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Dynamic Properties of the Compensation System for Doppler Shifts in the Bat, *Rhinolophus ferrumequinum**

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Summary. 1. Echolocation sounds of the bat *Rhinolophus ferrumequinum* were played back to the bat as artificial echoes shifted in frequency by a few kHz (0–4 kHz) without distortion of the amplitude and frequency pattern of the sound. The simulated Doppler shifts in the echoes were modulated either sinusoidally or in step functions.

2. The bats did not compensate for frequency shifts within one sound, but in the sounds subsequent to the introduction of the shift.

3. Responses to symmetrical sinusoidal modulations of the echo from -2 kHz to $+2$ kHz demonstrate that in the dynamic situation the bat compensates for positive frequency shifts and ignores negative frequency shifts (Fig. 2). Asymmetrical sinusoidal modulations between 0 Hz and different positive frequency shifts (1, 2, 3, and 4 kHz) yielded amplitude and phase response curves for modulation frequencies between 0.01 and 2 Hz (Fig. 5, 6). The response to step functions gave the time course for positive and negative changes of the frequency shift (Fig. 7).

4. The Doppler compensation system shows nonlinearities: The response of the system depends on the sign of the frequency shift change. Positive changes of the frequency shift in sinusoidal modulations are optimally followed by the system, when it is considered as a sampling system, in which the pulse repetition rate is the sampling rate. The response to negative frequency shift changes is much slower (Fig. 6). With an increase of the modulation frequency the response is DC-shifted. The amplitude and phase response curves depend on the amplitude of the frequency shifts presented in the modulation (Table 1, 2).

5. The maximum compensation between two succeeding bat orientation sounds was 1400 Hz, giving a frequency change of about 10 Hz/msec. This value is about the same as the minimum frequency modulation of the constant frequency portion of the sound detected by the bat.

6. The dynamic properties of the Doppler shift compensation system are discussed in the context to neurophysiological findings on the hearing system of the bat.

Introduction

The echolocating bat, *Rhinolophus ferrumequinum*, emits echolocation sounds composed of a short upward frequency modulated portion at the beginning of a 10–60 msec long constant frequency portion (about 83 kHz), which is terminated by a short 13–16 kHz downward frequency modulated portion. When flying, the bat receives echoes which are shifted in frequency due to Doppler effects. As the bat approaches a reflecting target, the echo frequency is higher than the emitted frequency of the sound (positive frequency-shift). When the target moves away from the bat, negative frequency-shifts occur in the echoes. Bats hearing positive frequency-shifts lower the emission frequency of subsequent sounds in order to compensate for the frequency-shift (Schnitzler, 1968). In this way they receive

echoes at a frequency almost equal to the resting frequency, which is emitted, when no Doppler shifts occur. This result was first confirmed by Simmons (1974) who used an electronic device to produce artificial echoes with a frequency 1 kHz above the emitted frequency.

A different technique which simulated Doppler shifts in the echoes provided a higher accuracy and stability in frequency and allowed measurements of the performance of the compensation system for constant frequency shifts in the range up to 6000 Hz (Schuller, Beuter, Schnitzler, 1974). In these experiments it was confirmed that the bats control the frequency of outgoing orientation sound in a way that the echo frequency lies 50–300 Hz higher than the resting frequency.

Only a few indications of the dynamic properties of the control system for frequency-shift using data restricted to a positive Doppler step of 1 kHz were given by Simmons (1974). This paper reports data on the dynamic performance of the system for frequency-shifts up to 4000 Hz obtained by measuring the response of the compensation system to sinusoidal and square wave modulations of the Doppler frequency-shift in the echo.

The dynamic properties of linear systems can be completely described by their response to such modulations. The control system for frequency-shifts in this bat is not strictly a linear system. The responses to sinusoidal modulations can therefore give only an approximate description of the dynamic properties. They can, however, give evidence on the nature of the nonlinearities present in comparison to well-known linear systems.

Methods

Bats of the species *Rhinolophus ferrumequinum* were used as subjects in the studies. The artificial echoes were shifted in frequency by a controllable increment relative to the frequency of the emitted sounds of the bat by a double heterodyning technique which is fully described elsewhere (Schuller, Beuter, Schnitzler, 1974).

Fig. 1 shows frequency spectra measured with a wave analyzer (HP 3590 A) at the different stages of heterodyning. The spectra show that the intensities of spurious sideband signals were always 30 dB lower than the intensity of the artificial echo played back to the bats.

The frequency of the constant-frequency portion of the emitted sounds was continuously monitored with a frequency-measuring device described in the previous work. The time constant of the frequency meter was 2 msec. The frequencies of the constant frequency portions of the emitted sounds and the frequency shifts were stored on magnetic tape and plotted on a strip-chart recorder (Helcoscriptor He-1, Hellige). The frequency recording methods allowed an accuracy of ± 50 Hz. The bats were fixed in a special animal holder so that they faced the loudspeaker and the microphone at a distance of 68 cm.

In one experiment the artificial echoes were played back through two loudspeakers situated bilaterally to the head of the bat in order to avoid possible echoes reflected from straight ahead by the loudspeaker. Both loudspeaker arrangements gave the same results regarding the properties of the compensation system for frequency shift studied in this work. The intensity of the artificial echo was 20–40 dB lower than the intensity of the bat's sound.

The frequency shift in the artificial echoes relative to the emitted frequency of the bat's sonar sounds could easily be modulated by applying a signal to the VCG-input of the Wavetek (Type 136) generator which delivered the heterodyning frequency of the second stage. Thus simulated Doppler shifts varying in time according to sinusoidal and rectangular functions were produced and the frequency and step response of the compensation system could be evaluated. The modulating functions could be offset, resulting in symmetrical or asymmetrical
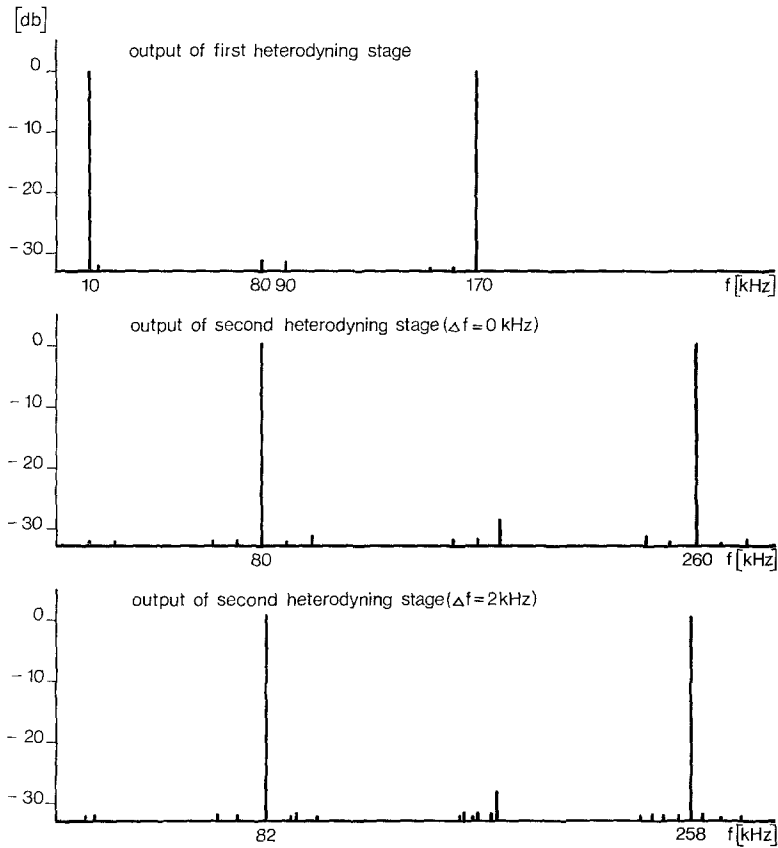
[db]

output of first heterodyning stage

0

- 10

- 20

- 30

10   80 90   170   f[kHz]

output of second heterodyning stage (△f = 0 kHz)

0

- 10

- 20

- 30

80   260   f[kHz]

output of second heterodyning stage (△f = 2kHz)

0

- 10

- 20

- 30

82   258   f[kHz]

Fig. 1. Frequency spectra of the output signal at different stages of heterodyning in the playback equipment. Frequency of the input signal: f_t; heterodyning frequency of first stage: f_0; variable frequency of the second heterodyning stage: f_v. Top: output of the first stage ($f_t = 80$ kHz, $f_0 = 90$ kHz). Middle: output of the second stage ($f_t = 80$ kHz, $f_0 = 90$ kHz, $f_v = 90$ kHz). Bottom: output of the second stage ($f_t = 80$ kHz, $f_0 = 90$ kHz, $f_v = 88$ kHz)

Doppler shifts relative to the emitted frequency. For the sinusoidal Doppler shifts modulation frequencies from 0.01 Hz to 2 Hz were used. The maximum Doppler shifts ranged up to 4 kHz.

Results

In all the experiments done with simulated Doppler shifted echoes the frequency changes within the constant frequency portion of the sounds never exceeded those measured during emission of the resting frequency. This indicates that the response to Doppler shifts occurs for subsequent sounds, but not during one single sound.

Symmetrical Sinusoidal Modulation. When the simulated Doppler shifts were modulated symmetrically relative to the resting frequency, the bats compensated only for positive shifts.
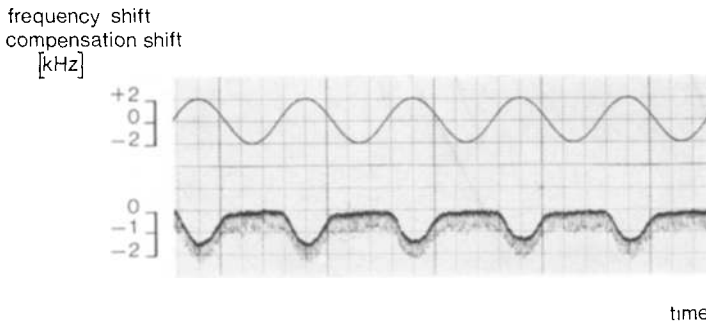
frequency shift
compensation shift
[kHz]

time

Fig. 2. Response of the compensation system to symmetrical modulations of the frequency shift ($\Delta f = \pm 2$ kHz). Top: modulating waveform (modulation frequency is 0.05 Hz). Bottom: compensation shift of the bat's response. The black dots represent the constant frequency portion of the sound

Fig. 2 represents the emission frequency of a bat that is hearing its echoes at frequencies shifted sinusoidally by ± 2 kHz relative to the emitted frequency, at a modulation frequency of 0.05 Hz. This response resembles the output of a half-wave rectifier and demonstrates that the bats compensate only for positive frequency-shifts and continue to utter the resting frequency as long as negative frequency-shifts occur in the echoes. The compensation shift of the bats is slightly smaller than the total positive frequency shift, an offset that was demonstrated in the previous work on constant frequency-shifts (Schuller, Beuter, Schnitzler, 1974).

Sinusoidal Positive Shifts. In all other experiments the simulated Doppler shifts were varied sinusoidally between zero and a maximum positive shift. The response of the compensation system to such asymmetrical modulations was measured for the artificial Doppler shifts of 1, 2, 3 and 4 kHz at modulation frequencies between 0.01 Hz and 2 Hz.

Fig. 3 represents typical responses from the compensation system to Doppler shifts varying between 0 and 2000 Hz at different modulation frequencies. With more rapid changes of Doppler shifts the errors in Doppler shift compensation increase. Typical properties of the system for increasing modulation frequencies are:

1. At all modulation frequencies the bats control the emission frequency in such a way that the maximum occuring frequency-shift is compensated.

2. As modulation frequency increases, the response of the bat gets progressively more distorted from the driving sinusoidal waveform. The bat compensates rapidly for increasing frequency-shifts but returns rather slowly towards resting frequency when the frequency-shifts decrease.

3. At higher modulation frequencies the bat's emitted frequency no longer returns to the resting frequency, even for zero Doppler shifts. In this case the frequencies of both the emitted sound and the returning echo lie below the resting frequency (Fig. 4).

4. Whereas the phase lag between the maximum Doppler shift and the maximum compensation shift in the bat's response increases only slightly, the phase

frequency shift
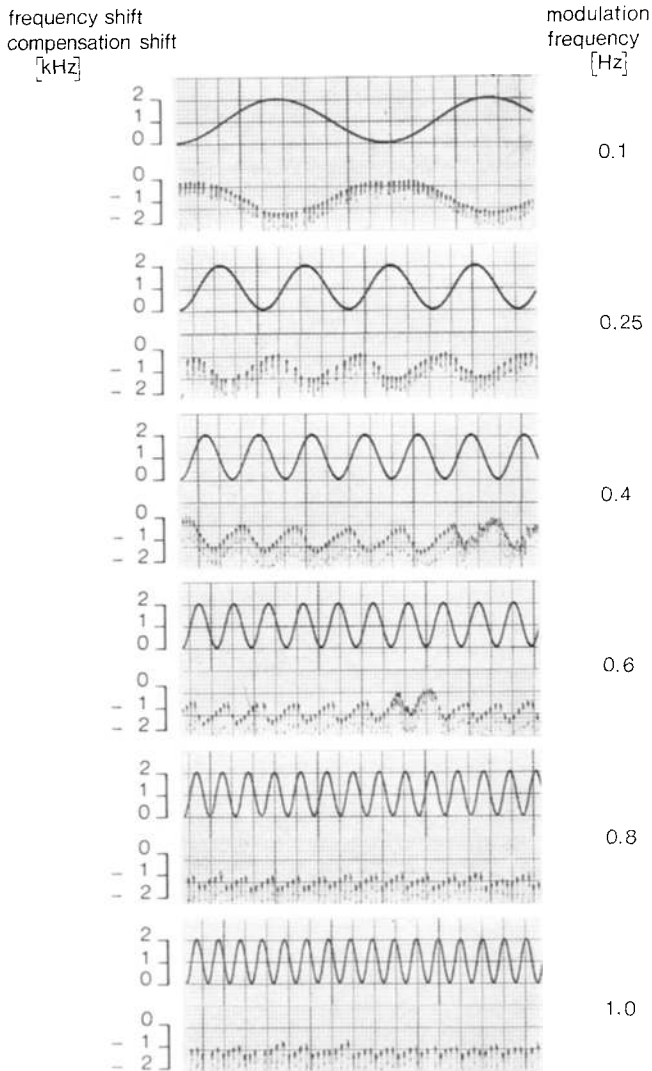compensation shift
[kHz]

modulation
frequency
[Hz]

Fig. 3. Response of the compensation system to sinusoidal modulations of positive frequency shift (2 kHz) for different modulation frequencies. In each graph the upper curve represents the modulating waveform and the lower graph the compensation shift of the bat's response. The dots represent the constant frequency portion of the sounds

lag between zero shift and the minimum compensation shift in the bat's response grows rapidly with increasing modulation frequency.

The records from five bats yielded amplitude and phase response curves. At each modulation frequency the mean value of the differences between the minimum and maximum compensation shift of 10 modulation cycles was taken as the amplitude response. Fig. 5 shows the normalized amplitude response for one
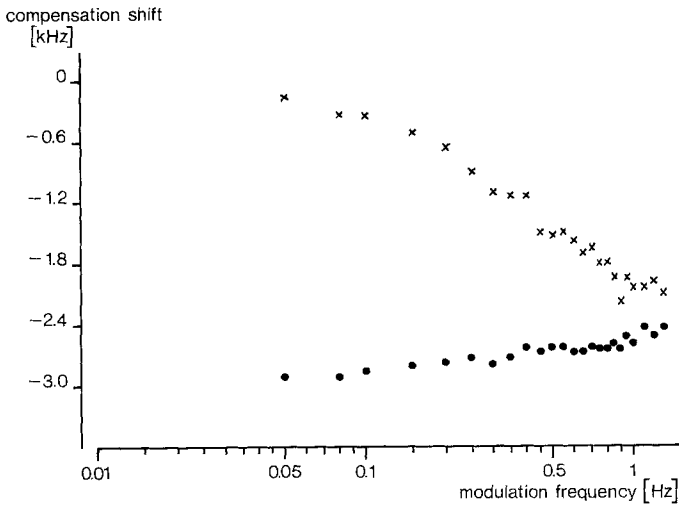
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Fig. 4. Compensation shifts at maximum frequency shifts (3 kHz, circles) and zero frequency shift (crosses) as a function of the modulation frequency

bat at four different maximum frequency shifts. The amplitude response curves of the other bats are well characterized by this example and differ only in the frequency at which the amplitude response curve reaches its half value, or − 6 db point. The half value frequencies for all bats are listed in Table 1.

The phase lags were calculated from the time lags between the peaks in the modulation cycles and the corresponding peaks in the bat's response measured from parallel records of the modulation waveform and the response of the compensation system. The phase lag between the maximum frequency-shift and the maximum compensation shift in the emitted sound characterizes how quickly the compensation system follows increasing frequency-shifts. The phase lag between zero frequency-shift and the minimum of the compensation shift in the response shows how rapidly the system goes back towards the resting frequency when the Doppler shifts are decreasing. The phase response curves from one bat are represented in Fig. 6 for the four different maximum frequency-shifts. A major limitation to the accuracy of the time delay evaluation arises from the variable repetition rate and duration of the bat's sounds. The repetition rate for the different bats varied between 3 Hz and 7.5 Hz, i.e., the sounds were separated on the average by 130 msec to 330 msec. The sounds themselves lasted from 30 to 60 msec. A sampling system that ideally follows a continuous sinusoidal input function can only follow the input changes without considerable phase lag if the sampling rate is much higher than the frequency of the input waveform. For a constant sampling rate the phase lag can be calculated for sinusoidal input waveforms as a function of the input frequency, using the formula: phase lag $= 2\pi$ (modulation frequency/sampling rate). The curves describing an ideal sampling system for repetition rates of 4 Hz and 7 Hz are drawn as bold curves in Fig. 6. The phase lag values measured at maximum frequency-shifts fall in the range
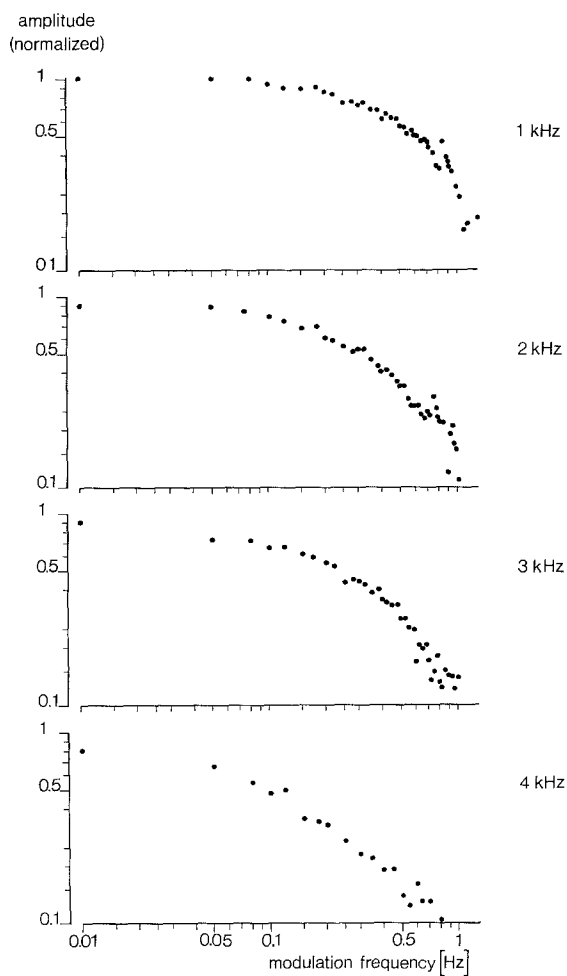
Fig. 5. Amplitude response curves for maximum frequency shifts of 1, 2, 3 and 4 kHz

Table 1. Modulation frequency at the −6 db point of the amplitude response curves

| Frequency shift (Hz) | Bat | | | | |
	RF 1 (Hz)	RF 2 (Hz)	RF 3 (Hz)	RF 4 (Hz)	RF 5 (Hz)
1000	0.62	—	0.5	0.75	0.64
2000	0.32	0.62	0.4	0.27	0.52
3000	0.25	0.5	0.31	(0.16)	0.36
4000	0.1	0.2	0.18	0.12	0.22

phase lag

1 kHz

2 kHz

3 kHz

4 kHz

modulation frequency [Hz]

0.01   0.05   0.1   0.5   1
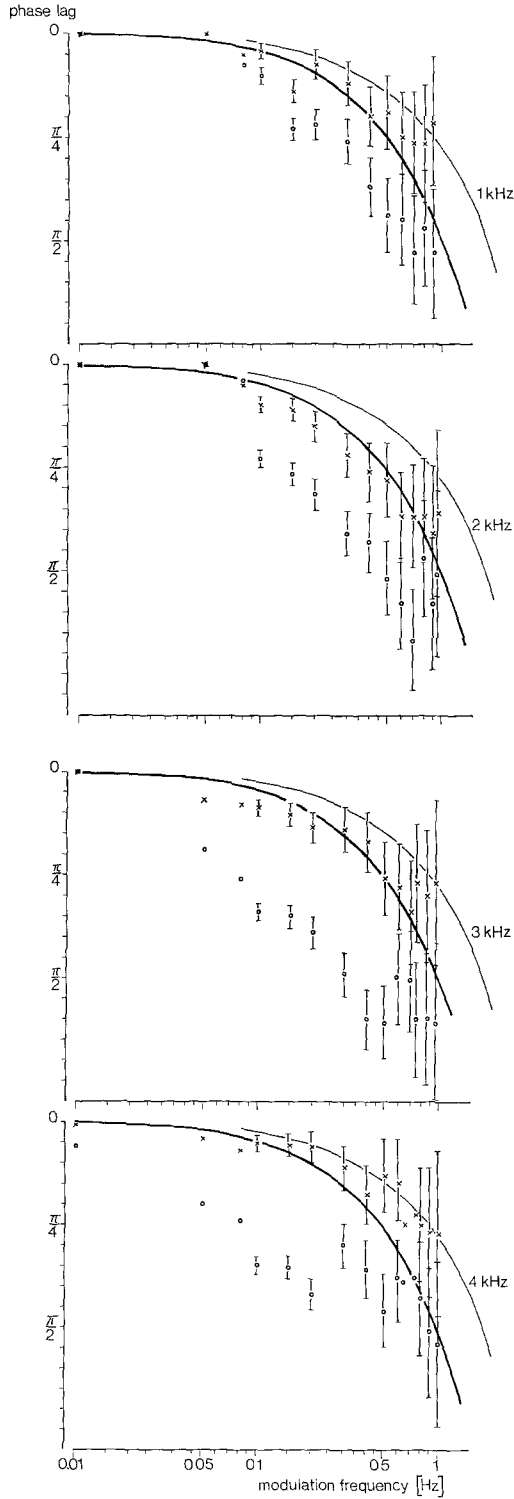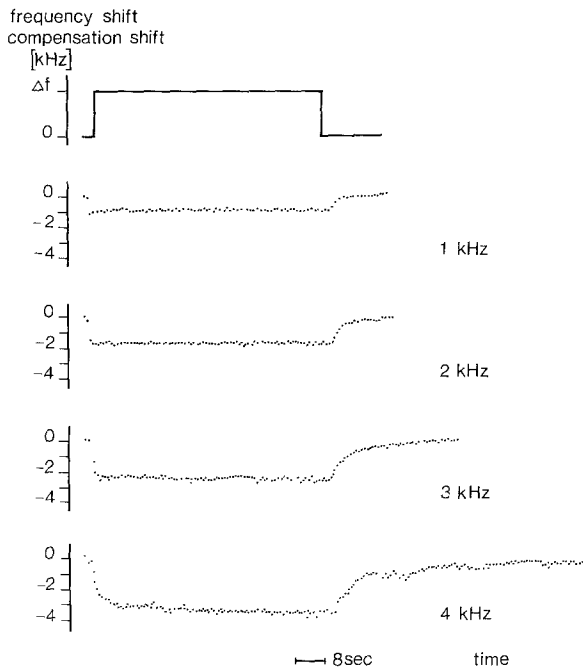
Fig. 6

frequency shift
compensation shift
[kHz]

Fig. 7. Response of the compensation system to frequency steps of 1, 2, 3 and 4 kHz. The upper curve represents the modulating waveform of the frequency-shift. The four lower curves give the compensation shifts of the bat's response

between these two curves. The scattering of the values is due to changing repetition frequencies used by the bat. The phase lag at zero frequency-shifts is much higher than the theoretical values for the sampling system. The bars around each measured value indicate the error in the phase lag measurements due to the distance in time between two succeeding sounds. This systematical error is larger than all measurement errors.

Frequency Steps. Rectangular frequency-shift modulations were used in addition to sinusoidal modulations. In these rectangular modulations the frequency shifts in the artificial echoes were raised suddenly to a constant value (pos. step). When the bat had reached the compensation shift level corresponding to the given frequency shift and stabilized to this emission frequency the frequency shift was suddenly lowered to zero shift again (neg. step). In this way the time needed for the system to reach a steady compensation state, and the time needed for return to the resting frequency could be evaluated. Fig. 7 shows the bat's response to rectangular modulation waveforms. The times needed for the bats to reach full compensation for positive steps in Doppler shift are presented in

Fig. 6. Phase response curves for maximum frequency-shifts of 1, 2, 3 and 4 kHz. Crosses: phase lag of the response at the maximum frequency-shift. Circles: phase lag of the response at zero frequency-shift. The bold lines give the phase lags for an ideally following sampling system at pulse repetition rates of 4 Hz (lower line) and 7 Hz (upper line)

Table 2a. Time needed to reach full compensation for positive steps in Doppler shift

Frequency shift (Hz)	Bat		
	RF 2 (sec)	RF 4 (sec)	RF 5 (sec)
1000	0.27 ± 0.09	0.42 ± 0.27	0.35 ± 0.11
2000	0.45 ± 0.10	0.57 ± 0.32	0.40 ± 0.12
3000	0.72 ± 0.11	0.56 ± 0.15	0.74 ± 0.20
4000	2.16 ± 0.82	2.05 ± 1.21	1.58 ± 0.50

Table 2b. Time needed to return to $1/e$ (0.37) of the maximum compensation shift after a negative step in Doppler shift

Frequency shift (hz)	Bat		
	RF 2 (sec)	RF 4 (sec)	RF 5 (sec)
1000	0.35 ± 0.05	2.15 ± 1.50	0.44 ± 0.12
2000	0.59 ± 0.04	2.74 ± 0.73	1.16 ± 0.46
3000	1.28 ± 0.43	2.25 ± 1.17	2.70 ± 0.90
4000	1.23 ± 1.08	3.46 ± 1.98	2.15 ± 0.92

Table 2a. Whereas the time course of the response to positive frequency steps was rather uniform that for the return to the resting frequency could vary somewhat. Usually the response to the negative step was similar to an exponential decay function but could also be much faster. In all cases the times taken by the bat to reach $1/e$ (0.37) of the maximum compensation shift after a negative frequency step was measured. They are given in Table 2b. One bat (RF 4) continued to utter a frequency lower than the resting frequency even when no artificial frequency shifts occured in the echoes. As this phenomenon lengthened the return times considerably for frequency shifts of 1 kHz and 2 kHz, the values for RF 4 are not directly comparable to those of the other bats in Table 2b. In all experiments with time-dependent Doppler shifts the maximum frequency change between two succeeding bat sounds was below 1.4 kHz. Maximum values between 900 and 1400 Hz occured predominantly at positive frequency steps of 2 and 3 kHz. On the basis of the reported measurements it cannot be decided how the performance of the system depends on the repetition rate of the echolocation sounds. Momentary changes in the repetition rate could not be evaluated and were not correlated with the time course of Doppler shifts. They may have been more dependent on the bat's state of attention than on any other experimental parameter.

Discussion

The control system for compensation of Doppler shifts in the CF-FM-bat, *Rhinolophus ferrumequinum,* consists of a feedback loop involving parts of the

auditory system and parts of the motor innervation system for the vocalization. The acoustical information is received by the ear and processed through acoustical centers up to a level at which information is directed to vocalization command centers. This feedback loop has the purpose to keep the frequency of the returning echo at the so called reference frequency lying about 50–300 Hz above the resting frequency. Where the connection between the acoustical and the vocalization centers occurs has not yet been localized within the brain.

In the experiments reported here the artificial Doppler shift was added to the bat's emitted frequency. By this method the control system of the bat can be analyzed during normal operation of the system without affecting the integrity of the feedback loop itself. Simulated Doppler shifts differ somewhat in the frequency-shifts during the FM-component of the sound from natural Doppler shifts. As removal of the frequency modulated component in the echo did not affect the performance of the Doppler compensation system (Schuller, in preparation) it may be concluded that the bat needs only the information coded in the "cf-part" of the sound for Doppler shift compensation. Frequency changes during the "cf-part" of the sounds were not bigger when the bat was compensating for Doppler shifts than in situations without Doppler shifts. Preliminary experiments in which a frequency-shift was introduced during one sound showed that no response to the frequency-shift occurred within this sound. Therefore, compensation for the frequency-shift is always done in sounds following the introduction of the frequency-shift. The emission of standardized narrow band frequency patterns in the sound fits the neurophysiological specialization of a very narrow sensitivity peak of the auditory system just at about the resting frequency (Neuweiler, 1970). The compensation for frequency-shifts offers the great advantage that the echoes are kept in the frequency range where the auditory system is best specialized for this task. In this way small frequency and intensity modulations can be detected in the "cf-portion" without interfering with the Doppler shift compensation system. As negative frequency-shifts are not compensated for, the compensation system of the bat seems to be adapted to follow only decreasing relative distance or closing target range, i.e. the most important situation when the bat is hunting its prey. The asymmetry of the compensation system can be explained by different models; one simple hypothesis based on beat note detection will be discussed here: Suga (1975) showed that beats produced by overlapping sounds of different frequencies (up to 3 kHz difference) are coded in the neural activity at the 8th nerve of another cf-fm-bat, *Pteronotus parnellii*. Neurophysiological findings of Neuweiler (1970) and behavioural experiments of Long and Schnitzler (in preparation) showed that the hearing threshold of *Rhinolophus ferrumequinum* increases rapidly in the range of a few kHz below the resting frequency, whereas the corresponding increase in hearing threshold for frequencies higher than the resting frequency is less rapid. For a given signal this asymmetry could result in different effective intensities of the bat's sound depending on the frequency deviation from the resting frequency. When the bat is compensating for positive Doppler shifts, the strong outgoing sound would be heard in a region of low sensitivity but the weak echo would be received near the resting frequency with high effective intensity. Since overlap of the outgoing sound and the echo is necessary for compensation (Schuller, 1974), the beats

resulting from these two sounds with similar effective intensities would be strong. If the bat gets negative Doppler shifts the weak echoes fall in a frequency range of low sensitivity whereas the strong outgoing sound is received near the resting frequency, resulting in a very weak beat modulation. In order to decide whether the bat's compensation system uses this beat note information, it should be determined whether the neural activity in this bat follows the beat frequency and how this neural activity depends on the modulation index of the beats.

The different response times for increasing and decreasing Doppler shifts seen for rectangular modulations in Fig. 7 are also responsible for the two different phase response curves (Fig. 6): The response times to the beginning and termination of a positive Doppler shift of 1 kHz, given by Simmons (1974) coincide well with the values measured in this work. The measured phase lags for increasing frequency shifts are scattered between the theoretical curves of minimum phase lag calculated for pulse repetition rates of 4 and 7 Hz (Fig. 6). This scattering can be explained by the changing of the pulse repetition rate of the bat between these two repetition rates. The system seems to be able to follow increasing Doppler shifts with an optimum speed only determined by the sound repetition rate. The phase lags for decreasing frequency shifts are, on the other hand, significantly higher than the theoretical curve and therefore the system is less adapted to follow decreasing Doppler shifts. Since the response for increasing Doppler shifts is faster than that for decreasing shifts the mean value of the compensation shift increases with increasing modulation frequency (Fig. 3). Such a DC-shift is found in systems with time constants dependent on the sign of the input signal. As additional nonlinearity the cutoff frequencies of the amplitude response curves (Table 1) depend on the amplitude of the input Doppler shift, unlike the response of a linear system in which the cutoff frequency is independent of the amplitude of the input variable.

The compensation steps from one sound to the next were always smaller than the frequency shift introduced in the echo. Thus overcompensation did not occur and no modulation waveform was found that produced an unstable behaviour of the compensation system. The system appears to be well-damped. The quantitative properties of this compensation system and possible models will be treated in a separate paper (Beuter, in preparation). The question at which stage of the information processing system these nonlinearities are located must be decided by a physiological approach. The maximum speed of compensation for increasing frequency shifts of up to 1.4 kHz per interpulse interval corresponds to 7–10 Hz/msec frequency change. Evoked potential measurements in the inferior colliculus (Schuller, 1972) and threshold measurements by behavioural experiments (Flieger, in preparation) yielded minimum frequency modulations of about 4–6 Hz/msec detectable within one sound. In the natural situation fast Doppler shift changes generally produce small frequency shifts, which can be detected without compensation during one sound. Doppler shift changes caused by lesser accelerations as in flight movements often yield high frequency shifts. These are properly compensated for in order to keep the echo frequency near the reference frequency. The control system for compensation of frequency shifts cancels therefore large frequency shifts and keeps the echoes in the most sensitive fre-

quency range, where the fast frequency modulations within one echo can be processed in an optimum way.

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