

Movement as a specific stimulus for prey catching behaviour in rhinolophid and hipposiderid bats

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Summary. 1. The echolocating 'long CF/FM-bat' *Rhinolophus rouxi* and the 'short CF/FM-bats' *Hipposideros bicolor* and *Hipposideros speoris* were tested for catching responses to moving and non-moving targets.

2. Under our experimental conditions (freshly caught caged bats in a natural environment) *Rhinolophus rouxi* and *Hipposideros speoris* only responded to insects of any sort that were beating their wings. The bats showed no reactions whatsoever to nonmoving insects or those walking on the floor or the sides of the cage.

3. *Hipposideros bicolor* responded in the same way as the above species to wingbeating insects but in addition also attacked walking insects. In 27 presentations 15 walking insects were caught (Fig. 2).

4. *Rhinolophus rouxi*, *Hipposideros speoris* and *Hipposideros bicolor* also detected, approached and seized tethered cockroaches hanging from the ceiling when these were vibrating up and down (Fig. 3). This indicates that any oscillating movement and not specific aspects of wing beating were the key releasers for catching behaviour in all three species. However, a wing beating insect is strongly preferred over a vibrating one in all three species (Fig. 4).

5. *Rhinolophus rouxi*, *Hipposideros speoris* and *Hipposideros bicolor* attacked and seized a dead bait when it was associated with a wing beating device (Fig. 1). All three species responded effectively to beat frequencies as low as 10 beats/s (peak-to-peak amplitude of the wing excursion 20 mm). For lower frequencies the response rates rapidly deteriorated (Fig. 5).

Abbreviations: CF constant frequency; FM frequency modulated

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6. Horseshoe bats no longer responded to wing beats of 5 beats/s when the wing beat amplitude was 2 to 1 mm or to wing beats of 2 to 1 beats/s when the amplitude was 3 mm or lower (Fig. 6). This suggests that the speed of the wing is a critical parameter. From these data we infer that the threshold for the catching responses is at a wing speed of about 2 to 1 cm/s.

7. In horseshoe bats (experimental tests) and the two hipposiderid species (behavioural observations) one single wing beat was enough to elicit a catching response (Fig. 8).

8. It is concluded that 'long' and 'short' CF/FM-bats feature a similar responsiveness to fluttering targets. The sensitivity to oscillating movements is considered as an effective detection mechanism for any sort of potential prey.

Introduction

Rhinolophid and hipposiderid bats are closely related families which not only share common morphological traits such as nose leaves, but also emit a type of echolocation signal different from that of other bat families. All species of the two families so far studied emit a composite sound consisting of a pure tone (CF) terminated by a brief frequency downward modulated sweep (FM; for reviews see Pye 1980; Neuweiler 1983). However, there is a marked difference in the duration of the echolocation sounds between the two families: in hipposiderid species the pure tone component never lasts longer than 5 to 10 ms (Grinnell and Hagiwara 1972; Schuller 1980) whereas in rhinolophid species the pure tone components last about 50 ms and are never briefer than 10 ms (Schnitzler 1968; Schuller 1980; Neuweiler et al., submitted).

Rhinolophid (Neuweiler 1970; Schuller 1980; Jen and Suthers 1982; Taniguchi 1985) as well as hipposiderid species (Grinnell and Hagiwara 1972; Schuller 1980; Neuweiler et al. 1984) feature extremely narrow auditory filters tuned to the species-specific frequencies of the CF-components. Both rhinolophid and hipposiderid species compensate for Doppler shifts of the complete echo signals caused by the bat's own flight speed in such a way that the heard CF-echo frequency matches the center frequency of the auditory filter whereas the emitted ones are shifted to lower frequencies (Schnitzler 1968; Gustafson and Schnitzler 1979; Trappe and Schnitzler 1982). Behavioural studies have shown that *Hipposideros bicolor* and *H. speoris* performed less perfect and less consistently than rhinolophids in this so-called 'Doppler shift compensation' (Habersetzer et al. 1984).

From neurophysiological (Schuller 1972; Neuweiler et al. 1980; Ostwald 1984; Schuller 1984) and behavioural studies (Goldman and Henson 1977; Schnitzler and Flieger 1983; Vogler and Neuweiler 1983) it was inferred that echolocation with such a pure tone system is an adaptation to the detection of fluttering targets since the wingbeats of insects are imprinted in the pure tone echo as repetitive frequency and amplitude modulations which are distinctly coded by auditory neurons (Schuller 1984). It is even conceivable that these rhythmic wingbeat echoes may be used for differentiation of the insect prey by its wingbeat frequencies (Goldman and Henson 1977; Schnitzler et al. 1983).

For differentiation of these frequencies a bat should encode at least two wingbeats in one echo or else integrate information from echo sequences over time. So far there is no evidence for such a temporal integration. In any case, a long lasting tone is better adapted for coding wingbeat sequences of insects than brief ones. Since hipposiderid bats only emit brief CF-components the question arises whether they detect fluttering targets less well than the horseshoe bats.

From free field observations (Habersetzer 1982) we had the impression that not only rhinolophid but also hipposiderid bats were specifically alerted by insect wing movements of any speed. Bell and Fenton (1984) reported that *Hipposideros ruber* attacked fluttering targets but not stationary ones. We assume that in rhinolophids and hipposiderids the sensitivity of the long and brief CF-component to moving prey mainly alerts the bat to any moving target irrespective of wingbeat frequency. We therefore initiated comparative experiments to test the attacking responses of *Rhinolo-*

phus rouxi, *Hipposideros speoris* and *Hipposideros bicolor* to natural prey specimens and fluttering target dummies. Since these bats rapidly accommodate to captive conditions and then no longer show the full range of their responsiveness we conducted experiments with naive bats kept in cages in the field.

Material and methods

The experiments on *Hipposideros speoris* and *Hipposideros bicolor* were carried out in Madurai from February 1st to May 30th 1984 and those on *Rhinolophus rouxi* in Sri Lanka from 1st to October 30th, 1984. The bats were captured from the caves and individually kept in net-covered cages (65 × 65 × 130 cm for *Rhinolophus rouxi*, 40 × 40 × 80 cm for *Hipposideros bicolor* and 80 × 80 × 80 cm for *Hipposideros speoris*). In Madurai the bats were kept in an outdoor cage which provided dark shelters. In this cage also the experiments were done. In Sri Lanka the horseshoe bats were maintained in a dark room at 29 °C and about 90% relative humidity during daytime. At night the caged bats were brought in a garden where the experiments were performed within the activity period of the bats from 20.00 to 24.00 h under natural environmental conditions, except for a dim light used for observation. Control experiments in complete darkness, where observations were made with an infrared night vision device, showed that the dim light did not influence the behaviour of the bats.

In preliminary studies we had noticed that within two weeks all three species became accustomed to the experimental situation and had learned to accept any kind of suitable food offered by the experimenter. To avoid such an influence on the catching behaviour of the bats, we used freshly caught bats. We used four specimens of each species for each experiment, and replaced them by a new group of four bats after at most 10 days.

For testing the catching response of the bats cockroaches were used which could be easily induced to beat their wings. The bait was tethered on a string within the cage. As a positive catching response we counted all flights towards the bait at which the prey was seized or touched by the bat. If the bat did not react in this way within 15 min it was considered as a negative test. Apart from the number of responses under various experimental situations described below, the latency of the response was also recorded, i.e. the time elapsed from introduction of the bait to touching of the bait by the bat.

For measuring the influence of wingbeat amplitudes and frequencies on the catching response of the bats two, identical custom-made wingbeat simulators were introduced. The membrane of a loudspeaker was replaced by a thin metal rod which was 32 cm long. A small mechanical device at the end of the rod transformed the vertical oscillations of the speaker into symmetrical up and down movements of two thin plastic membranes (9 × 23 mm) which served as artificial wings. A sound absorbing metal box covered the loudspeaker which effectively reduced the noise of the machine to a low level. The loudspeaker was driven by a Wavetec oscillator with amplifier. The simulator was checked for sinusoidal movements of the membranes. The device produced sinusoidal excursions for frequencies up to 200 Hz. For higher frequencies the movements were heavily distorted and therefore the working range was limited to frequencies below 200 Hz and wing tip excursions of up to 42 mm. The average speed of the artificial wings was calculated from the peak amplitude and frequencies of the sinusoidal movements. Tests were performed with the two simulators running

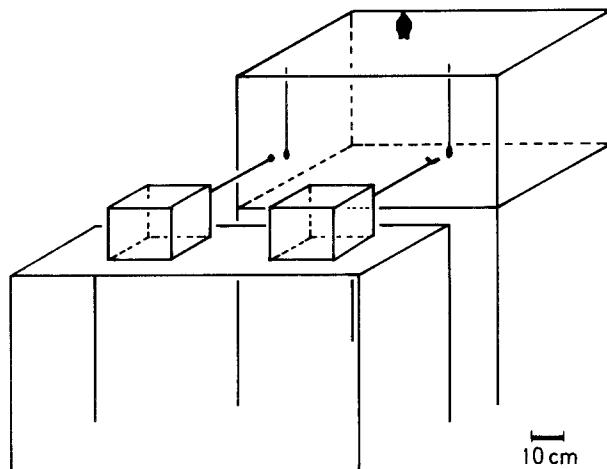


Fig. 1. Diagram of the experimental set up used in the fluttering target experiments. The bat responded by flying towards the beating one of the two wingbeating flutter simulators placed outside of the cage and was rewarded by a piece of cockroach tethered to the ceiling of the cage in front of the two fluttering target simulators

and presented simultaneously, however, one with wings attached and the other one with wings removed (Fig. 1). These tests showed that the bats only responded to the moving wings and not to the noise of the simulators. Since the bats frequently attacked and destroyed the beating artificial wings, we presented a tethered dead cockroach inside the cage and backed it by the wingbeat simulator placed outside of the cage-netting for protection. Details of the specific experimental set-ups are briefly described for each experiment in the 'Results' section.

Results

Reaction to natural prey

We first offered the bats insects caught at a light trap. These were various moths, beetles, grasshoppers, crickets and other insects (Table 1). As soon as certain insects placed into the cage started to fly or to flap their wings they were caught by the bats. The bats usually flew directly to the prey and did not circle around before seizing it. Small flying moths were frequently ignored or could not be captured. The body length of the accepted items ranged between 2 and 70 mm. Horseshoe bats and *Hipposideros speoris* mainly reacted to flying or wing flapping insects whereas *Hipposideros bicolor* also got alerted and caught insects jumping or running on the floor or the walls of the cages. All bats took no notice at all of any stationary insect.

Some of the insect species were avoided by the bats (Table 1). In this case the bats repeatedly hovered in front of the prey without touching it and then turned away or they caught the insect and dropped it immediately. Interestingly those moths and plant bugs that were most often avoided had

conspicuously red and orange colored bodies and wings, very hairy bodies or possessed defensive glands which secreted stinking fluids or sticky hairs.

The bats sometimes had problems with big sized prey, such as large mantis, grasshoppers or sphingid species. For instance a *Hipposideros speoris* attacked a wing flapping death's head hawk moth (Sphingidae). The bat briefly hovered over the prey and then descended and covered the prey by its wings. The moth reacted with strong body vibrations and emitted a loud audible sound. The bat released the moth but several times attacked again. Each time the moth escaped, even from the mouth of the bat, by frantic wing flappings. Even though the moth was hurt it finally crawled away and the bat gave up. A *Hipposideros bicolor* was confronted with a grasshopper (bodylength 48 mm) which jumped towards the bat with its strong thorny hindlegs. The bat responded to the insect with head and ear movements. However, when the grasshopper was only a few cm away the bat flew away. When we offered the same grasshopper a second time the bat hovered above the crawling insect, touched it shortly and then returned to its roost. The bat repeatedly approached the grasshopper but never attacked it. When we had removed the strong hindlegs of the grasshopper the bat again hovered over the insect and then finally caught it. In a second test with a similar grasshopper another *Hipposideros bicolor* behaved in the same way, however, the grasshopper without hindlegs was not caught. Horseshoe bats were more reluctant to chase flying insects in the cage. They most successfully caught beetles whereas moths smaller than about 2 cm body-length usually escaped because of their fast and erratic flights.

All these observations showed that movements of the insects were a powerful stimulus for releasing catching behaviour irrespective of the kind of prey offered and whether it was palatable or not. We therefore performed experiments to define more clearly which kind of movements are the most powerful releasers for catching responses. To avoid influences of the sort of bait offered all experiments were uniformly performed with cockroaches as baits.

1. Catching responses to non-moving and walking prey

In this experiment single wingless nymphs of cockroaches, about 2.5 cm long, were placed onto the floor of the cage for 15 min or until they were

Table 1. List of insects taken or rejected by the bats

Insects accepted	Insects rejected
Dragonflies (Anisoptera)	Damselflies
Grasshoppers (Acrididae)	Hydrophylid beetles
Crickets	Scarabid beetles
Cockroaches (<i>Periplaneta americana</i>)	<i>Helicopris bucephalus</i> (Scarabidae)
Praying mantis	<i>Halys dentatus</i> (Pentatomidae)
Dytiscid water beetles	<i>Nezara viridula</i> (Pentatomidae)
Various dung beetles	<i>Creatonotus gangis</i> (Arctiidae)
<i>Camponotus</i> spec. (black ant)	<i>Uteheisa pulchella</i> (Arctiidae)
<i>Dorylus labiatus</i> (ant)	<i>Pericallia ricini</i> (Arctiidae)
Belostomatid water bug (nymph)	<i>Hypsa ficus</i> (Hypsidae, Lepidoptera)
<i>Spodoptera litura</i> (Noctuidae)	<i>Argina cibraria</i> (Hypsidae)
<i>Plusia orchalsia</i> (Noctuidae)	
<i>Grammodes geometrica</i> (Noctuidae)	
<i>Heliothis armigera</i> (Noctuidae)	
<i>Melanitis leda ismene</i> (Satyridae)	
<i>Catopsilea crocata</i> (Pieridae)	
<i>Eupterote mollifera</i> (Euptroptidae)	
<i>Euploca core</i> (Nymphalidae)	
<i>Hippotion celerio</i> (Sphingidae)	
<i>Acherontia styx</i> (Sphingidae)	
<i>Amata</i> spec. (Lepidoptera)	

All species have been identified by the Department of Agriculture, Madurai Kamaraj University

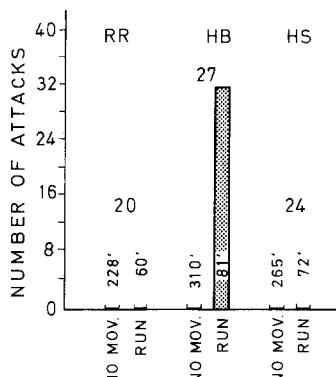


Fig. 2. Responsiveness of the bats to nonmoving (no mov) and moving (run) cockroaches placed on the floor of the cage. RR *Rhinolophus rouxi*, HB *Hipposideros bicolor*, HS *H. speoris*. Numbers above columns indicate number of trials. Figures with 'give total time in minutes during which the bat was exposed to the specific prey

caught by a bat. The total time a nymph stayed motionless and the total time it was walking in the cage were recorded. Only those tests during which a cockroach walked at least for a total time of 3 min within the 15 min test period or the nymph was caught before the end of the test time were counted.

None of the 14 bats of all three species ever showed the slightest reaction to the presence of a motionless insect positioned about 20–60 cm in front of the bat (Fig. 2). For nonmoving nymphs no catching responses occurred during a total ex-

posure time of 228 min in *Rhinolophus rouxi*, 310 min in *Hipposideros bicolor* and 265 min in *Hipposideros speoris*. When the nymphs walked along the floor or on the sides of the cages *Rhinolophus rouxi* and *Hipposideros speoris* again showed no response to the walking prey, even when it was close by (total exposure to walking cockroach nymphs 60 min in *Rhinolophus rouxi* and 72 min in *Hipposideros speoris*). However, in six presentations *Hipposideros speoris* circled over the walking nymph but never approached or attacked it.

Interestingly, the four *Hipposideros bicolor* behaved differently. Out of 51 cockroaches released into the cage 18 did not move at all within 15 min. These nonmoving insects did not release any reaction in *Hipposideros bicolor*. Of the other 33 cockroaches which started walking or running nine were caught by *H. bicolor* within 3 to 35 s by one attack, and another 15 cockroaches were caught after several attacks. As indicated by their fast alternating ear movements *H. bicolor* frequently followed the walking bait by echolocation and directing the head towards the prey. Now and then the bat flew off and landed closer to the cockroach. When this happened, the cockroach usually stopped moving. During these motionless periods the bats were apparently unable to detect the prey and kept searching for it by fast head and ear movements. As soon as the cockroach started running again the bats tried to catch it immediately. Only nine cockroaches ran so fast that they es-

caped within the 15 min test period. In only two tests *H. bicolor* did not take notice of a cockroach which walked rather slowly on the floor. However, as soon as this cockroach happened to move faster it was attacked by the bat. Thus, insects moving on the ground initiated an attack in *Hipposideros bicolor* but not by *H. speoris* and *Rhinolophus rouxi*.

2. Catching responses to vibrating baits

Since only *Hipposideros bicolor* but not *Hipposideros speoris* and *Rhinolophus rouxi* caught walking prey, we next asked if oscillating movements of the prey are better stimuli for releasing catching responses of these bats. To test this we simultaneously offered two dead tethered cockroaches hanging from the ceiling of the cage about 30 cm apart and 25 cm away from the sides and the ceiling of the cage. The bat's head was about 2–3 cm above and 50 cm away from the baits. As a control both cockroaches were presented motionless for two minutes. Then one of the tethered cockroaches was made to vibrate by slightly shaking the thread it was tethered to by hand from outside of the cage. The vibrating cockroach was presented for a two minute period or until the bat attacked. If the bat did not respond within two minutes the test was considered to be negative. Care was taken that the bait only vibrated vertically up and down and did not swing sideways.

In all three species the control tests never elicited any reaction from the bats in a total of 158 tests, except for *Hipposideros speoris* which happened to fly once towards one of the dead cockroaches. In contrast, vibrating dead cockroaches induced a catching response and subsequent attack of the vibrating cockroaches in 58 of 66 trials in *R. rouxi* and 44 of 55 trials in *H. bicolor* (Fig. 3). *R. rouxi* and *H. bicolor* nine times flew to the motionless bait. Again *Hipposideros speoris* responded less distinctly which also shows up in the latencies of the responses. They exceed 20 s on the average for *H. speoris* whereas the other two species responded within 10 s after vibration had started (Fig. 3, lower graph).

Figure 3 clearly shows that a vibrating dead prey quickly elicits catching responses in *Rhinolophus rouxi* and *Hipposideros speoris* whereas living walking prey had no effect at all (compare Fig. 3 and Fig. 2). Only occasionally a bat flew towards the nonvibrating bait and only when it was induced to fly off by a vibrating cockroach. These results suggest that rhythmical brief and brisk movements of dead insects are more effective stimuli for induc-

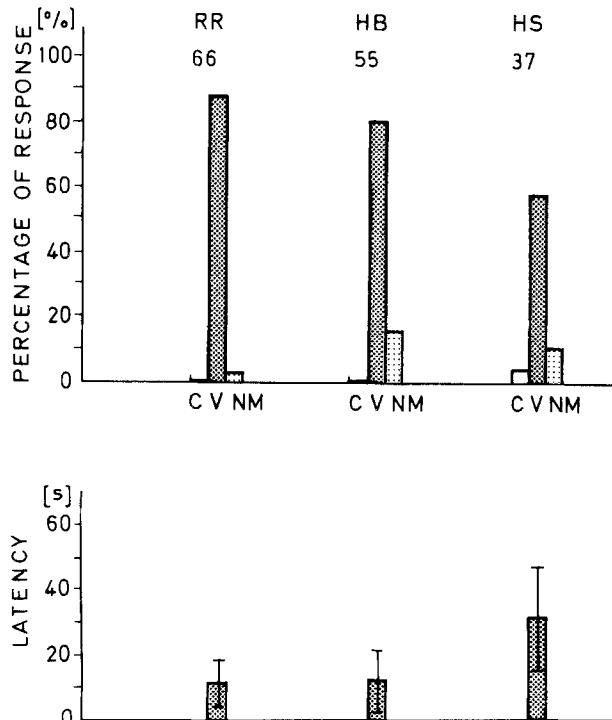


Fig. 3. Upper graph: Responsiveness of the bats (RR *Rhinolophus rouxi*, HB *Hipposideros bicolor*, HS *H. speoris*) to vertically vibrating (V) and nonmoving (NM) baits. C controls: neither of the two baits were moving. Numbers above columns indicate number of trials. – Lower graph: Latency of responses with standard deviations (vertical bars)

ing catching behaviour in rhinolophids and hippo-siderids than normally walking prey.

3. Catching responses to wingbeating against vibrating prey

In the same arrangement as in the previous experiment, a simultaneous choice was offered between a vibrating and a wingbeating cockroach. Wingless cockroach nymphs serving as vibrating bait and winged male cockroaches serving as a wingbeating target were tethered to the end of a string. The males can be easily induced to wing flapping sequences of several seconds by shaking the thread as in the vibrating bait. The cockroaches beat their wings at a rate of about 40 beats/s and the maximal wing tip excursion was about 40 mm. Again for a control both baits were presented motionless for two minutes and then both were shaken by hand which resulted in flights in the male and vibrations in the nymphs. Again number and latency of the catching responses of the bats were recorded.

In the 31 to 47 control experiments the motionless baits were never approached by the three bat species, except once by *Hipposideros bicolor*. In all

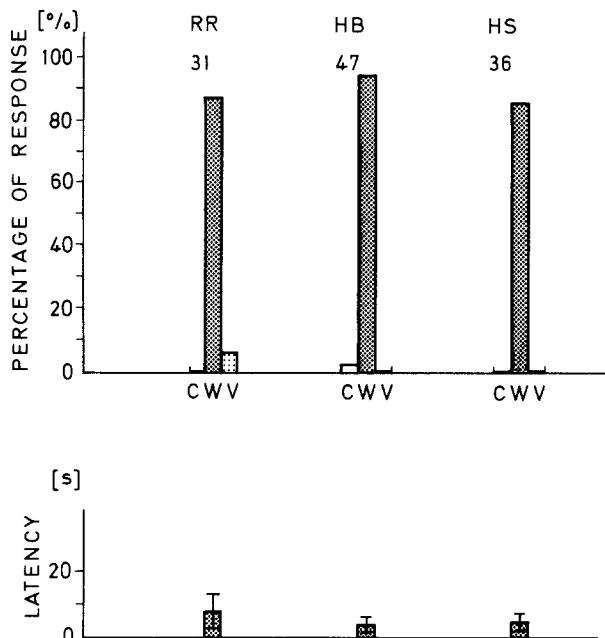


Fig. 4. Upper graph: Responsiveness of the bats (RR *Rhinolophus rouxi*, HB *Hipposideros bicolor*, HS *H. speoris*) to wingbeating (W) and vibrating (V) cockroaches. C control experiments: neither of the baits were moving. Numbers above columns indicate number of trials. – Lower graph: Latency of responses with standard deviations (vertical bars)

three species the wingbeating cockroach was attacked in nearly all experiments whereas the vibrating prey was not approached even once by the hipposiderid species (Fig. 4). Only *Rhinolophus rouxi* flew towards the vibrating cockroach twice in 31 tests. Remarkably the latency of the catch response to wingbeating prey was about three times faster in *Hipposideros bicolor* and six times faster in *Hipposideros speoris* than the one to vibrating cockroaches. The latency of the response was 5 s or less in *H. speoris* and *H. bicolor* and below 10 s in *R. rouxi* (Fig. 4). Only in the rufous horseshoe bats was the latency of response to vibrating and wingbeating targets about the same (compare Figs. 3 and 4). *Hipposideros speoris* did not respond to walking prey and clumsily reacted to vibrating prey but attacked wingbeating insects with the lowest response latency of the 3 species. This species seems to be the one most specialized to wingbeating prey as a releaser for catching behaviour. In any case for all three species wingbeating was the most effective stimulus for eliciting catching responses.

4. Catching responses to the wingbeat simulator

Since wingbeating proved to be the most effective stimulus we presented artificial wingbeats to exam-

ine the effects of wingbeat amplitude and frequency on the reactivity of the bats. In order to guarantee that the bat only differentiated wingbeating versus motionless targets and their choices were not influenced by the identical noises made by the active devices, both simulators were active with the same frequency and amplitude but in one of them the wings were removed from the oscillator. The simulators were placed 50 cm apart and 60 to 70 cm away from the bat. Inside the cage, in front of each simulator a piece of cockroach was tethered to the ceiling as in the previous experiments. When the bat responded to the wingbeats by a catching flight it seized the cockroach bait as a reward. Again, as control the bats were tested for two minutes with inactive simulators. Then one of them started to beat until a bat responded for maximally up to 2 min. If after 2 min no response had occurred the test was considered to be negative.

When the bats were attracted by the beating artificial wings outside of the cage they flew towards the gauze of the cage and hit the piece of cockroach tethered inside the cage. In cases where the bat failed to seize the reward it returned to its resting site and started to fly again towards the still beating artificial wings. When the first approach was successful in getting the reward we call it a single attack, and when the bat had to approach it several times it is called a repetitive attack.

We first presented the beating wings at a fixed peak-to-peak amplitude of 20 mm and frequencies varying from 1–30 beats/s. During an initial two minute or control period the hungry bats were faced with the two tethered stationary baits and the nonoscillating simulators just behind the baits, outside of the cage. All the bats showed hardly any reaction to the baits and nonoscillating simulators. The bat's behaviour immediately changed into one of complete alertness when one of the simulators started wingbeating. The bat directed its attention towards the wingbeating device outside of the cage, whereas no attention at all was paid to the nonbeating device equally baited. *Hipposideros bicolor* (twice in 31 tests) and *Hipposideros speoris* (once in 16 tests) flew to the bait backed by the nonmoving simulator only at a low beat frequency of 5 beats/s.

As Fig. 5 demonstrates *Rhinolophus rouxi* and *Hipposideros bicolor* in most presentations seized the bait in front of the wingbeating target by a single or a repetitive attack as long as a wingbeat machine was moving with frequencies above 10 beats/s. At lower wingbeat rates the number of

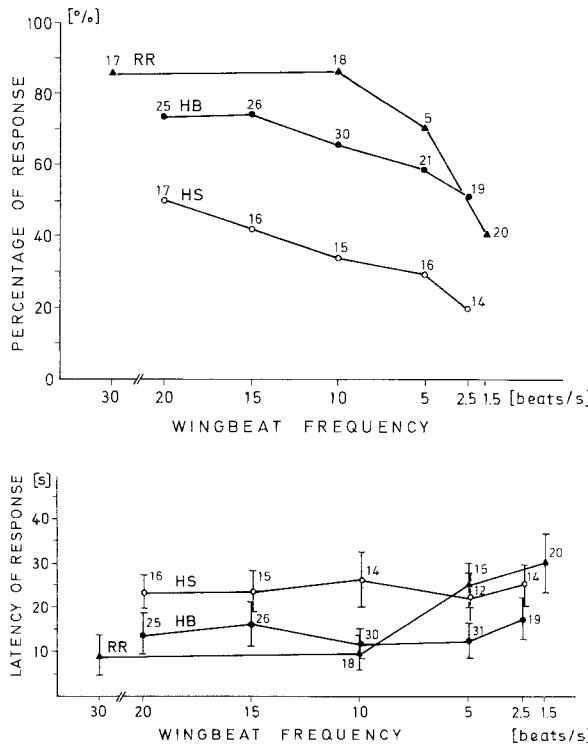


Fig. 5. Upper graph: Correlation between the percentage of attacks and the wingbeat frequency of the fluttering target simulator (max. wing excursion 20 mm). RR *Rhinolophus rouxi*, HB *Hipposideros bicolor*, HS *H. speoris*. Numbers above data points indicate number of trials. – Lower graph: Latency of attacks (vertical bars give standard deviation)

attacks fell and dropped sharply for frequencies of 2.5 to 1.5 beats/s. At this low repetition rates *Rhinolophus rouxi* was induced to approach the bait only 8 times in 20 presentations and *Hipposideros bicolor* 10 times in 19 presentations. Thus at a peak-to-peak excursion of the wings of 20 mm, wingbeat frequencies of 2 to 1 Hz were about the lower limit which induced the catching responses in horseshoe bats and *Hipposideros bicolor*.

Hipposideros speoris had more problems with the experimental set up. Even at 30 beats/s in seven of 87 tests this species did not react within 2 min. The rate of positive responses steadily declined with decreasing wingbeat frequencies (Fig. 5). This reduced responsiveness also shows up in the latencies of the positive responses. In *Hipposideros speoris* it was about 25 s for all frequencies tested whereas in *Hipposideros bicolor* latencies were mostly around or below 15 s, and only rose to about 18 s at wingbeat frequencies below 5 beats/s (Fig. 5, lower graph). The fact that in *Hipposideros speoris* latencies were long and did not change even at low beat frequencies suggests to us that this species may have detected the wingbeating target as well as the other species, but for some reason

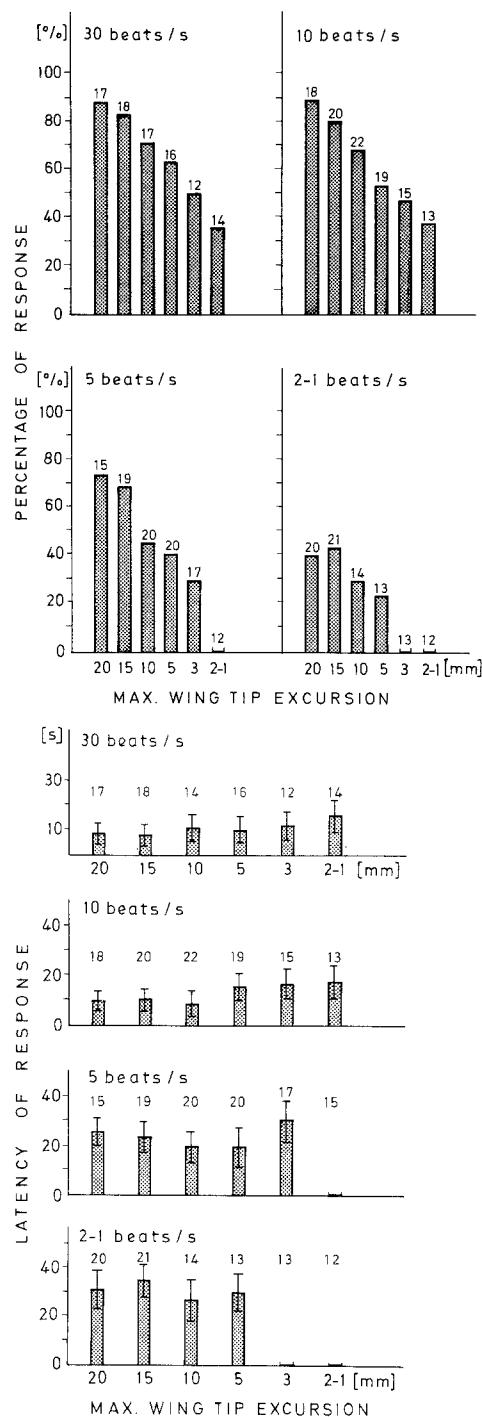


Fig. 6. Upper graph: Correlation between the responsiveness of *Rhinolophus rouxi* and the extent of the maximal wing tip excursion (abscissa) at four different wingbeat frequencies. Numbers above columns indicate number of trials. – Lower graph: Latency of responses with standard deviations (vertical bars)

were less responsive in this experimental situation. In contrast, *Rhinolophus rouxi* responded fastest with latencies below 10 s for wingbeat rates of 10 beats/s. For lower rates in this species not only

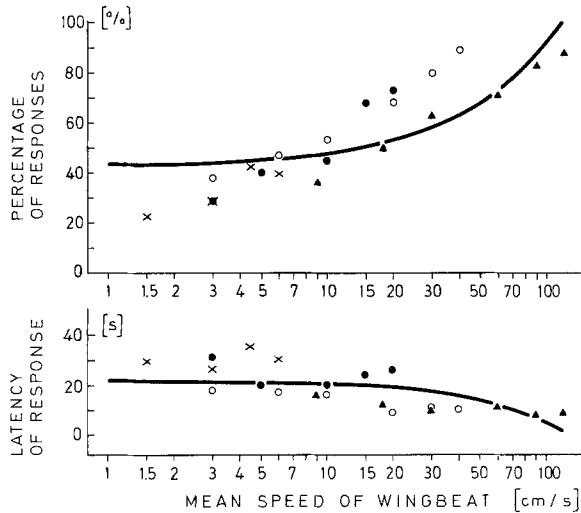


Fig. 7. Upper graph: Correlation between the responsiveness of *Rhinolophus rouxi* and the mean wing speed of the fluttering target simulator at four different wing beat frequencies: 30, 10, 5, 2–1 beats/s. The curves are the calculated linear regressions. Lower graph: Latency of responses

the number of responses dropped but also the latency of responses increased up to 30 s (Fig. 5). In any case the experiments show that horseshoe and hippostriderid bats can detect and respond to wingbeating frequencies as low as 2 to 1 beats/s.

For technical reasons the following experiments could only be performed on *Rhinolophus rouxi* in Sri Lanka. We tested the responsiveness of three rufous horseshoe bats to wing beats of various peak-to-peak amplitudes at fixed beat frequencies. The results shown in Fig. 6, upper graph, disclose that the bats still responded to wing beat amplitudes of 2 to 1 mm as long as the frequency was not below 10 beats/s. At frequencies of 5 beats/s the bats still reacted to 3 mm excursions of the wings, although at a low response rate. However, at peak amplitudes of 1–2 mm the bats no longer reacted at all, and at wingbeat frequencies of 2 to 1 beats/s the threshold of responsiveness was between amplitudes of 5 and 3 mm. These figures suggest that the relevant parameter for detection might be the speed of the wings which is about 1 cm/s at threshold levels. In contrast, as shown in Fig. 6, lower graph, latency of the response was not clearly correlated to the amplitude of the wing beats. It remained more or less the same until the threshold of the response was reached. The same average wing speed may be achieved by either a high wing beat frequency and small wingtip excursion or vice versa. The percentage of responses increased with wing speeds (Fig. 7). In the same way the latency of the response decreased with wing velocity. However, in all cases but one the latency

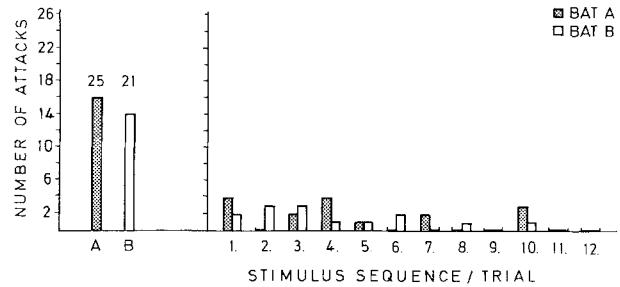


Fig. 8. Responsiveness of *Rhinolophus rouxi* (Bat A and B) to a sequence of single, discrete wing excursions. Left: Total number of attacks during presentation of discrete wingbeat sequence. The numbers above the columns indicate number of trials. Right: The numbers of sequentially presented wingbeats necessary to elicit an attack for each trial

was shorter for an identical average wing speed when it was achieved with higher beat frequencies than with lower ones.

5. Response to single wing beats

In horseshoe bats we tried to elicit catching responses to single wing beats in the same set up as described above. In these tests the artificial wings were only moved by hand through one up and down cycle. The maximal excursion of the wing was about 42 mm, and the wings were moved rather slowly through one cycle within about 1 s. These single wing beats were presented to the horseshoe bats at a repetition rate of 1/10 s. If the bat did not respond within 2 min, i.e. after 12 presentations of single wingbeats, the test was considered as negative.

Two horseshoe bats were tested and both responded to such single wingbeats. Bat A was attracted to the fluttering target in 16 out of 25 experiments within 2 min and 4 times attacked the bait after the first single wingbeat. Bat B reacted in 14 out of 21 experiments within 2 min and seized the bait twice after the first and three times each after the second and third single wingbeat presented. Most responses occurred after the first four single wing beat presentations (Fig. 8). It is obvious, that in horseshoe bats one single wing movement was sufficient to elicit a catching response.

6. Echolocation

Under the experimental conditions described all three bat species continuously emitted echolocation sounds. Design of the sounds, repetition rates during searching phases and attacks of prey were the same as reported in Habersetzer et al. (1984) for hippostriderids and in Neuweiler et al. (submitted) for *Rhinolophus rouxi*. Briefly, before take off

Hipposideros speoris (in brackets corresponding figures for *H. bicolor*) emitted CF/FM sounds of 5–7 ms (4–5 ms) duration and intervals between sounds of 6–15 ms (6–12 ms). When the bats flew towards the prey final buzzes of up to 20 sounds occurred with sound durations of 3.5–4.5 ms (3.0–4.0 ms) and intervals of 4–6 ms (4–6 ms). The frequencies of the pure tone components varied between 142.8 and 144.4 kHz (156.6–157.2 kHz).

Rhinolophus rouxi also emitted CF/FM sounds which frequently started with an additional frequency upward modulated component. Sound durations varied between 38 and 46 ms during searching phases and were shortened to about 10 ms in final buzzes. The frequency of the pure tone component varied between 74 and 78 kHz. No differential echolocation behaviour towards various species of prey and different kinds of their movements were observed.

Discussion

One of the aims of the study was to test if the hipposiderid bats which only emit brief CF components of 2–6 ms duration also depend on fluttering target detection to the same degree as horseshoe bats do. The latter species emitted pure tone components lasting about 45 ms (Neuweiler et al. submitted). The results obtained unequivocally demonstrate that both hipposiderid and rhinolophid species only detected and attacked prey which was moving. Thus bat species emitting either short or long pure tone components only responded to moving prey.

This behavioural result in specific detection of movement is consistent with auditory adaptations to the pure tone echo component rendering pure tone echolocation highly sensitive to fluttering targets. These neural and peripheral adaptations have been described in all rhinolophid and hipposiderid species so far studied (Neuweiler 1970; Schuller 1980; Jen and Suthers 1982; Taniguchi 1985; Grinnell and Hagiwara 1972; Neuweiler et al. 1984). Apparently, both long and brief pure tone signals are equally well suited for fluttering prey detection provided the auditory analysis of the species-specific echo frequency is fine enough. Indeed, all three species feature an acoustical fovea for the echo tone frequency (*Rhinolophus rouxi*: Schuller 1980; Vater et al. 1985; *Hipposideros speoris* and *H. bicolor*: Schuller 1980; Neuweiler et al. 1984; Rübsamen et al., in prep.). As demonstrated by Schuller (1984) the acoustical fovea renders neurons specifically sensitive to minute frequency and amplitude modulations. Such modulations are im-

posed onto echoes reflected from wingbeating insects. Thus pure tone echolocation in horseshoe bats and hipposiderids is an adaptation to fluttering target detection.

On the other hand, there are bat species which do not apply pure tone echolocation and yet also only are alerted to prey when it is moving (e.g. *Antrozous pallidus* (Bell 1982) and *Megaderma lyra*). In the latter species it has been recently shown that prey is only detected by noise produced by a moving target (Marimuthu and Neuweiler, in prep.). Wenstrup and Suthers (1984) have demonstrated that *Noctilio leporinus* gets information on the movements of prey by the change of distance information in the echoes and not by Doppler shifts of the emitted pure tone components in the echo signals.

Interestingly *Hipposideros bicolor* was the only species which also attacked walking or running insects on the floor or the sides of the cages and skilfully caught them. It also regularly flew off when some rustling noise (e.g. rubbing fingers) was made behind the nylon clothing of the cage. The bat localized the noise source correctly and bit the clothing in front of the fingers. This behaviour could not be evoked in the other two species. Rustling noises contain a large amount of sound energy in the frequency band of 15 to 40 kHz. Audiograms in *H. bicolor* but also in *H. speoris* show, that both species are sensitive in the lower ultrasonic frequency range (Neuweiler et al. 1984). Thus both species should hear rustling noises. However, in *H. bicolor* the outer ears are considerably larger than in *H. speoris*. All species which have been shown to detect prey by noise have unusually large ears (e.g. *Macroderma gigas* (Guppy and Coles, submitted), *Megaderma lyra* (Fiedler 1979), *Antrozous pallidus* (Bell 1982)). This correlation between large pinnae and high sensitivity to rustling noises suggests that *H. bicolor* also is adapted to detect prey by its walking noises.

This difference in stimuli eliciting catching behaviour between *H. bicolor* and *H. speoris* nicely conforms to the differences in foraging behaviour in the natural habitat (Habersetzer 1982). *H. speoris* was observed to catch insects only on the wing about half a meter away from vegetation and in our experiments this species was most specialized on fluttering targets as key stimuli for catching behaviour. In contrast *H. bicolor* frequently foraged within foliage, picked up insects from walls and from the ground, and in our experiments this species was the only one which responded to noises and to prey walking on the floor of the cages. These observations, however, do not exclude the

possibility that *H. speoris* and *Rhinolophus rouxi* might also localize and catch insects on the ground when, for instance, insect abundance is low. From horseshoe bats such a behaviour has been reported (Southern 1964). In any case, the observations in the natural habitat, our experimental results and the presence of large outer ears suggest that *H. bicolor* is more adapted to detecting prey by noise than the other two species studied.

In our experiments *Rhinolophus rouxi* and *Hipposideros speoris* vigorously attacked fluttering insects or nonmoving prey backed by a fluttering dummy. However, they never reacted to prey walking or running on the ground. Apparently, for these two species fluttering, i.e. oscillating fast movements are the only stimuli which induced catching responses. Even in *Hipposideros bicolor*, which also attacked walking insects, fluttering targets also were the most attractive stimuli. This specific sensitivity to fluttering targets in all three species is best explained by the peculiar pure tone echolocation system as described above (Neuweiler et al. 1980).

However, fluttering wings were the most effective but not the *only* releasers of catching behaviour. When there were no fluttering targets present tethered cockroaches vibrating up and down from the ceiling of the cage were effectively detected and attacked. This suggests that oscillating movements of any sort and not specific features of wing movements are the key stimuli for detecting prey. In *Hipposideros speoris*, however, the latencies for catching baits vibrating up and down were longer than to fluttering prey and the response rate to vibrating and fluttering targets was lower than in the other two species. There is no apparent explanation for this difference in responsiveness. Habersetzer (1982) reported that *H. speoris* only forages for flying insects on the wing. Therefore this species might be more specialized to fluttering prey detection and hence might respond less frequently to vibrating targets.

All three species respond well and with brief latencies to wingbeat frequencies of 10 to 100 beats/s. The response rates rapidly deteriorate for lower wingbeat frequencies and they release only little attraction at frequencies between 1 to 2 beats/s in all three species. Interestingly there is no substantial difference in reactivity to different wingbeat frequencies between the three species even though horseshoe bats use a pure tone signal ten times longer than that of the two hipposiderid species.

At the least attractive wing beat frequencies of 2 to 1 beats/s the peak excursions of the wing tips

were 20 mm which results in an average wing speed of about 40 mm/s. In horseshoe bats thresholds for catching responses were reached at wing beat frequencies of 5 beats/s and peak amplitudes of 2 mm or at 2 to 1 beats/s and amplitudes of 3 mm. In both cases average wing speed was between 15 and 20 mm/s. It is most likely that the critical parameter for eliciting a response is the speed of the wings and its threshold would have been around 1–2 cm/s in our experiments. This corresponds to the low speeds (24 mm/s) discriminated by *Rhinolophus ferrumequinum* in the experiments of Schnitzler and Flieger (1983).

The experiments in horseshoe bats show that a single wing movement may be sufficient to elicit a catching response. The repetition rates of wingbeats were therefore not involved in the decision of the bat to attack a potential prey. Unfortunately for technical reasons the same experiments were not performed in hipposiderids. However, from many behavioural observations in the field and from hipposiderid bats in captivity fed by living insects we know that frequently an insect is caught if it happened to flap its wings just once.

From these results and observations we conclude that in rhinolophids and hipposiderids echolocation with a pure tone component primarily serves as a device to detect any wingbeating target irrespective of its prospective palatability. As shown above hipposiderids achieve a similar reactivity to such movements as horseshoe bats even though their pure tone signals are much briefer.

Why then do horseshoe bats consistently make the effort to emit long pure tones which are never shorter than 10 ms and always longer than those of hipposiderids? Field studies have unequivocally shown that *Rhinolophus rouxi* emits long pure tones with no or only faint FM components while searching for flying prey from their vantage points (Neuweiler et al., submitted). These observations again prove that the pure tone primarily serves as a detection signal. The last few echolocation tones emitted before a take-off for catching a detected insect lasted about 60 ms compared to an average sound duration of 45 ms. This prolongation of the tone might suggest that the horseshoe bats also used the long echoes for prey differentiation. Schnitzler et al. (1983) have shown that pure tone echoes from wingbeat sequences of different insect species carry specific modulations by which differentiation of prey species might be possible. Differentiation on the basis of echoes from wingbeats should be better the longer the sequence encoded in the echo, hence the longer the echo signal. Perhaps long pure tone emission in horse-

shoe bats makes prey differentiation by echolocation easier than in hipposiderids. However, our observations in all three species do not favor this attractive hypothesis since the bats mostly decided to catch or not to catch a prey after take-off and when they were at very close range to the prey (Habersetzer 1982; pers. observ.). Bell and Fenton (1984) also reported that hunting *Hipposideros ruber* do not prefer one insect species over any other, but in behavioural experiments they closely approached some very big moths without attacking them. The same happened with an electrical insect dummy when it was fluttering. The authors suggested that *H. ruber* selects prey only at close range based on textural echo features in the FM component of their echolocation call. Since the responsiveness to fluttering target detection under nearly natural conditions is of the same order for horseshoe bats and hipposiderids the significance of emitting long pure tones for echolocation remains obscure. This problem will be a challenge for further behavioural studies.

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