

## Control of Doppler Shift Compensation in the Greater Horseshoe Bat, *Rhinolophus ferrumequinum*

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*Summary.* Flying *Rhinolophus ferrumequinum* lower the frequency of the constant frequency part ( $f_A$ ) of the emitted sounds in order to compensate for Doppler shifts caused by the flight speed. The echo frequency ( $f_E$ ) is kept constant within a frequency band of about 200 Hz, the center frequency of which is about 150 Hz above the average or resting frequency ( $f_R$ ) emitted by roosting bats shortly before take off. For the compensation they use a feedback control system in which the emission frequency is changed to hold the echo frequency at a criterion value. This feedback system was demonstrated by experiments with bats flying in an experimental wind tunnel and in a He-O<sub>2</sub>-mixture. In the wind tunnel *Rhinolophus* lowers the emission frequency in order to compensate for Doppler shifts which are caused by the ground speed flown by the bat. In the He-O<sub>2</sub>-mixture *Rhinolophus* compensates for Doppler shifts which correspond to the different sound speeds in the gas mixture.

### Introduction

*Rhinolophus ferrumequinum* emits orientation sounds consisting mainly of a long portion of constant frequency (the cf-part) followed by a short terminal frequency-modulated part (the fm-part) in which the frequency drops by about 13–16 KHz. The duration of the sounds depends upon the orientation situation. In free flight it is 50–65 msec and in the terminal phase near an obstacle or an insect it is shortened to a minimal 10 msec (Novick, 1958; Griffin, 1962; A. Pye, 1966; Schnitzler, 1967, 1968; Airapetianz and Konstantinov, 1967; Konstantinov and Sokolov-1969). In roosting bats, the frequency of the cf-part measured in the middle of the orientation sound varies as much as  $\pm 100$  Hz around the average or resting frequency ( $f_R$ ). The resting frequencies of 24 bats were between 81.0–84.2 KHz with a majority between 82.4–83.3 kHz. Previous experiments showed that flying *Rhinolophus* lower the emission frequency ( $f_A$ ), that is the frequency of the cf-part of the emitted sound, in order to compensate for Doppler shifts caused by the flight speed (Schnitzler, 1968). At ordinary flight speeds toward stationary targets the frequency difference or frequency decrease between the resting frequency and the emission frequency ( $f_R - f_A$ ) averages about 150 Hz less than the frequency difference or Doppler increase between emission frequency and

echo frequency ( $f_E - f_A$ ). The echo frequency is, therefore, kept constant on the average at about 150 Hz above the resting frequency measured shortly before take off.

The two most probable systems to explain how the bats are able to maintain a constant echo frequency are:

1. The bats compare in a control system the echo frequency with a criterion value frequency which is about 150 Hz above the resting frequency. If there is a difference between these frequencies the emission frequency is changed until the echo frequency is equal to the criterion value frequency. This system works with feedback and will be called a feedback control system.

2. The bats measure their air speed directly—perhaps with mechanoreceptors at the bases of the facial hairs—and use this information to choose the appropriate emission frequency. As this system works without feedback it will be called a control system without feedback.

The following experiments show which of these two systems is used by the bats.

### I. Echolocation in a Wind Tunnel

The air speed ( $v_A$ ) of a bat flying against a headwind ( $v_W$ ) differs from the ground speed ( $v_G$ ) as  $v_A = v_G + v_W$ . If a bat flying against a headwind echolocates a non-moving object the Doppler increase between  $f_A$  and  $f_E$  depends upon the ground speed  $v_G$ . In a feedback control system, the frequency decrease of the difference between the resting frequency and the emission frequency of the flying bat should, therefore, be dependent upon the Doppler increase caused by  $v_G$  whereas in a control system without feedback it should depend upon the air speed  $v_A$ . To solve this problem the frequency decreases of a bat flying against headwinds of different strengths were measured in an experimental wind tunnel.

#### *Methods*

*Wind Tunnel.* The experiments were made in an experimental wind tunnel developed by Griffin and Brown (Fig. 1). The tunnel consisted of 2 chambers (C1 and C2; 190 cm high, 190 cm wide and 60 cm long) connected by 190 cm long tapering sections (TS1 and TS2) with the working section (WS). The working section was 240 cm long, 90 cm wide and 60 cm high. The air was drawn successively through a first net N1, C1, TS1, WS, TS2, C2, a second net N2, and another tapering section TS3 into a blower (B) operated by a DC motor. By changing the DC voltage with an AC variable transformer plus rectifier the wind speed in the working section could be varied continuously from 0–18 m/sec. Measurements of the wind speed with an anemometer at different places in the working section did not vary more than 3% from measurements in the middle of the working section. The air flow was somewhat turbulent but the bats flew normally as far as could be judged by direct observation.

*Training.* One *Rhinolophus* was first trained to fly in still air from C2 to C1 or from C1 to C2 and to land at the nets N1 and N2. It began a flight after being

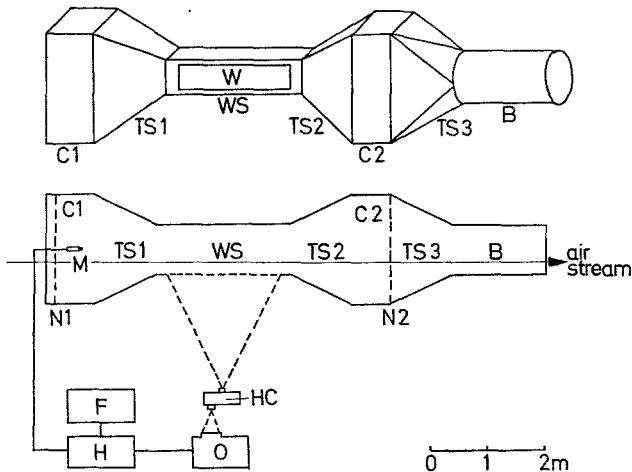


Fig. 1. Diagram of the wind tunnel and horizontal section. For further explanations see Methods

touched by a long wire. In the experiments this bat flew several times at each wind speed, with headwind from C2 to C1 and with tailwind from C1 to C2.

*Filming the Flights and Recording the Orientation Sounds.* A 2 m long window (*W*) at the front side of the working section made possible the filming of every flight with the first lens of a 16 mm Hycam Model K2001R high speed motion picture camera (*HC*) at 100 frames/sec. The orientation sounds emitted during flight were detected by the microphone (*M*) of a Holgate ultrasonic detector and, after being heterodyned (*H*) with a frequency of about 84 KHz (*F*), they were displayed on a 502 A Tektronix oscilloscope (*O*). The heterodyned sound were photographed without a shutter on continuously moving film by a second lens of the Hycam camera. The ground speed  $v_G$  and the frequency of the cf-parts of the sounds detected by the microphone ( $f_M$ ) could be determined by analyzing the 16 mm films.

*Doppler Shifts in the Wind Tunnel.* Before each experiment the windspeed  $v_W$  was measured in the working section. With  $v_W$ , the microphone frequency  $f_M$  and the ground speed  $v_G$  the emission frequency  $f_A$  and the echo frequency  $f_E$  had to be calculated for the following situation.

*Rhinolophus* flew in the working section with the ground speed  $v_G$  in a headwind  $v_W$  and emitted sounds with cf-parts of the emission frequency  $f_A$ . These sounds were propagated with the sound speed  $c$ . After the working section the sounds passed through areas of lower wind speed (TS1 and C1) and finally arrived at the microphone *M*. Under these conditions the Doppler shift contained in the microphone frequency is mainly caused by the ground speed  $v_G$  of the bat during sound emission. A slight additional frequency shift caused by the windspeed in the working section is for  $v_W \ll c$  below the accuracy of measurement for  $f_M$  and was, therefore, not considered at the following calculation of  $f_A$ .

$$f_A = f_M \frac{c - v_G}{c}.$$

In calculating the echo frequency, it was assumed that the slight frequency changes caused by the windspeed in the sounds traveling from the bat to the located end of the wind tunnel are inverse to those in the returning echoes. Therefore in calculating the echo frequency only the ground speed has to be considered. One Doppler shift originates at the emission of the sounds (moving source) and a second at the detection of the echoes (moving receiver). The echo frequency is therefore:

$$f_E = f_A \frac{c + v_G}{c - v_G}.$$

If  $v_G$  is small in comparison to the sound speed  $c$  the underlined terms are very small and can be neglected:

$$\begin{aligned} f_E &= f_A \frac{1 + \frac{v}{c}}{1 - \frac{v}{c}} = f_A \left(1 + \frac{v}{c}\right) \left(1 - \frac{v}{c}\right)^{-1} \\ &= f_A \left(1 + \frac{v}{c}\right) \left(1 + \frac{v}{c} + \frac{v^2}{c^2} + \frac{v^3}{c^3} + \dots\right) \\ &= f_A \left(1 + \frac{v}{c}\right) \left(1 + \frac{v}{c}\right) = f_A \left(1 + \frac{2v}{c} + \frac{v^2}{c^2}\right) \\ &= f_A \left(1 + \frac{2v}{c}\right) = f_A + f_A \frac{2v}{c}. \end{aligned}$$

The Doppler increase is therefore:

$$f_E - f_A = f_A \frac{2v_G}{c}.$$

At a  $v_G = 4$  m/sec the Doppler increase calculated with the simplified equation is 22 Hz lower than with the exact equation. The accuracy of measurement for  $v_G$  and  $f_M$  allowed the calculation of  $f_E$  and  $f_A$  with an accuracy up to about 100 Hz. The amounts of the frequency decreases ( $f_R - f_A$ ) may be influenced by the fact that the resting frequency was measured for only a few sounds before take off. Further experiments must show whether  $f_R$  measured in this way differs from an  $f_R$  measured over a longer time with roosting bats.

### Results

For these experiments it was important to know how *Rhinolophus* changed  $v_A$  and  $v_G$  at different wind speeds. The results (Fig. 2) are similar to results with *Myotis lucifugus* (Schnitzler, 1971). With no wind, *Rhinolophus* flew in the wind tunnel with airspeeds between 4.3–4.9 m/sec (average 4.6 m/sec). With increasing headwinds it increased  $v_A$  and lowered  $v_G$ . At  $v_W = 7.8$  m/sec,  $v_A$  was 8.3 m/sec and  $v_G$  was 0.5 m/sec. At higher wind speeds, the bat would not fly. With rising tailwinds,  $v_A$  was lowered and  $v_G$  increased. At  $v_W = -4.65$  m/sec, the bat flew with  $v_A = 1.2$  m/sec and  $v_G = 5.85$  m/sec.

The ground speed  $v_G$  during emission of the sounds and detection of the echoes, the emission frequency  $f_A$  and the echo frequency  $f_E$  could be calculated for every flight in the working section after analyzing the

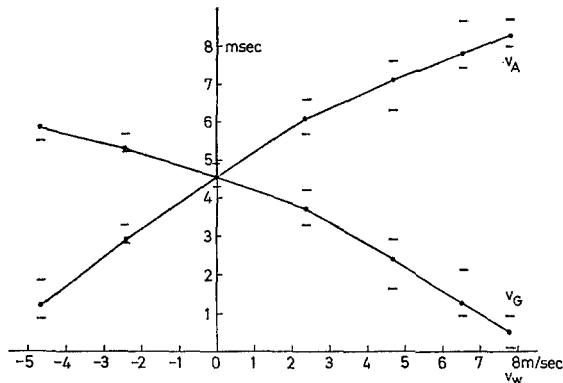


Fig. 2. Average air speed  $v_A$  and average ground speed  $v_G$  of a *Rhinolophus* at different wind speeds  $v_W$ . Range of speeds is marked by horizontal lines below and above the average

16 mm films. The resting frequency  $f_R$  was measured shortly before every flight. It was, therefore, possible to compare the *Doppler increase* ( $f_E - f_A$ ) and the *frequency decrease* by the bat ( $f_R - f_A$ ) at different ground speeds (Fig. 3). Without wind, results similar to those of earlier experiments were obtained (Schnitzler, 1968). The frequency decreases of the measured sounds were about 50–250 Hz less than the corresponding Doppler increases for these flight speeds. That means, that the echo frequency is kept within a frequency band about 200 Hz wide, the center frequency of which is about 150 Hz above the resting frequency. With a  $v_G = 4.5$  m/sec, the frequency decrease is about 2000–2100 Hz.

With headwinds,  $v_G$  is lowered as shown in Fig. 2. At these values of  $v_G$  the measured frequency decreases were also as much as 250 Hz lower than the corresponding Doppler increases. The echo frequencies are, therefore, kept within the same frequency band as in still air. The results in Fig. 3 show for every value of  $v_G$  a clear relation between the frequency decrease and the corresponding Doppler increase. This means that a feedback control system must exist.

The measured frequency decreases were not related with  $v_A$ , as a control system without feedback would demand. This can be demonstrated by the following example: At  $v_G = 1$  m/sec the  $v_A$  was 7 m/sec (from Fig. 2). In a control system without feedback the bat would have to lower  $f_A$  by about 3400 Hz. The frequency decrease, however, was only 400 Hz.

Experiments with tailwinds were also made. In this situation turbulences at the membrane of the microphone made it difficult to get good records of the orientation sounds. The few results, however, indicate that

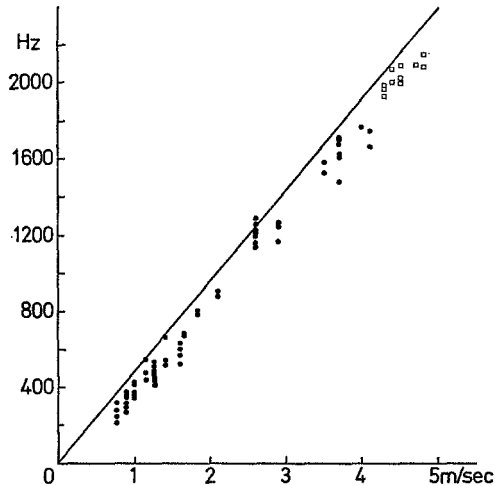


Fig. 3. Comparison of Doppler increases  $f_E - f_A$  (solid line) and frequency decreases  $f_R - f_A$  in still air (squares) and in headwinds (dots) at different ground speeds  $v_G$

the frequency decrease corresponded approximately to the Doppler increase caused by  $v_G$ .

## II. Echolocation in a Helium-Oxygen-Mixture

In a mixture of 20% Oxygen and 80% Helium the speed of sound  $c$  is higher than in air and the Doppler increase is lower, given that  $f_E - f_A = f_A \cdot 2v_G/c$ . If *Rhinolophus* uses a feedback control system to keep the echo frequency constant, its frequency decrease should depend upon the Doppler increase in the He-O<sub>2</sub>-mixture, whereas in a control system without feedback, the frequency should be lowered according to the measured air speed  $v_A$ . In order to determine which of the two systems is used by *Rhinolophus*, the frequency decrease of a bat flying in a He-O<sub>2</sub>-mixture was measured.

### Methods

The experimental chamber (240 cm long, 60 cm wide, 120 cm high) consisted of a collapsible wooden frame covered by a transparent plastic tubing (seamless beer barrel lining). At both ends of the chamber there were nets where the bat could land and at one end the microphone of a Holgate ultrasonic detector. The filming of the flights, the recording of the orientation sounds and the analysis of the 16 mm films were the same as in the experiments with the wind tunnel. Before filling the experimental chamber with a mixture of 20% O<sub>2</sub> and 80% He the collapsible wooden frame was folded up and most of the air was drawn out with a vacuum cleaner. Afterwards, the tubing was inflated with the gas mixture and the wooden frame was opened again. It was not possible to keep the chamber gas tight. Therefore, it was

necessary to measure the speed of sound during the experiments by measuring the time between sound emission from a loudspeaker at one end, and the arrival of sounds at a microphone situated at the opposite end of the chamber. The highest sound speed measured was 550 m/sec. Due to loss of Helium this decreased to 500 m/sec within about 60 minutes.

### *Results*

The high sound speed in the He-O<sub>2</sub>-mixture not only changed the Doppler increases, but also affected the sound production and lowered the time lapse between sound emission and echo detection.

In air, the main intensity of the cf-part is in the second harmonic at about 83 KHz, whereas the first and the third harmonic are of low intensity. In a mixture of 20% O<sub>2</sub> and 80% He, the frequency of the second harmonic is the same as in air, but its intensity is lowered to such an extent that it can no longer be recorded within the dynamic range of a Kay Sonagraph. The first and the third harmonic, however, are now accentuated. This change suggests that the laryngeal membranes of the bat vibrate with the frequency of the first harmonic. In air, cavity resonances in the respiratory tract accentuate the second harmonic and suppress the first and higher harmonics. In He-O<sub>2</sub>-mixture the sound speed and, consequently, the cavity resonances are different. Therefore the second harmonic is filtered out and other harmonics can pass through. This is consistent with Pye's (1967) hypothesis that the waveform produced within the larynx contains several harmonics and that the respiratory tract acts as an acoustical filter. The intensity of the cf-part at the second harmonic was still high enough to allow the orientation sounds to be analyzed after heterodyning them with a frequency of about 84 KHz.

Assuming that the bats measure distances by using the time lapse between sound emission and echo detection, the shorter time lapse in He-O<sub>2</sub>-mixture (due to the higher sound speed) should affect the orientation behavior of R.F. Indeed, the bat would not fly spontaneously when it was released in the experimental chamber. After poking it, the first 5-10 flights were hesitant, the bat flew often against the plastic wall and it had great difficulties in landing. The sound pattern was also different. The bat produced mostly groups of 3-4 sounds per wing beat and, at landing, no final group (buzz) was emitted. Afterwards the sound pattern became normal, a final group of pulses was emitted at landing, and the bats had learned to fly and to land at the net. From these experiments it cannot be judged whether or not the bats regained the same echolocation abilities as in air. Further experiments, e.g. obstacle avoidance tests in a He-O<sub>2</sub>-mixture should be made in order to solve this problem.

As the bat learned to fly in the gas mixture its *frequency decrease* ( $f_R - f_A$ ) could be measured and compared with the *Doppler increase*

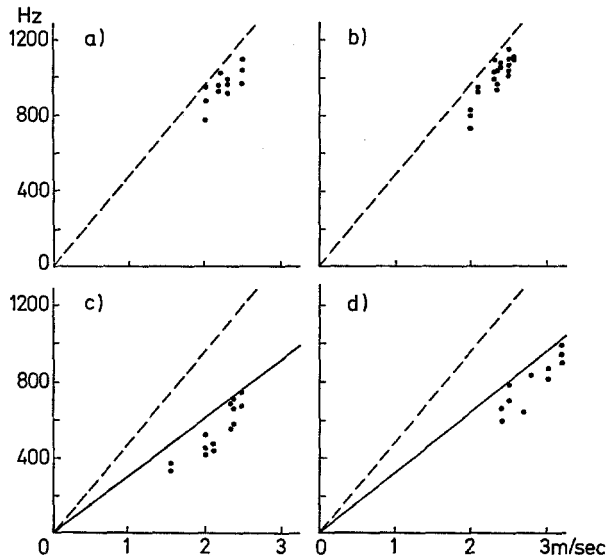


Fig. 4a-d. Comparison of the Doppler increases in air (dashed line) or in He-O<sub>2</sub>-mixture (solid line) and the frequency decreases (dots) of a bat flying in air (4a and 4b) or in He-O<sub>2</sub>-mixture (4c and 4d) at different ground speeds  $v_G$ . The speed of sound was 535 m/sec in 4c and 510 m/sec in 4d

( $f_E - f_A$ ) at different values of  $v_G$  (Fig. 4.) The frequency decrease was measured only for the sounds emitted during flight in the central part of the flight chamber. Control measurements were made with a bat flying in an air-filled chamber (Fig. 4a and 4b). The results confirmed earlier findings. The frequency decreases were about 50–250 Hz less than the corresponding Doppler increases. Fig. 4c and 4d show a comparison between frequency decreases and Doppler increases at sound speeds of 535 m/sec (4c) and 510 m/sec (4d). In He-O<sub>2</sub>-mixture the Doppler increase (solid line) is lower than in air (dashed line). The measured frequency decreases by the bat are also about 50–250 less than the Doppler increases in He-O<sub>2</sub>-mixture. The echo frequencies are, therefore, kept within a frequency band of about 200 Hz the center frequency of which is approximately 150 Hz above the resting frequency. This result also confirms the conclusion from experiment I that a feedback control system must be used by *Rhinolophus*.

### Discussion

These experiments show that *Rhinolophus* compensates for Doppler shifts which correspond to  $v_G$  in flights in the wind tunnel and to the different sound speed in flights in the He-O<sub>2</sub>-mixture. This proves that



RF must use a feedback control system, in which the frequency of the cf-part of the returning echo is compared with the criterion frequency of the system. If there is a difference between the two frequencies the emission frequency is changed until the echo frequency is kept within a frequency band approximately 200 Hz wide the center of which is about 150 Hz above the resting frequency emitted shortly before take off.

In these experiments the bat echolocated stationary objects and the Doppler shifts were caused only by its ground speed. When *Rhinolophus* locates moving objects, additional Doppler shifts come about. Up to now it has not been possible to test in an experiment whether these additional Doppler shifts are also compensated. Additional support for a feedback control system was provided by an earlier experiment (Schnitzler, 1968), where a resting bat tried to compensate for Doppler shifts created by a swinging pendulum. The feedback control is complicated by the fact that the system works with pulses. The comparison between echo frequency and criterion frequency is only possible during detection of an echo.

What are the physiological capacities demanded by such a feedback control system ?

*Rhinolophus* needs fine frequency discrimination in the range of the criterion frequency in order to ascertain deviations of the echo frequency from the criterion frequency. Differences between the two frequencies must be transposed into commands to the vocalisation apparatus. Neurophysiological studies made by Neuweiler (1970), Neuweiler, Schuller and Schnitzler (1971), with *Rhinolophus ferrumequinum* and Schnitzler, Neuweiler and Schuller (1971) with *Rhinolophus euryale* showed that the auditory threshold for on-responses of evoked potentials in the inferior colliculus has a minimum at about the resting frequency of the cf-part and rises steeply at the frequencies below and above. A maximum of threshold can be recorded at about 2 KHz below this minimum. Therefore, at first we assumed that by the Doppler shift compensation the echo frequency is kept at the frequency where the on-response threshold curve has its minimum. New measurements of evoked potentials in the inferior colliculus of awake bats (Schnitzler, 1972) showed, however, that at about 0.5 KHz below the on-minimum the off-response threshold curve has an even sharper minimum and that, after preliminary measurements with two bats, the echo frequency is most probably kept at that frequency where the off-response threshold curve has its minimum. The lowest point of the off-threshold is at a position where the on-threshold curve has the steepest slope towards lower frequencies and it has about the same value as the on-threshold at this position. The extremely narrowly tuned area of low off-threshold suggests that there must be narrowly tuned neurones which make possible the fine frequency discrimination necessary for the feedback control system.

It is not yet known how *Rhinolophus* compares the echo frequency with the criterion value frequency and how differences between the two are transposed into commands to the vocalisation apparatus. Another problem is how the bats manage to control the emission frequency of about 83 KHz within about  $\pm 100$  Hz (1.2<sup>0</sup>/<sub>100</sub>).

What are the advantages gained by RF by using a long cf-part in the orientation sounds and by compensating for Doppler shifts ?

### 1. Measurement of the Relative Speed between Bat and Echolocated Object

The orientation sounds of RF are so long in all orientation situations that there is always an overlap between the outgoing sound and the echoes which return from the echolocated objects. The differences between the frequencies of the cf-part of the echo and the cf-part of the emitted sound can be used as a measure for the relative speed between bat and located object. The compensation for Doppler shifts simplifies the measuring of this difference in frequency. In flying bats, the frequency of the cf-parts of the emitted sounds is within a frequency range where the on-threshold is high (e.g. at about 81 KHz at a speed of 4/msec) whereas the echo frequency is kept at the off-minimum and, therefore, within a frequency range of lower on-threshold. The danger of masking between the emitted sounds and the weak returning echoes is therefore reduced.

### 2. Facilitated Detection of New Objects Moving towards the Bat

An object, e.g. an insect, which moves towards a bat causes additional Doppler shifts. The echo frequency of the echoes from such an object is, therefore, higher than the echo frequency of echoes from non-moving objects. If, as we assume after some preliminary experiments, the echo frequency is kept at the frequency of the off-minimum the higher echo frequencies of echoes from objects moving towards the bat fall in the frequency area of lowest on-threshold. The first detection of such objects is, therefore, facilitated.

That *Rhinolophus* reacts strongly to movements towards it is confirmed by the observation that even small movements towards a roosting bat cause a frightened reaction whereas even strong movements away from it don't disturb the bat.

### 3. Discrimination between Echoes from Moving and Non-Moving Objects

If after the first detection the frequency of the echoes from an echolocated object moving toward a bat is kept constant by the feedback control system (which is for a moving object not yet proved but highly

probable) the echo frequency of adjacent stationary objects are lower and fall in an area of high on-threshold. Therefore, they cannot mask the echoes from the moving object, which are in an area of lower on-threshold. This would be an ecological advantage for *Rhinolophus* if, as Brosset (1963, 1966) reports, it hunts in areas which are full of obstacles, e.g. under trees and bushes.

#### 4. Analysis of Frequency and Amplitude Modulations Caused by the Located Object in the cf-Part of the Echoes

Schuller (1972) showed that at the frequency band of lowest off-threshold frequency-modulated sweeps within cf-tones evoked responses in the inferior colliculus down to sweeps of 6 Hz/msec. It has been calculated that such modulations in the cf-part of the echoes could be caused by the wing movements of flying insects. The wing movements also cause amplitude modulations in the echoes (Roeder, 1963). In preliminary experiments we recorded evoked potentials to 60 msec long sinusoidal amplitude changes of about 0.6 db.

A long cf-part makes it possible to collect this kind of information which may be used for prey recognition. As the feedback control system keeps the echo frequency constant, the system for analyzing frequency and amplitude modulations is needed only in the small frequency area of low threshold. Schuller's results show that for frequency modulation this is the case. The highest sensitivity for fm-sweeps is restricted to the area of the off-minimum.

#### 5. Improved Directionality of Echo Detection

The amount of Doppler increase depends upon the cosine of the angle between the forward direction and the direction of the returning echo. The echo frequencies from greater angles are, therefore, lower and fall in a frequency area of high on-threshold. This means that the detection of echoes from a forward direction is favored.

#### 6. Determination of Target Direction

The angular dependence of the echo frequency also gives some information on the target direction. The lower the echo frequency is, the greater is the angle between target and forward direction. More information may be gained by measuring the intensity difference between the long cf-parts of the echoes received by both ears. As the ears are moved during echo reception (Schneider and Möhres, 1960; Griffin, Dunning, Cahlander and Webster, 1962; Pye, Flinn and Pye, 1962;

Webster, 1967) and the directionality of the ears is, therefore, changed (Neuweiler, 1970) a continuously changing intensity difference results at the binaural comparison. Grinnell and Grinnell (1965) showed evidence for the hypothesis that bats with frequency-modulated orientation sounds can locate a target in space by the binaural comparison of intensities at many different frequencies with the same ear position. *Rhinolophus* and other bats with cf-parts in the orientation sounds make a binaural intensity comparison at one frequency but with continuously changing ear positions. If they have proprioceptive information on the positions of the ears the pattern of the continuously changing intensity differences would define a unique angle in space (Schnitzler, 1972).

That *Rhinolophus* uses the binaural comparison of echo intensities for the localization of targets show the results of Flieger and Schnitzler (1972). They found that by slightly plugging one ear (attenuation of 15–25 db) the number of free flights through a wire obstacle diminished whereas by slightly plugging both ears the location ability was nearly as good as with unplugged ears. If one ear was tightly plugged (about 60 db attenuation) the bat was unable to locate the obstacle.

The long cf-parts seem to have no meaning for the measuring of distances. Probably *Rhinolophus* determines distances by measuring the time lapse between the frequency-modulated terminal part of the emitted orientation sound and the fm-part in the returning echo (Schnitzler, 1972).

It is possible that a similar feedback system also exists in the bat *Chilonycteris rubiginosa*, for these bats when flying also compensate for Doppler shifts caused by the ground speed (Schnitzler, 1970) and show similar on- and off-threshold curves as *Rhinolophus* (Grinnell, 1967, 1970).

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