), for various frequency shifts Δf. Most of the animals were able to compensate frequency shifts up to 4400 Hz properly. In a few bats compensation of frequency shifts up to 6000 Hz was found. For frequency shifts bigger than these com-

Table 1

Animal	Mean value or resting frequency (Hz)	Standard deviation (Hz)	number of sounds
Green	81760	53	651
	81680	42	585
	81730	46	806
	81760	38	1140
Red	83310	30	333
	83330	29	278
	83290	45	319
Black	82210	29	465
	82220	37	321
	82250	34	456

pensation limits, three different reactions in different bats could be observed. Some animals compensated the frequency shift by lowering their emission frequency by a constant amount, but did not reach full compensation as found for lower frequency shifts. A second group of animals tried compensation, but they changed the emission frequency irregularly before reaching full compensation. The third group of animals continued emitting their resting frequency, i.e. they did not compensate the high frequency shifts at all.

Fig. 2 shows histograms for the compensation shifts made by one *Rhinolophus ferrumequinum* at different positive frequency shifts. Figs. 3 and 4 give the means and standard deviations of the compensation shifts for positive and negative frequency shifts obtained from two other bats. The dashed diagonal line corresponds to a complete compensation of the frequency shifts. In all bats studied the compensation shifts were smaller than the corresponding frequency shifts. The echo frequency $(f_t + \varDelta f)$ is, therefore, always above the resting frequency. The difference between the echo frequency and the resting frequency are shown in the upper parts of Figs. 3 and 4. In an individual compensating bat this difference, i.e. the compensation offset, is about the same size over the whole compensation range. The compensation offsets in all bats studied varied between 50–300 Hz. The constant compensation offset results in a constant echo frequency over the whole compensation range in every bat. This echo frequency, which is controlled by the compensation system, we will call reference frequency. The linearity of the compensation system was very high over the whole compensation range.
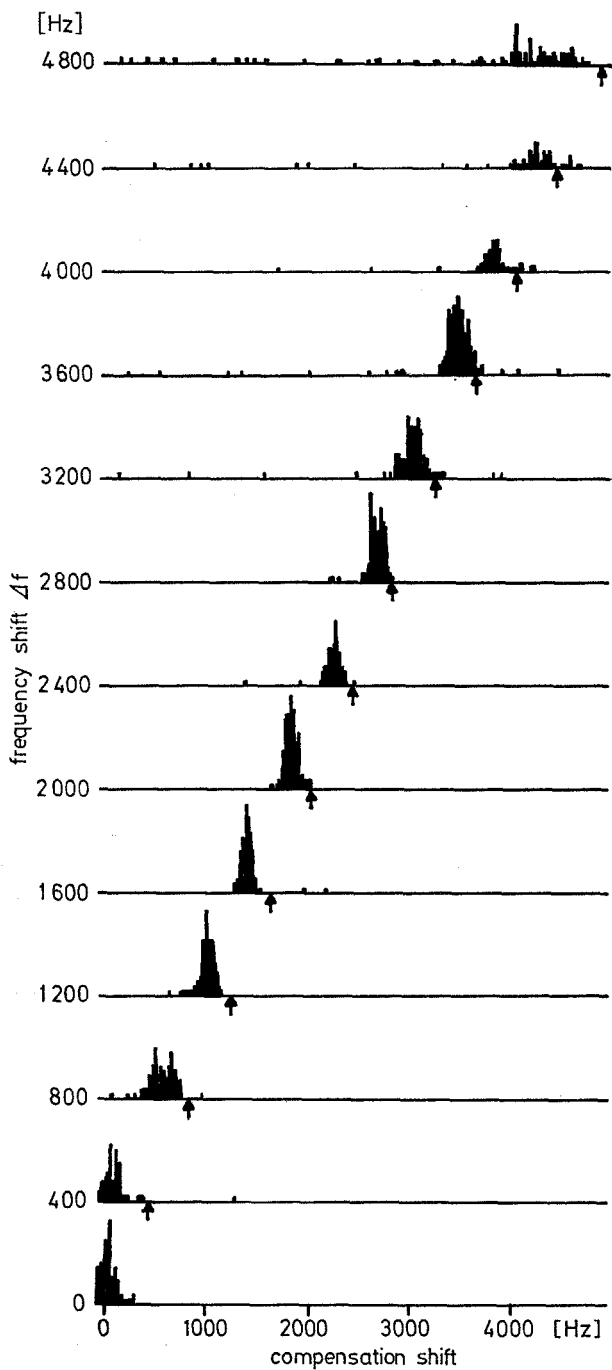
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Fig. 2

The results displayed in Figs. 3 and 4 differ somewhat. The bat of Fig. 3 starts to compensate at an upward shift of about 50 Hz and has a compensation offset of 50–100 Hz whereas the other bat of Fig. 4 did not compensate for shifts below 250 Hz and had an offset of about 250 Hz. Similar relationships were found in all investigated bats. That means that the compensation offset is about as large as the minimum frequency shift which is compensated for.

The standard deviations of the compensation shifts did not vary significantly throughout this range and were only slightly larger than the standard deviations for the resting frequency. They were typically between 50 and 200 Hz.

Decrease of the Frequency in Artificial Echoes. Playing back artificial echoes shifted by negative $\varDelta f$ relative to the emitted frequency was not responded to by an increase of the emission frequency. Instead the bat continued to utter its sounds at the resting frequency. This is represented for a large range of negative frequency shifts on the left side of the graphs in Figs. 3 and 4. The emitted frequency is however less accurate than the resting frequency, yielding larger standard deviations. Most animals reacted to the negative frequency shifts in the echo with a short increase of the intensity of the emitted sounds.

The effect of intensity of the artificial echoes on the compensation of frequency shifts was not systematically evaluated in these experiments. The artificial echoes were played back with intensities between 60 and 20 db of attenuation relative to the intensity of the emitted sounds. The performance of the frequency compensation system did not vary within this intensity range.

Discussion

In the natural situation frequency shifts in the echoes of echolocating bats occur due to movements of the bat and the prey. This is known as Doppler shift, which in first approximation is proportional to the relative movement between the bat and the reflector and proportional to the frequency of the emitted sound. Movements which decrease the distance between bat and target increase the frequency in the echo, whereas movements, which increase this distance decrease the echo frequency. In our experiments the artificial echoes differ from the naturally encountered echoes in the echolocation situation and do not exactly simulate a naturally moving target. Whereas the Doppler shift

Fig. 2. Frequency histograms for the constant frequency portions of echolocation sounds in a bat compensating for upward frequency shifts in the echo. Vertical: frequency shift $\varDelta f$ in the echo. Horizontal: compensation shift, that is the frequency decrease of the emitted sound relative to the resting frequency. The arrows indicate the compensation shifts necessary for full compensation of the frequency shift $\varDelta f$
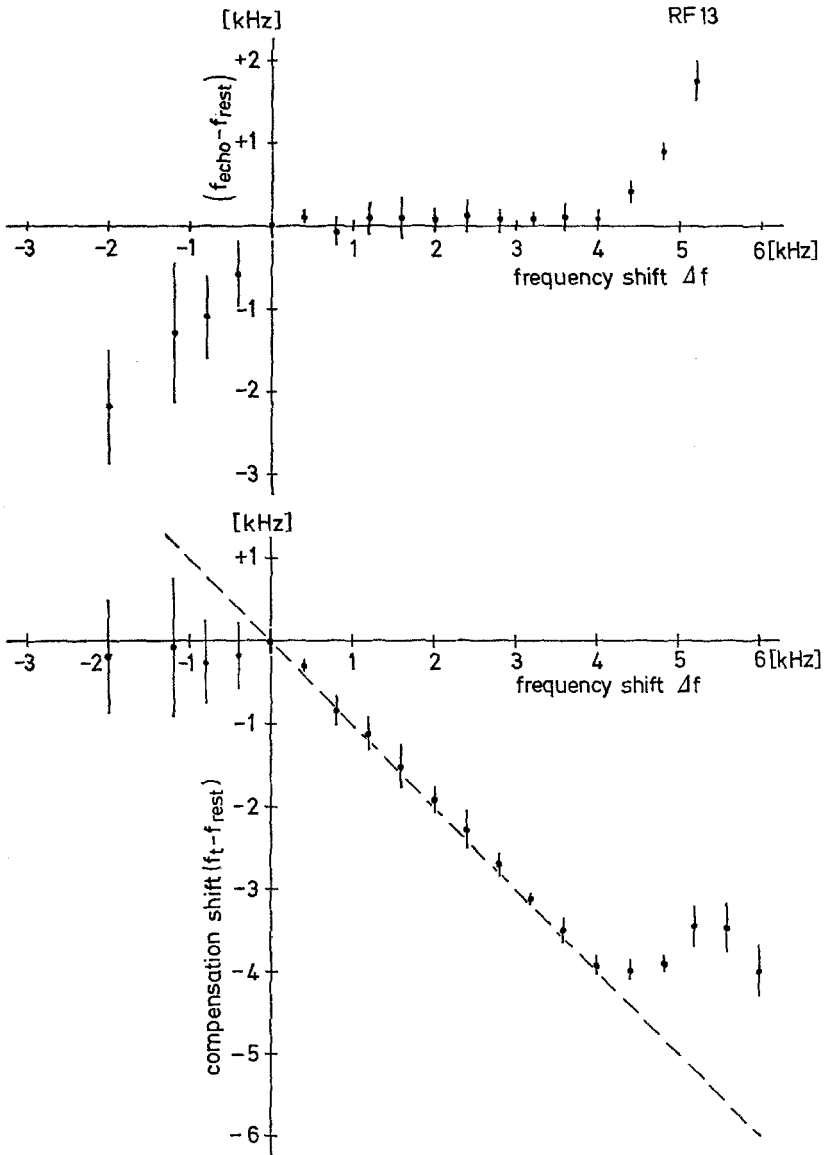
Fig. 3

Figs. 3 and 4. Lower graph: Compensation shift $(f_t - f_{rest})$ as a function of the frequency shift Δf. Upper graph: Difference between echo frequency and resting frequency $(f_{echo} - f_{rest})$ as a function of the frequency shift Δf. The vertical bars indicate $\pm$ standard deviation (68% of all CF-frequencies fall in this frequency range)
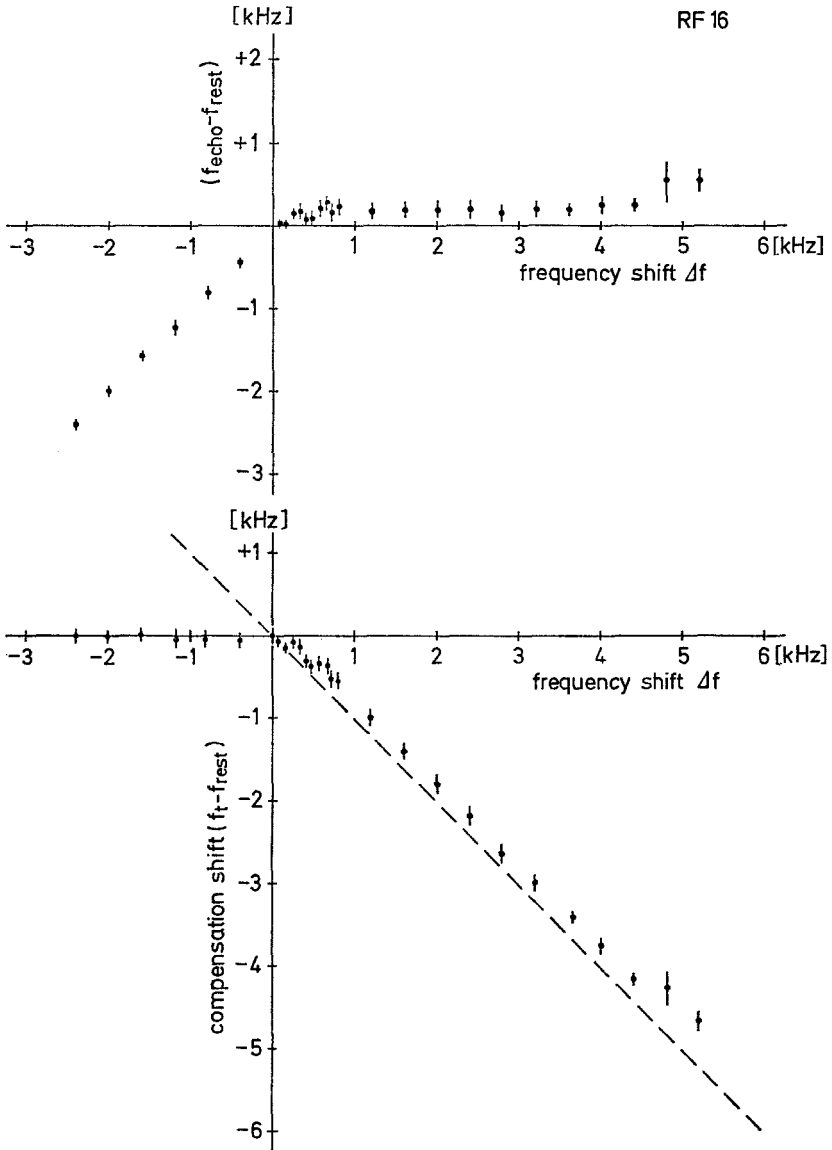
Fig. 4

is frequency dependent and causes a decreasing frequency shift in the final frequency modulated portion of the echolocation sound, the artificial echoes were shifted by the same amount over both the constant and final frequency modulated portion of the echolocation sound.

As the artificial echoes were played back with a constant intensity attenuation relative to the emitted intensity and as the delay between the echo and the emitted sound was constant the artificial echo corresponds to a Doppler shifted echo encountered in the natural situation only in its frequency domain and in its constant frequency portion. The simulated target was therefore moving in the frequency domain, but resting in regard to time and intensity parameters.

A common result in all our experiments was the accuracy with which the resting bat controls its emission frequency.

The results indicate a high performance of the vocalization system as the bats were able to maintain their resting frequency typically within 0.06% standard deviations and in the worst case within 0.15% standard deviations from the center frequency.

The mechanism which keeps the resting frequency in such a narrow band is unknown. It may be that it is also controlled by the frequency compensation system.

The pendulum experiments of Schnitzler (1968), in which the Doppler shifts in the echo were produced by a swinging reflector indicated an almost symmetrically working compensation system in the bat, i.e. that it compensated for upward and downward Doppler shifts. The described experiments revealed an asymmetrically working system, which compensates only upward frequency shifts in the echo in all investigated *Rhinolophus ferrumequinum*. This corresponds to the situation in which the reflector and the bat are approaching. On downward frequency shifts, corresponding to withdrawing targets, the bats did not alter the emission frequency but their accuracy to center on the resting frequency decreased somewhat.

The discrepancy of our experiments from the pendulum experiments may be explained by the experimental conditions in the pendulum experiments, where the maximum frequency shift was rather low (500 Hz) and the pendulum frequency rather high (about 0.7 Hz). When the compensation system regulates for upward frequency shifts the emitted frequency is always decreased in a way that keeps the echo frequency at a reference frequency. For downward shifts the echo frequency is below the reference frequency.

In terms of a control system the compensation system is sensitive to echo frequencies above the reference frequency but not to echo frequencies below the reference frequency. These properties will be discussed later in the light of neurophysiological results. Most attention was payed to the properties of the compensation system, when it responded to upward frequency shifts.

It has been shown that the system performs compensation in a highly linear way up to frequency shifts of 6000 Hz in some bats and

up to 4400 Hz in most of the investigated animals. These upper compensation limits correspond to the speed of approximation between bat and target of about 12 and 9.5 m/sec respectively. The maximum flight speed measured in *Rhinolophus ferrumequinum* was about 9 m/sec (Schnitzler, 1973a).

The linear compensation range covers therefore the velocities important in the natural echolocation situation of the bat. The threshold at which the bats started to compensate upward frequency shifts varied in different animals between 50 and 300 Hz. In compensating bats the compensation shift, that is the difference between the emission frequency and the resting frequency, was always lower by the same amount than the frequency shift throughout the whole linear range. The reference frequency, that is the frequency at which the echo frequency was kept constant by the compensation system, was therefore always higher than the resting frequency. The difference between the resting frequency and the reference frequency, called the compensation offset, was related to the compensation threshold. In bats which started to compensate at small upward shifts the compensation offset was also small and vice versa. These results confirm the measurements of Schnitzler (1968, 1973a), who found similar compensation shift offsets. The standard deviation of the compensation shifts, which is a measure for the accuracy with which the reference frequency is kept, was revealed to be the same in the total linear compensation range and to be slightly higher than for the resting frequency. These results suggest that in the compensation system the echo frequency is compared with the reference frequency and the emission frequency is changed until the echo frequency equals the reference frequency. This is consistent with the results that the echo frequency is controlled with the same accuracy over the whole compensation range independent of the size of the frequency shift.

Neurophysiological measurements of Neuweiler (1970), Neuweiler, Schuller, and Schnitzler (1972), Schuller (1972) and Schnitzler (1973b) gave evidence that *Rhinolophus ferrumequinum* has a highly specialized auditory receiver system. Evoked potential measurements in the inferior colliculus gave extreme minima for thresholds of the on- and off-responses in the frequency range of the resting frequency. The off-response minimum lies about 0.5 kHz below the on-minimum. In this frequency range the auditory system is very sensitive to frequency modulations as small as 5 Hz/msec occurring during a constant frequency stimulus (Schuller, 1972). Unfortunately in most neurophysiological experiments the resting frequency of the bats used has not been measured. In preliminary experiments on two animals it was found that the resting frequency and the reference frequency fall in the range of the off-response minimum (Schnitzler, 1973b) and high sensitivity for frequency modulations.

Echo frequencies higher than the reference frequency, produced by approaching targets, fall in a frequency range of low on-response thresholds, whereas echo frequencies lower than the reference frequency, caused by withdrawing targets, fall in the range of high on-response thresholds. Further the emitted sounds of a bat compensating for upward frequency shifts, and therefore lowering its emitted frequency, fall in the range of high on-response thresholds and possible masking of the echoes is therefore reduced. As the compensation system keeps the echo frequency in the frequency range, where the performance for the detection of frequency modulations during the CF-portion of the sound is high, the bat has available its full detection capabilities for accelerated movements independent of its own flight speed.

Further advantages of the Doppler shift compensation of *Rhinolophus ferrumequinum* were extensively discussed by Schnitzler (1973a, b)

It guarantees to the bat a high selectivity of detecting a target of a specific velocity in surroundings of a high variety of movements. The system is able to cut out a small section of the velocity space and use there its whole detection and discrimination capabilities.

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