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Object recognition by echolocation: a nectar-feeding bat exploiting the flowers of a rain forest vine

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Abstract In the bat-pollinated vine *Mucuna holtonii* only the first visit to a flower is rewarded with a substantial amount of nectar, which is released when a bat lands on the flower and triggers an explosion mechanism. During later visits the bats receive only small amounts of nectar. Nevertheless, the inflorescences as a whole remain attractive, since further buds successively open during the night. Nectar-feeding bats *Glossophaga commissarisi* selectively visit unexploded, “virgin” flowers. They can discriminate buds, virgin and exploded flowers using echolocation. In field experiments bats exploited virgin flowers, the vexillum of which had been replaced by a same-sized triple mirror or by an artificial vexillum. Such flowers were frequently inspected, but not as often exploited as natural flowers. In two-alternative-forced-choice experiments the bats learned to discriminate between replicas of the vexillum and triple mirrors. The recognition distance was between 15 and 50 cm. Echoes of the three flowering stages differ in their spectral composition, which changes in dependence of the sound incidence angle in a characteristic way. We conclude that glossophagine bats are able to recognize small motionless structures like flowers and to accurately adjust their landing manoeuvres by using their echolocation system alone.

Keywords Echolocation · Echo-acoustic object recognition · Foraging behaviour · *Glossophaga* · *Mucuna holtonii*

Introduction

Since Donald Griffin’s discovery of bat echolocation intense research over half a century brought some insight in the problems a bat has to solve when detecting and locating insect prey (Neuweiler 1989, 1990). The mere ability to hunt insects in open air or in the “clutter-free window” (the range corresponding to the time interval between overlap of echoes with their own echolocation signal and with clutter-echoes originating from objects and obstacles close to the prey) is amazing enough, but some bat species of both CF- and FM-type are even able to locate insects although the echoes of prey and background overlap (Siemers and Schnitzler 2000; Jensen et al. 2001). CF-bats may use glints and Doppler shift-induced frequency modulations to detect and localize fluttering insects, while FM-bat species utilize very faint rustling noises that allow passive localization of prey (reviewed in Schnitzler and Kalko 1998; Arlettaz et al. 2001). But how bats detect, recognize and localize motionless and silent objects in highly cluttered surroundings (Kalko and Condon 1998; von Helversen and von Helversen 1999; Schmidt et al. 2000) is still, if at all, only poorly understood.

Nectar-feeding glossophagine bats, visiting motionless and soundless flowers, find their plants guided by visual and olfactory cues (e.g. Suthers et al. 1969; Knudsen and Tollsten 1995; Thies et al. 1998; von Helversen et al. 2000) and by echolocation. While olfaction and echolocation are important in darkness, vision may only support the search for flowers in moonlight or crepuscular times. Before the faint calls of these “whispering bats” could be recorded, odour was thought to be the only orientational cue, and undoubtedly it is important for long range orientation and in dense vegetation. However, the detection of flowers by echolocation plays a major role below 2–3 m down to a few centimetres. Thus, flower-visiting bats may be an excellent model system to investigate how the amplitude/time functions of echoes arriving at the two ears may be

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transferred to an internal representation of the outside world.

Bat-pollinated plants, in competition for these effective pollinators, have evolved structures that facilitate the detection of their flowers, such as clutter-free position of the flowers on the tips of twigs or on long perpendicles hanging down from the canopy (Vogel 1958, 1968/1969; Dobat and Peikert-Holle 1986). Flowering phenology that ensures availability of nectar over long periods matches the excellent spatial memory of bats and reduces the time, risk and energy costs of foraging (von Helversen 1993; Winter and von Helversen 2001).

Most neotropical bat-pollinated plants are exploited while the bat hovers at the flower for a few hundred milliseconds (von Helversen and Winter 2003). *Mucuna* is an exception in that newly opened (virgin) flowers cannot be exploited during hovering flight. To reach the nectar the bat has to land on the flower and trigger an "explosion mechanism" (also known from other papilionaceous flowers). Pressure at a distinct point between the alae bursts the keel, releasing the staminal column and the pollen load to the bat's back. Virgin flowers contain about 100 μl of nectar but exploded flowers have only 6–10 μl standing crop (O. von Helversen, unpublished observations). Nevertheless, the inflorescence as a whole remains attractive, since, for a flowering time of about 6 weeks, during each night up to eight buds successively raise their vexilla, signalling a reward. Thus, the most effective foraging tactic for a bat would be to seek for virgin (unexploded) flowers selectively, which requires them to discriminate between buds, virgin and exploded flowers.

Here we ask whether bats indeed discriminate between the different stages of the flowers in the field, i.e. whether they are able to recognize a specific form even in a highly variable and clutter-rich surrounding. A next step was to investigate how well bats can discriminate between two such forms as used in the field and to identify the possible cues allowing recognition. In parallel we measured the echoes of natural flowers to investigate the echo-acoustic cues that may allow recognition.

Materials and methods

Study site

We studied the pollination of *Mucuna holtonii* at the OTS Station La Selva (Caribbean lowlands of Costa Rica), where this vine is abundant high in the canopy, but also overgrows medium-sized trees in adjacent secondary forest. In these situations the long flagelliferous inflorescences hang down to less than 2 m above the ground, which allowed us to manipulate flowers and record pollination behaviour.

In La Selva, the most abundant glossophagine bat visiting *Mucuna* is *Glossophaga commissarisi*, but *Hylonycteris underwoodi* and *Lichonycteris obscura* have also been observed to land and explode the *Mucuna* flowers. The large *Lonchophylla robusta* was seen to only hover in front of exploded flowers (Tschapka 1998; personal observations).

Field experiments with manipulated flowers and infrared-video recording

To register bat visits to flowers, we either checked whether previously virgin flowers were exploded, or we monitored one to several inflorescences with an infrared (IR)-sensitive camera (Sanyo VCB 3572). We used a custom-built infrared strobe (flash duration 200–500 μs) and a digital video recorder (Sony GV D900). The flashes were synchronized with the video camera (50 half-frames s^{-1}) allowing frame-by-frame evaluation. The flash was an array of 36×24 IR diodes (TSHA 5203) measuring 16 cm×12 cm. Altogether we monitored 49 virgin flowers and 42 exploded flowers at various inflorescences and different sites for more than 10 h of recording.

We tested the attractiveness of artificial vexilla (plastic replicas of real vexilla) and triple mirrors of the same size using the explosion of flowers as an indicator for visitation. Small triple mirrors (see Fig. 3, inset) consisted of three rectangular triangles perpendicular to each other and were folded out of stiff plastic foil (thickness 0.5 mm). The artificial vexilla were replicas of a natural vexillum: In a first step a natural vexillum was used to produce a negative form by embedding it in Permadyne Garant (ESPE Dental-Medizin). The negative was then filled with the bi-component system Protemp Garant (ESPE), which hardened within several minutes. One negative form allowed the production of about three to six replicas. Both artificial forms were treated with the same clear varnish to make the surface quality equal.

To increase the number of virgin flowers for the tests, early in the evening we covered a number of inflorescences with bags to prevent bats visiting newly opened flowers before manipulation. We carefully removed the vexilla by pulling them out of the calyx and replaced them with either an artificial vexillum or a triple mirror, which was pinned with a thin insect needle (000) to the dorsal surface of the calyx. This did not interfere with the function of the explosion mechanism, which could be released as easily in natural as in manipulated flowers. Occasionally, an explosion was released during manipulation and the flower had to be discarded. Intact virgin flowers served as a measure of the normal visitation rate. We checked the status of each flower every 2 h.

Training experiments on object recognition

In the lab we trained three bats in a two-alternative-forced-choice paradigm to discriminate between an artificial vexillum and a triple mirror of the same size. The bats were rewarded when they had chosen the vexillum. A replica of a *Mucuna* vexillum and a plastic triple mirror (as used in the field experiments) were mounted at the ends of a motor-driven axis (24 cm) allowing us to position either the one or the other object directly above a feeder (while the other pointed backwards). The visits of the bat were registered by small photoelectric IR sensors at the feeder. Their signals were fed into a computer, which, in case of a correct choice, triggered a valve (Jucomatic) to release a reward. As the reward was small (ca. 20 μl of 17% sugar-water consisting of fructose, glucose and saccharose) a bat made more than 1,000 decisions per night. Using two such units (46 cm apart), both objects, the rewarded vexillum and the unrewarded triple mirror, could be presented at the left and right side simultaneously. Two such pairs of feeders were housed at the two ends of a U-shaped tunnel. While the bat visited a feeder at the one end, the presentation order of the objects at the other was changed in a pseudo-random order to avoid preferences of the left or right location. Only the first correct choice in a compartment was rewarded. Thus, the bat had not only to learn which form indicated a reward but also to alternate between the two compartments. This alternation guaranteed that the bat made its decision while approaching the objects from the front. The experiments were run in complete darkness.

Estimation of recognition distance

To estimate the distance at which an approaching bat might recognize a small object, we recorded an area of 60 cm×160 cm in front of one pair of feeders. A video-camera (short focus) and four

IR flashlights were mounted about 2 m above the midline to record the approaching bat, which was marked with a tiny piece of reflecting foil. Since the feeders were mounted 25 cm above ground the bat approached them flying at a fairly constant height of about 20 cm above ground. At that height we recorded a scale to correct for distortions of the objective. Out of a 2-h video recording all correct visits to one of the four feeders were selected as a short clip. With the program NIH-Image the coordinates of the bats position were determined frame by frame and further processed in Excel.

Measurements of flower echoes

To estimate the echoes received by a bat's ear, we used a speaker and a receiver as close to each other as possible. A custom built condenser loudspeaker (TH Darmstadt) with an active membrane of 15 mm diameter and a microphone (Brüel & Kjaer 4135 and amplifier 2209) were mounted on a tripod, the centres of the speaker and the microphone membrane being 17 mm apart. The reflecting object was glued to a needle at the tip of a thin holder (diameter 3 mm) which was fixed on a rotating disc. The distance between loudspeaker and object was 20 cm.

To measure the impulse response of the objects we used the MLS method. A specific sequence of 1- and 0-values (16,383 samples) was repeatedly broadcast and recorded synchronously at a rate of 500 kHz. Using the fast Hadamard transformation the impulse response function was computed in the time domain. The echo was selected and the spectrum calculated using the fast Fourier transformation. All calculations were performed with the program Monkey Forest (Audio & Acoustics Consulting, Aachen). For a detailed description see von Helversen et al. (2003).

Single fresh flowers were brought into the lab and mounted on the turntable. The front view of the object was adjusted to face the speaker and microphone at 0°. Revolving the turntable in steps of 2° the object was irradiated in one plane between +90° and -90°. Depending on whether the object was mounted upright or tilted by 90° we recorded the echoes rotating on the vertical or transversal axis of the flower.

Results

The *Mucuna* flower

The inflorescences of *M. holtonii* hang down from the canopy on long perpendicles, which often measure several meters (Figs. 1, 2). An inflorescence consists of numerous small buds and normally three to eight ripe flowers (5.5 cm from top to bottom, Fig. 1), which open successively during night. A flower signals to contain nectar by raising the upper petal, the 'standard' or vexillum, a conspicuous concave structure that reflects sound and functions as a "target" for echolocation (von Helversen and von Helversen 1999). In addition, the two alae become visible (Fig. 1, top right). When a bat presses its snout between the two 'wings' (or alae) right below the vexillum the flower 'explodes': The lower part of the flower, the 'keel', bursts and the staminal column being under tension protrudes (Fig. 1, three flowers at the left and one at the lower right).

Foraging flights

To learn how *G. commissarisi* searches for virgin flowers, we videotaped a cluster of 15 *Mucuna* inflorescences hanging above an area of about 2 m×4 m (Fig. 2) with



Fig. 1 Inflorescence of the papilionaceous vine *Mucuna holtonii* with buds, one virgin and four exploded flowers. Note the vexillum covering the alae and part of the keel in the bud (upper right), the raised vexillum, the narrow slit between the alae and the closed keel in the virgin flower (left of the bud), and the widely gapping keel with the protruding staminal column in the exploded flowers

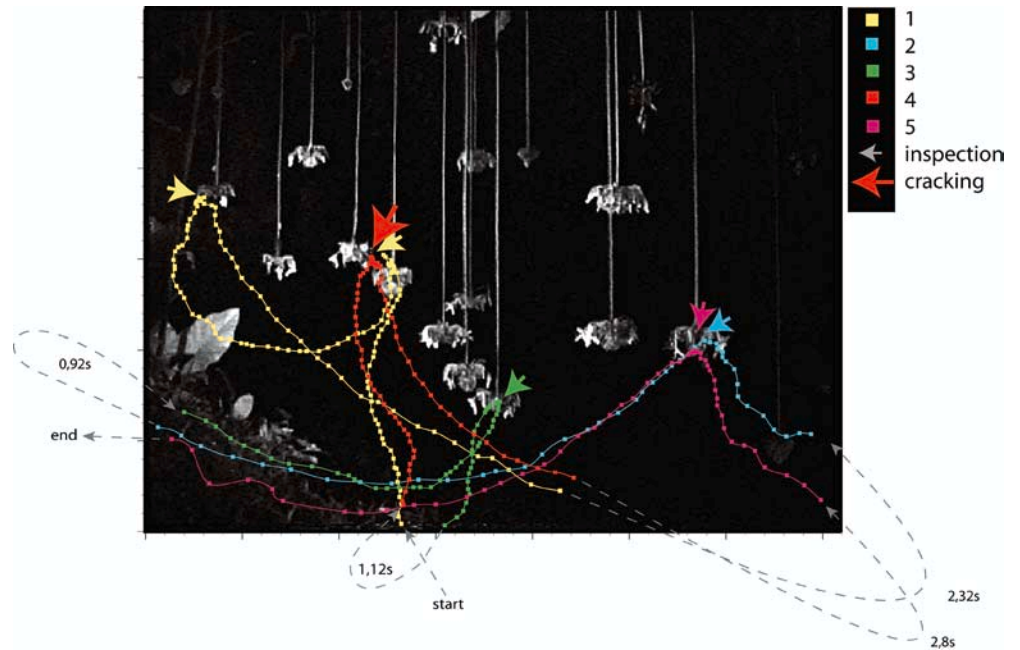
an IR-sensitive camera during several nights. At the same time we observed the bats foraging around that place with a night-vision scope, which allowed us to follow their routes in a much more extended area than monitored by the videocamera. At intervals of 4 to 10 or more minutes, we observed a bat cruising below and among the inflorescences for about 2–5 min, sometimes flying close to an inflorescence, hovering briefly in front of a flower, and occasionally landing for about 500–800 ms ($n=20$). The foraging flights were straight back and forth across the whole cluster of inflorescences (Fig. 2).

Close videos with only one to three inflorescences revealed that virgin flowers usually were "inspected" once or twice before the bat landed to explode the flower (85%, 51 recordings). Typically, during such a brief inspection the bat came very close (up to 1–2 cm) to the raised vexillum of a virgin flower. One quarter of the flowers was exploited within the next 5 s after an inspection visit, i.e. immediately after detection. However, as exemplified in Fig. 2, the bat could also inspect further flowers at other inflorescences before it returned to exploit a flower already inspected.

Do *Glossophaga* discriminate between buds, virgin and exploded flowers of *Mucuna*?

In a previous field experiment it was shown that the bats recognized a virgin flower by the raised vexillum and thus were able to discriminate between buds and virgin flowers: virgin flowers with the vexillum removed or filled with a small pad of cotton wool were exploded much less often than intact control flowers. Since vision and olfaction could be excluded as possible nectar guides, the bats must have recognized the status of the flowers by echolocation (von Helversen and von Helversen 1999).

Fig. 2 Fifteen seconds of a typical foraging bout, during which the bat crossed and re-entered the video frame five times. The time intervals outside the monitored space are indicated at the margin. On its search flight the bat repeatedly crossed the whole area of inflorescences rather than checked them one by one for newly opened flowers. In this example the bat inspected four different virgin flowers at four different inflorescences (*small arrowheads*) before it exploited the flower that it had detected first (*large arrowhead*), and then continued inspecting a further flower at the rightmost inflorescence

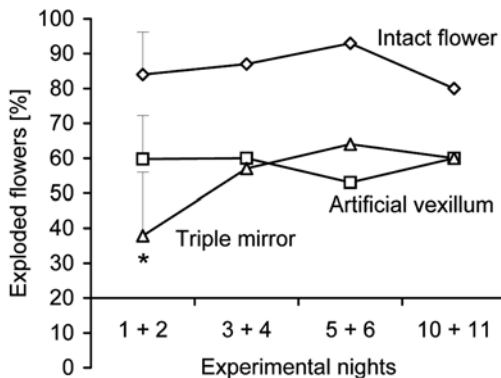


Whether they also discriminated between virgin and exploded flowers could not be tested simply by counting exploded flowers, but had to be observed directly. In Table 1 the average number of hovering flights and landings is listed for virgin and exploded flowers. Typically, virgin flowers were inspected once or twice before they were exploded. The value of 0.98 landings/virgin flower indicates that the detected flowers were nearly always exploded at the first landing. Once exploded, we observed only one landing at an exploded flower.

Table 1 Hovering and landing visits at virgin and exploded flowers of *Mucuna holtonii*. Hoverings in front of virgin flowers were always “inspections”, hoverings in front of exploded flowers could be inspections or exploitation visits, which typically occurred immediately after explosion, when the bat returned to completely empty the flower. Total observation time (tape recorded): 554 min

	Hoverings	Landings	Flowers
Virgin	86	48	49
Exploded	61	1	42

Fig. 3 Percentage of exploitation of natural and manipulated flowers during subsequent nights (data of two successive days and different locations were pooled). At each place tested about one-third of the virgin flowers was left intact (*diamonds*), while the vexilla of the rest were replaced either by a triple mirror (*triangles*) or an artificial vexillum (*squares*). Bars indicate standard deviation. Data were collected at 7, 5, 3 and 3 different locations for successive pairs of nights ($n_{int}=190, 86, 57, 30$; $n_{vex}=110, 66, 30, 15$; $n_{triple}=119, 74, 33, 20$ flowers for each data point). The percentage of exploded flowers was significantly different in the first two nights. Flower types of each data set were exposed for the same time, 4 h in most cases



These observations demonstrate that the bats discriminated between buds, virgin flowers and exploded flowers.

Experiments with artificial replicas of the vexillum and with triple mirrors: how important is the shape of the vexillum to attract bats?

Previous measurements of the echoes revealed the vexillum to function like an acoustic cat's eye, reflecting



most of the energy back into the direction of sound incidence (von Helversen and von Helversen 1999). An even more effective structure to reflect sound back into the direction of incidence should be a so called “triple mirror”, a structure consisting of three right-angled triangles perpendicular to each other, like an inner corner of a cube. This geometry implies that within a range of $\pm 45^\circ$, all echoes are reflected back to the sender. However they lack spectral specificity which characterizes the echoes of the natural and artificial vexillum (see echoes Fig. 7).

To test whether such triple mirrors are also attractive for bats or even act as supernormal stimuli, at several sites in the field we manipulated virgin flowers: In two thirds of the virgin flowers the natural vexillum was carefully removed and replaced by either a triple mirror or an artificial vexillum (see inset Fig. 3). The latter should control for the manipulation and allow a comparison between the attractiveness of natural and artificial vexilla. The rest of the flowers remained intact. The percentage of exploded flowers of each type is plotted in Fig 3 for subsequent nights.

Both artificial stimuli attracted bats and resulted in exploded flowers at a rate that was similar for both artificial stimuli but lower than that of the natural vexillum. Only during the first two nights flowers with a triple mirror were less frequently exploded than flowers with an artificial vexillum. This was probably due to a learning effect: since we did not remove the nectar of the manipulated virgin flowers, a bat landing on a manipulated flower could release the explosion and was rewarded. Thus, at least some bats could have learned that triple mirrors were attractive.

For a better understanding of this result we videotaped inspections, landing attempts and landings at flowers, whose natural vexilla had been replaced. While natural flowers were inspected only once or twice before a landing, manipulated flowers were inspected more frequently (Fig. 4). The average value of 4.5 inspections of flowers with triple mirrors indicates that the echo of a triple mirror indeed made the flowers conspicuous and attractive.

However, the video-recordings also revealed that landings at manipulated flowers often were not successful (releasing no explosion of the flower) compared to those at unmanipulated flowers. This may explain why in the replacement experiment (Fig. 3) the percentage of exploded flowers did not reach that of natural flowers, but was about 20% below.

Presumably the correct spatial relations of the vexillum and the rest of the flower are important for an exact landing manoeuvre, the accuracy of which allows the bat to release the explosion mechanism. To test the relevance of correct spatial correlations, we videotaped a couple of inflorescences, with 11 intact flowers (controls) and 9 flowers, the vexillum of which had been pulled out and re-fitted rotated by 20–30°. Only 1 of the 9 manipulated flowers was exploded successfully, though the bats had inspected the flowers and started several

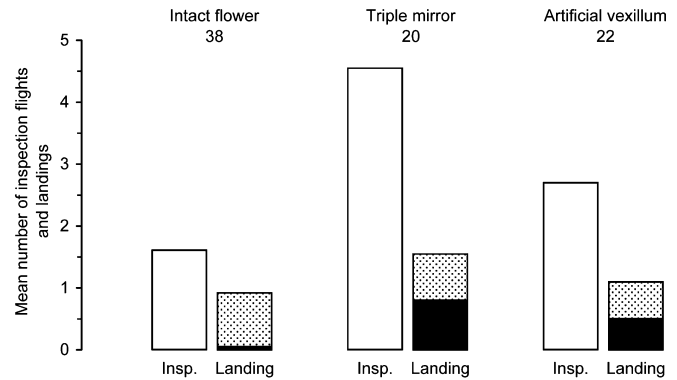


Fig. 4 Mean number of inspections (white, left columns) and landings (right columns) at intact and manipulated flowers as revealed by video recordings. Landings could be successful (stippled part of the columns) or unsuccessful (no explosion, black parts of columns). Note that intact flowers were exploded after 1–2 inspections and that the first landing normally was successful, while flowers with a triple mirror were frequently inspected but experienced many unsuccessful landings. Numbers of observed flowers as indicated above columns

landings and landing attempts. In contrast, 9 out of the 11 intact control flowers were successfully exploded at the first landing and a further one at the second trial.

*Can *Glossophaga* be trained to discriminate between an artificial vexillum and a triple mirror, and if so, at which distance?*

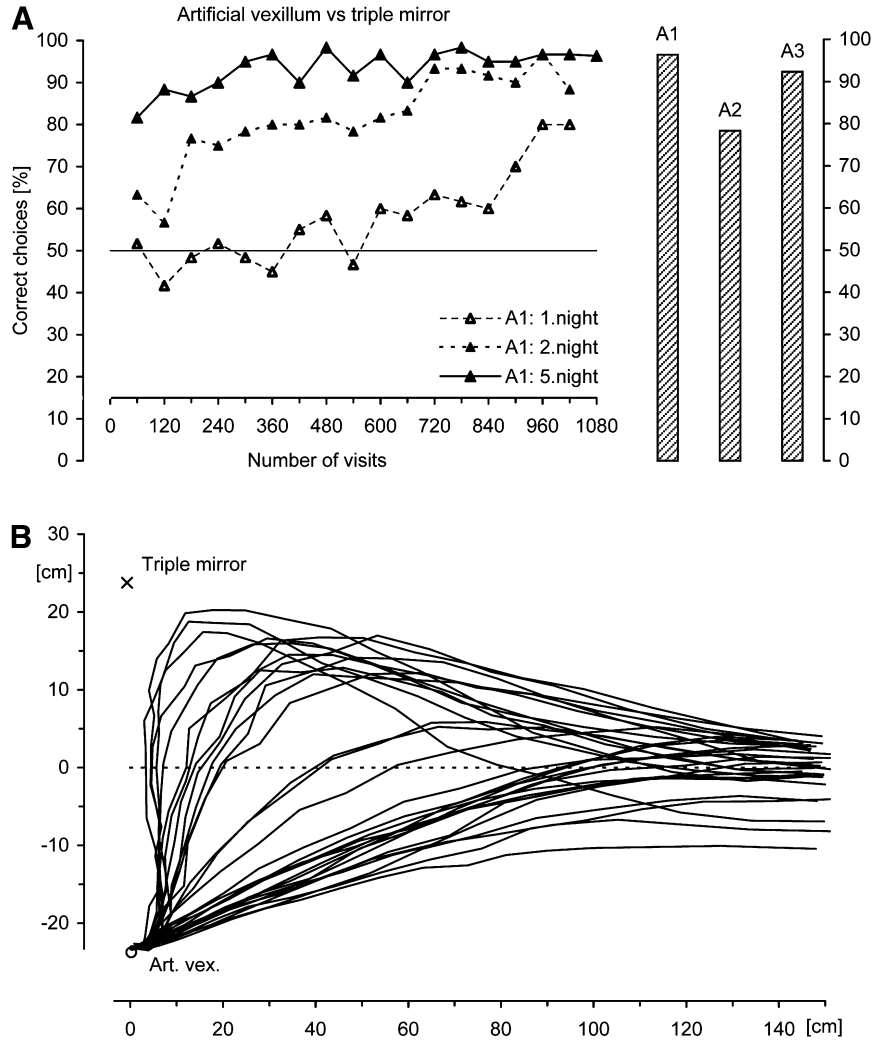
The finding that *Glossophaga* handled manipulated and intact flowers differently raised the question, whether and how well the bats would discriminate between an artificial vexillum and a triple mirror solely by their echoes. In the lab, three bats were trained to discriminate these two objects in a two-alternative forced choice experiment.

As an example, for one animal (A1), which was already familiar with the rewarding modus (see methods), the percentages of correct choices (for every 60 decisions) are plotted during the course of three nights (Fig. 5A). At the end of the first night of training about 70% of the bat’s decisions were correct. The level of correct choices increased during the second night and reached a level better than 90% for all further nights. Two other bats had very similar learning curves with saturation levels at 79% and 92% for the last 300 decisions of the respective night (Fig. 5A, columns A2 and A3).

The training experiments therefore corroborated our findings from the field that *Glossophaga* bats are able to discriminate small objects of the same size but different shape by echolocation alone.

To estimate the distance at which recognition of the correct object was possible, we plotted all flight paths to one feeder when it presented the correct form (Fig. 5, B). According to the two locations where, in principal, a reward could be obtained, about one half of the

Fig. 5A,B Percentage of correct choices (A) of three *Glossophaga soricina* and flight paths (B) of an individual bat trained to discriminate between a rewarded artificial vexillum and an unrewarded triple mirror in a two-alternative forced-choice paradigm. **A** The results of three successive nights of training are presented for one bat. For every 60 decisions the percentage of correct choices was calculated and plotted against the number of visits. At the right side the discrimination level attained by three different bats is shown. **B** Flight paths towards the left feeder when presenting the correct object. The bat steered to either side at about 50% (two bundles of traces right hand). Note that the recognition distance can be estimated only when the bat in the beginning had chosen the wrong route. In these cases it turned towards the correct side when it was between 15 and 50 cm distant to the feeder. Registration time was 90 min, all correct flights to the left feeder (30 out of 34) are shown



approach flights was directed to one or the other feeder. In case the correct form was at the end of the chosen route the bat continued its path, and it was therefore impossible to tell at which distance the bat might have realized to approach the correct object. However, if the wrong object was at the end of the flight path, the bat either slowed down and turned to the other feeder presenting the correct form (Fig. 5B, upper part) or it made a wrong decision (not shown here). The range of turning towards the correct side was between 15 and 50 cm. Thus, we conclude that the critical distance to recognize a small object (ca. 2 cm diameter) is within that distance.

Echoes of *Mucuna* flowers

To estimate the cues which might be used for recognition of a flower by echolocation, it is helpful to know how the echoes of the three different stages look like and which cues could be used for discrimination. Here we focus on the distribution of the overall reflected energy and the spectral composition of the echoes in dependence of sound incidence angle.

With a technique described in Materials and methods we determined the “spectral directional pattern” for the frequency range between 20 and 140 kHz, which can be regarded as an “acoustic fingerprint” of the three stages of the *Mucuna* flower (Fig. 6). However, echoes will be reflected only in the frequency range of the bats’ own echolocation calls, which are short multi-harmonic downward modulated sweeps in the range 140–60 kHz. Thus, only this frequency range is relevant for the bat.

The overall amplitude (measured between 60 and 140 kHz) of the echoes differs in the three stages. It is low in the bud between -50° and 50° , while the virgin flower shows a broad relative maximum in that range. In the exploded flower, probably due to the gaping keel, the maximum around 0° is even more prominent (compare Fig. 6, upper curves in A, B, C). In addition, the staminal column may produce an early faint echo, which may also contribute to recognize the exploded status of a flower.

Further information can be gained from the spectral composition of the echoes, which is plotted in dependence of angle of sound incidence (Fig. 6). For example, the virgin flower (Fig. 6B) facing speaker and

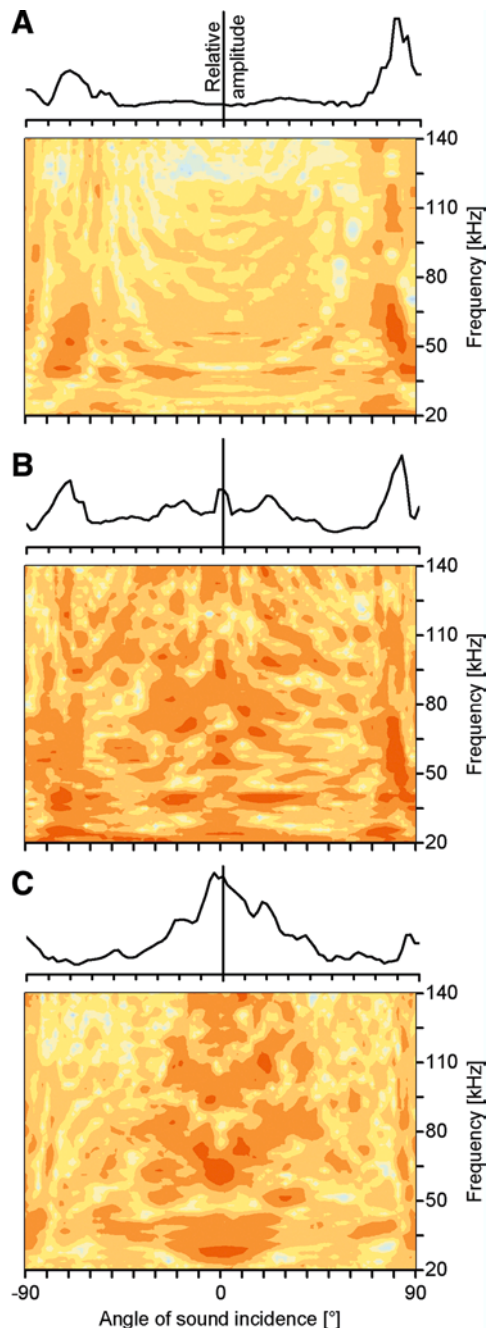


Fig. 6A–C Spectral directional echo pattern (“echo fingerprint”) of a bud (A), a virgin (B) and an exploded flower (C) of *Mucuna holtonii*, measured in dependence of the angle of sound incidence. The graded colours represent the intensity of the echo at a given frequency (*ordinate*) and angle of incidence (*abscissa*). 0 dB refers to an echo given by a metal plate at the same distance. For steps of attenuation compare scale in Fig. 7. Above the “fingerprints” the overall intensity of the echo is plotted for frequencies above 60 kHz. The flowers were mounted as in the natural situation facing speaker and microphone at 0°, ±90° corresponds to sound incidence from the left and right side of the flower, respectively

microphone at 0°, reflects a strong echo in the range 55–65 kHz, while around 70 kHz it is attenuated by more than 18 dB relative to the maximum value, and the echo is strong again at 90 kHz. Changing the angle

of sound incidence by only few degrees can result in dramatic changes of spectral composition of the echo. The concave shape of the vexillum gives rise to interferences of sound waves which result in enhancement of some frequencies and attenuation of others. Thus, circling around a flower, a bat will perceive a sequence of echoes with changing spectral composition from one call to the next.

Nevertheless, the patterns of the echoes are characteristic for each stage of the *Mucuna* flower due to the differences in their shape. In Fig. 6 these pattern of echoes are presented in one plane only; but, of course, different spectral patterns will result for any other plane of sound incidence. As an example, the directional spectral distributions for the horizontal and the vertical plane are given for a natural and an artificial vexillum (Fig. 7, upper two panels). Depending on the angle of approach a bat will receive very different sequences of echoes (cf. Fig. 7, horizontal, left and vertical, right). The rapidly changing spectral composition as a function of the inclination angle makes clear that the spectral distribution in the horizontal plane will be highly dependent on the inclination of the vexillum.

While the echoes of the isolated natural vexillum and the replica, in principal, show a similar spectral composition (Fig. 7), the echoes of a triple mirror (Fig. 7, lower left panel), due to its geometry, differ considerably in that (1) all frequencies are reflected nearly equally strong, and (2) the directional spectra of different planes are equal between +45 and –45°.

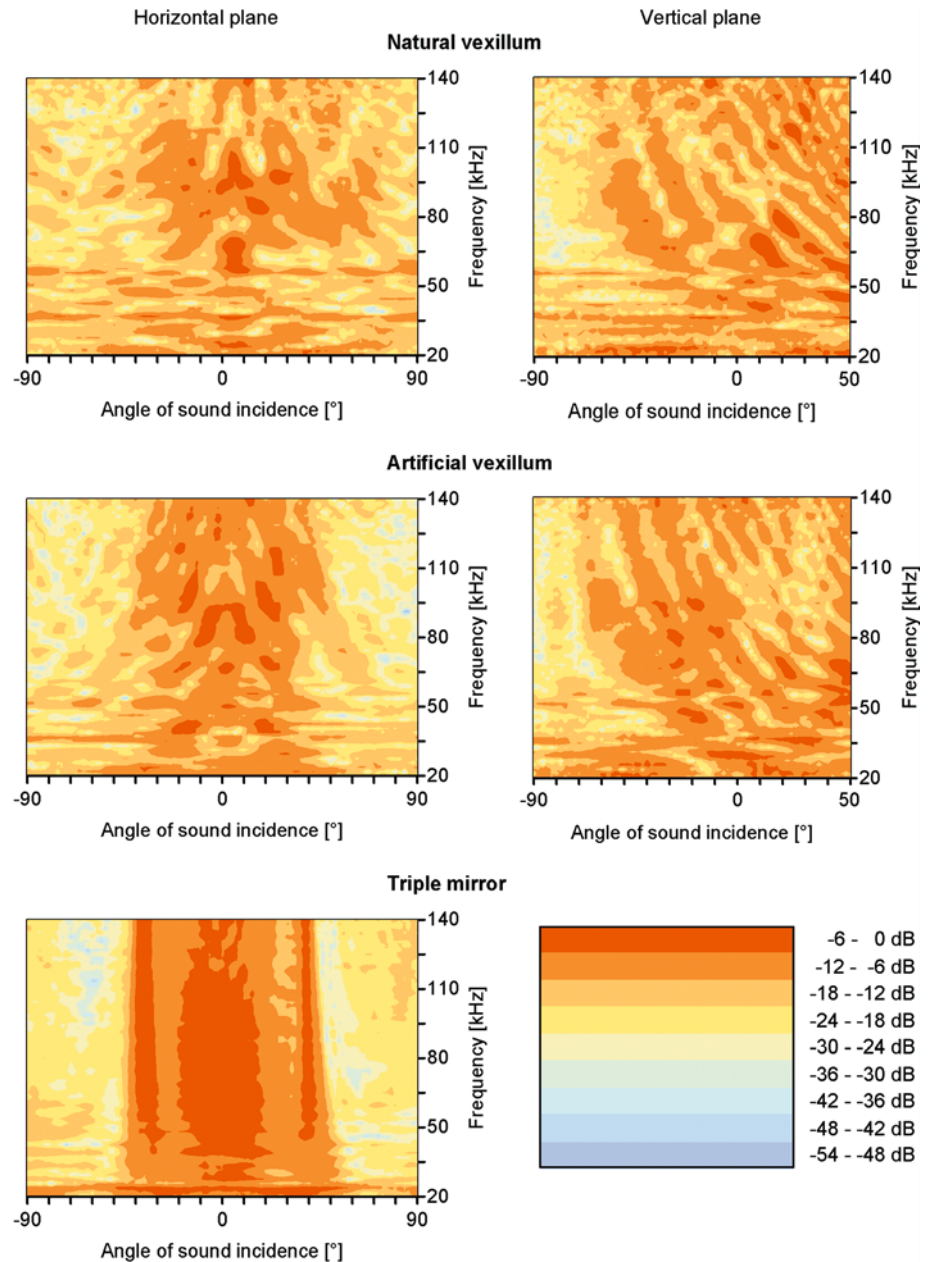
Discussion

Our field experiments show that the nectar-feeding bat *G. commissarisi* discriminates between the different flowering stages of the vine *M. holtonii*. The bats preferentially seek for the nectar-rich virgin flowers, land on them and, by triggering an explosion mechanism, obtain access to the nectar. Once exploded, a flower ceases nectar production and therefore is no longer attractive for the bats. The different flowering stages are characterized by different patterns of echo sequences, which may be used to discriminate between the flowering stages.

Object recognition by echolocation

The acoustic world of a bat primarily is built up by concentric spheres, defined by their time delays (Simmons et al. 1990). In a highly cluttered space many of these spheres will reflect echoes which superpose to one amplitude/time function at each of the two ears. Obviously, one such function will normally not contain enough information to reconstruct the surrounding world. To internally build up a three-dimensional representation of the outside world during flight, subsequent echoes of many calls have to be compared in relation to the

Fig. 7 Spectral directional pattern (“echo fingerprint”) of an isolated natural vexillum (*top*), an artificial vexillum (*middle*), and a triple mirror (*bottom*). *Top, middle—left panel*: the vexilla were mounted according to their natural position, i.e. inclined by about 20°. -90° refers to the left side of the vexillum (viewed from the speaker), +90° to the right side. *Top, middle—right panel*: rotation on the transverse axis of the vexillum. The front side of the vexillum (with the tip pointing to the left) was facing the speaker at 0°. At -90° the tip pointed to the speaker, at 50° the object was irradiated from its lower edge. The rapid change of the spectral components in the vertical plane makes clear that slight variations of the inclination can lead to drastic changes of the spectral composition in the recordings of the horizontal plane (this probably explains why the two fingerprints of the natural and the artificial vexillum are somewhat different). The triple mirror faced the speaker at 0°, tip and opposite edge being in a vertical plane. For geometrical reasons the echo of a triple mirror shows no spectral variation, irrespective of the axis around which the object is rotated. Gradation scale for attenuation is valid for Figs. 6 and 7



bat's changing own position, and echo components originating from different objects have to be extracted over calls, grouped and processed in parallel. This means anticipating echoes, confirming them with subsequent echoes, or correcting them by adding new information, and so on. Such a procedure may be called a “scene analysis” (Moss and Surlykke 2001).

For the task of recognition of small motionless objects, e.g. a *Mucuna* flower, characteristic features such as change of intensity, duration and spectral composition have to be extracted from the echoes. Subsequent echoes have to be compared, at the same time taking into account the position relative to the flower. Our training experiments and the echo fingerprints suggest that the changing spectral composition of the echo sequences, as shown in the echo fingerprints, seems to play

an important role for object recognition. This is in congruence with the suggestions of earlier authors claiming the spectral components to be the decisive cues (Bradbury 1970; Simmons et al. 1974; Habersetzer and Vogler 1983; Schmidt 1988; Mogdans and Schnitzler 1990; von Helversen et al. 2003).

The high-pitched, short downward modulated broad-band sweeps of glossophagine bats seem to be well suited for this task. The brevity of calls enlarges the clutter free window allowing the bats to come very close to the objects. The high frequency range allows a good resolution of small structures, although only applicable in short distances because of the high attenuation of high frequencies, especially in humid air. The broad spectrum (enlarged by the harmonics) contains multiple acoustic information, the spectral bands

of which may be analyzed in parallel. Thus, the calls of glossophagine bats, like most of the other phyllostomid bats, are similar to those of other gleaning bats like *Plecotus* (Vespertilionidae) or *Megaderma lyra* (Megadermatidae) (Schmidt et al. 2000; Leippert et al. 2002) that face similar tasks while foraging in close vicinity of vegetation. This similarity is independent of the phylogenetic relationship and can be regarded as a convergent development to optimize object recognition.

The function of the vexillum

The detection of a virgin flower occurs stepwise during the approach flight. The large free-hanging inflorescence of *Mucuna* probably produces a remarkable echo of its own, which may be assumed to be attractive for a bat over larger distances. Because of its concave shape, the echoes of a vexillum differ characteristically from the echoes of other surrounding structures mainly in two respects: first, by their persistence during several echolocation calls emitted by a passing bat, and second by their unique, angle-dependent spectral composition.

While a bat would receive a loud echo from plane objects such as leaves only when the wave front of the call arrives perpendicularly to the surface, the echoes of the concave shaped vexillum are reflected back to the bat within a much broader range of incidence angles. Like an acoustic cat's eye it is detectable from all directions within about $\pm 50^\circ$. Thus, for a passing bat, the echo of a vexillum will persist for many echolocation calls, and therefore may be conspicuous, while the echoes of plane structures appear as short glints here and there during one call only.

Multi-path reflections at the surface of the flower and the resulting interference of sound waves, cause the spectral distribution of the echoes to be "coloured" and characteristic, but different for various directions of sound incidence (von Helversen et al. 2003). Probably, not single echoes will allow recognition of an object, but sequences of echoes will provide enough information to the flying bat. The rapidly changing spectral composition of the echoes may contrast with the echoes of the surrounding, which do not show such drastic spectral changes (Müller and Kuc 2000). Moreover, flowers with a characteristic shape such as the *Mucuna* vexillum give rise to typical echo sequences, which could be learned and recognized by the bat.

Whereas a vexillum may be detectable out of a larger distance, the much shorter distance of 15–50 cm, measured in the discrimination experiment, may be necessary for the recognition of the fine structure. This would well correspond to the course of foraging flights observed in the field. It is clear that the vexillum acts as a target. Frame-by-frame evaluation of videotapes revealed, that a virgin flower generally is "inspected" (i.e. the bat approaches the flower hovering very close) at least once before the bat lands to explode the flower. This suggests that the bat needs accurate spatial information for the

following landing manoeuvre. This is corroborated by the observation that flowers with the natural vexillum rotated by 20–30° were not exploded, while intact flowers were mostly exploited during the first landing.

The experiments in which the vexillum was replaced by a triple mirror revealed similar results. Triple mirrors producing a loud echo over a wide range of frequencies and incident angles (see Fig. 7) were frequently inspected and thus were attractive (see Fig. 4). However, the bats seemed to have difficulties to land on the flower correctly and to find the point where to exert pressure to release the explosion mechanism. Thus, in the close range, the characteristic echo of the vexillum (in combination with the rest of the flower) may also act as an acoustic guide for an exact landing which is necessary to successfully release the explosion mechanism. Because the echo of a triple mirror is uniform over a broad range, a triple mirror might not be suited for this purpose.

Foraging behaviour

Mucuna is attractive for bats in that it offers a rich reward, especially when numerous inflorescences hang in close vicinity, each offering about four to eight flowers/night. Virgin flowers guarantee a high reward (100 μ l nectar at a time), while in other bat-pollinated plants the amount of nectar is unpredictable and may be even zero, when the flower was just emptied by another bat. However, unlike other plants with single flowers at a fixed place producing nectar throughout many hours during the night, in *Mucuna* the local spots of high reward change when virgin flowers are emptied and further flowers raise their vexilla during the course of the night. As a consequence, bats visiting *Mucuna* are permanently searching for newly opened flowers, of course, within a rather stable arrangement of inflorescences, which are expected to be well known to the bats. The function of the vexillum as an acoustic cat's eye being conspicuous within a broad range may be an adaptation to facilitate their detection. Once detected, a virgin flower should be exploited immediately before it might be found and exploited by another bat. Nevertheless, a foraging bat sometimes inspected several flowers before it started to crack them one by one, obviously memorizing various new flowers at different inflorescences during one foraging bout. The typical back and forth foraging flights below and among the inflorescences (Fig. 2) may be the energetically most efficient strategy for exploitation in an area of changing spots of reward. Thus, optimal foraging in *Mucuna* differs from the trap lining behaviour which may be efficient in plants offering nectar at one fixed place throughout the night.

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