

## ‘Binaural echo disparity’ as a potential indicator of object orientation and cue for object recognition in echolocating nectar-feeding bats

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### Summary

Echolocating bats emit ultrasonic calls through their mouth or their nostrils and receive echoes from objects with both their ears. Information conveyed in the echoes is the basis for their three-dimensional acoustic perception of the surroundings. The direction of an object is encoded in binaural echo differences, i.e. on the one hand in the different arrival times of its echo at the two ears, and on the other hand in spectral differences through direction-dependent frequency filtering of head and pinnae. Insufficient attention has been paid, however, to the fact that three-dimensional objects produce structured spatial echo fields, and that the position of the ear in this field determines the echo it receives. We were interested to determine whether the two ears, in addition to direction-specific echo differences, receive object-specific echo disparities that might be useful for the bat. Our measurements with an artificial bat head, which consisted of two microphones and a small ultrasound loudspeaker arranged to resemble a bat's ears and mouth, revealed that echoes at the two ears differed largely depending on

the shape and orientation of the echo-giving object. Binaural echo disparities of a bat-pollinated flower did indeed carry information about the orientation and, to a lesser extent, the shape of the flower. During flower approach such object-specific binaural echo disparities even exceed the binaural differences encoding direction of echo incidence, because the echo from the flower in front undergoes the same directional filtering by the two symmetrical ears. Nectar-feeding bats could use these object-specific binaural echo disparities not only to determine the object's orientation relative to the approaching bat, facilitating flight planning, but also to improve object recognition through spatial reconstruction of details of the object creating the echo. Our results suggest that the evaluation of binaural echo disparity has a greater importance for these tasks than has previously been assumed.

Key words: echolocation, acoustic object recognition, bat-pollinated flower, impulse response.

### Introduction

Sensory organs often come in pairs. Arthropods have pairs of antennae, bilateral-symmetric animals have pairs of main eyes and, with few exceptions, one pair of ears, irrespective of the amazing diversity of acoustic sensory organs. The advantage of this duplicity is that two spatially separated sensors will pick up differences in the complex spatial field of the adequate stimulus, which can be increased additionally through differing receiver characteristics. The resulting bilateral disparities between the outputs of both sensory organs are important perceptual cues not only for spatial perception but also for the recognition of objects.

Spatial vision, for example, is facilitated by binocular fixation of an object. Besides the angle of convergence of the two eyeballs and the degree of accommodation, the human central nervous system (CNS) utilizes differences between both retinal images of an object, i.e. the binocular disparity, to assess spatial information. Thereby, neurons of cortical area V1 systematically evaluate if structures lie before or behind the

focal plane or more specifically the binocular horopter (e.g. DeAngelis, 2000). Binocular disparities are used for judging both the position (distance and direction) and the three-dimensional structure of objects.

Echolocating bats derive a three-dimensional representation of their immediate environment by emitting ultrasonic vocalisations and listening for echoes generated by objects in their surroundings. Their CNS evaluates acoustic information contained in these echoes to construct an acoustic image of the world. This biological sonar allows bats to orient, avoid collisions in flight and to find and acquire their food (Griffin, 1958).

The two copies of each particular object's echo that reach the two eardrums can differ considerably, and bats evaluate such differences by the mechanisms of directional hearing to derive the position of objects. The CNS evaluates interaural differences in intensity (IID) and in time of arrival (ITD) that are indicative of the horizontal angle towards the echo-bearing object. By adding pinnae to their ears bats and other mammals

generate direction-specific spectral filtering, which encodes the vertical bat-to-target angle (Grinnell and Grinnell, 1965; Fuzessery, 1996; Wotton et al., 1995; Firzlaff and Schuller, 2003; Firzlaff and Schuller, 2004; Aytekin et al., 2004). Echolocating bats time the delay between call and echo as an indicator of object distance (Griffin, 1958). In behavioural tests bats reached remarkable acuity/resolution in range determination (Simmons et al., 1995a; Moss and Schnitzler, 1995).

A second important task of echolocation is object recognition, and bats evaluate the echo's fine structure to extract information about the object behind the echo. An echo arises whenever sound meets a discontinuity in the density of the transmitting medium. For flying bats this is often a solid object surrounded by air. Complex objects have a fine structure of several small surfaces perpendicular to the angle of sound incidence. Each such surface will generate a separate first-order reflection called a glint. The time course of glints in the complex echo shows the range distribution of reflectors in the complex object (Simmons and Chen, 1989; Kuc, 1997). The overall strength of the reflections is an indicator of object size [target strength (Urlick, 1983; Simon et al., 2006)], and the echo duration marks its depth (von Helversen et al., 2003).

There are several experiments showing that insectivorous bats can recognize characteristics of possible prey objects by echolocation (Griffin, 1958; Simmons and Chen, 1989; von der Emde and Schnitzler, 1990). However, relatively few experiments show that bats can recognise totally motionless objects by echolocation, particularly when close to clutter-generating background structures: *Phyllostomus* can recognize and find the fruits of the Cucurbitaceae *Gurania*, which is eaten by these bats, guided by their echolocation alone (Kalko and Condon, 1998). Carnivorous and insectivorous bat *Megaderma lyra* can detect its prey even when it is motionless (Schmidt et al., 2000). *Glossophaga commissarisi* finds the flowers of the bat-pollinated vine *Mucuna holtonii* with the help of echo orientation (von Helversen and von Helversen, 1999) and recognizes even the degree of ripeness of the bud (von Helversen and von Helversen, 2003). With artificial objects nectar-feeding bats were not only able to discriminate between different types of artificial hollow forms, but even generalized certain shapes independent of size, which might involve some kind of three-dimensional shape perception by the bats (von Helversen, 2004). However, our understanding of how bats can achieve this is poor at the theoretical level (but see Kuc, 1997; Kuc, 2001; Müller and Kuc, 2000) as well as at the neurophysiological level. Simmons and Chen discuss this problem (Simmons and Chen, 1989).

Yet, to the best of our knowledge, there has been no systematic study of whether the echoes heard by both ears of a bat can differ significantly, not through direction-specific spectral filtering, but also because the object itself sends two different echoes in the directions of the two ears. Such differences can arise when the object's three-dimensional gestalt presents two different range profiles towards each ear, but were often considered negligible because the ear distance

seemed too small to receive noticeable gestalt-specific disparities (e.g. Pollak, 1988; Pollak and Casseday, 1989). Simmons et al. mention such object-specific disparities on a temporal scale and their potential relevance for target discrimination (Simmons et al., 1995b).

It is thus of special interest to know if such gestalt-specific binaural disparities exist and whether they are useful for recognition of objects. Kuc designed a (large) biomimetic robot (Kuc, 1997), which could focus objects with two mobile ears and thereby align itself to the objects by evaluating direction-dependent binaural differences. Additionally, this system could differentiate the front and back of a coin based on the glint pattern generated by the coin's relief patterns. The authors also reported that their left and right microphones picked up different echoes, but did not evaluate such differences for object recognition, nor did they attempt to reconstruct object features from binaural echo disparities. Their biomimetic robot had a mouth-to-ear distance about 10 times wider than a bat.

In the following we report measurements of the disparity of the echo signals of a metal cube and a bat-pollinated flower, which are picked up by two microphones when the spatial arrangement of loudspeaker and microphones resembles the relative position of mouth or nostrils and the ears in an echolocating bat. We analyse whether gestalt-specific binaural disparities acoustically encode information about the objects' orientation, and also about its size and shape. Finally, we discuss whether such binaural disparities might actually be accessible to the bat with its limited acoustic information processing powers.

For this study we chose flowers of a bat-pollinated plant, because nectar-feeding bats depend on these flowers' echoes to localize them, to guide their in-flight approach and to find the right approach angle to reach the nectar chamber. Visits at a flower last for fractions of a second and often involve hovering (von Helversen and Winter, 2003). Because chiropterophilous plants gain fitness when they attract bats more efficiently, some of them have evolved flowers with echoacoustic features that are conspicuous to their echolocating pollinators (von Helversen and von Helversen, 1999; von Helversen and von Helversen, 2003; von Helversen et al., 2003). Here we discuss the binaural echoic features of a bat-pollinated flower on structural and evolutionary grounds.

## Materials and methods

### *Arrangement of loudspeaker and microphones – the 'artificial bat head'*

We used a custom-built condenser speaker of 15 mm diameter and two 1/4" microphones without protecting grid (GRAS 40BF with preamplifier 26AB and power module 12AA; GRAS sound & vibration, Holte, Denmark). This combination allows measurements up to 140 kHz, covering the frequency range of echolocation calls of flower-visiting bats.

The microphones were placed on top of either side of the loudspeaker. The distance between the centres of loudspeaker and microphones was 18 mm and 14 mm between the centres

of the microphones. Microphones and loudspeaker were pointing in the same direction and all three membranes were in the same plane (Fig. 1).

#### Measurement set-up

Target objects were presented on a thin holder mounted in the centre of a small turntable. The 'artificial bat head' was placed at a distance of 20 cm at the same height (20 cm) as the target object and pointed in its direction (Fig. 1). The turntable allowed the objects to be ensonified from all directions in one plane. The front view of the objects was adjusted to 0°. This arrangement resulted in a total angle between the centre of each microphone, the centre of the target and the midpoint of the loudspeaker membrane of 5°9'. The corresponding horizontal angle was 2°1'.

#### Echo measurements

Due to its small size, the loudspeaker could not produce a single broadband click of sufficient sound pressure. Therefore, we employed the so-called Maximum Length Sequence (MLS) method. A MLS is a deterministic sequence of impulses of variable length showing a perfectly narrow autocorrelation function. We used a custom-built sound generator (USSY, Technische Hochschule Darmstadt, Germany) to continuously replay a MLS of 16383 samples. At a rate of 500 kHz, each repetition lasted for 32.766 ms. The microphone signals were digitised with 12-bit resolution and recorded either on a custom-made hard disc recorder or a custom-made A/D DSP-Card in a desktop computer (both: Institut für Technische Elektronik, Universität Erlangen, Germany). Replay and recording were sample-synchronous.

From MLS recordings the echo's impulse response function was derived by a Fast Hadamard Transformation (FHT). The target's echo impulse response was then separated in the time domain, and its frequency response (spectrum) was calculated (FFT; window size 1024 samples; rectangular window). To

correct for the frequency characteristic of loudspeaker and microphones, we recorded the perpendicular reflections from a large metal plate (plate diameter: ~40 cm). The object's actual echo spectrum, without influence of loudspeaker and microphone, is the complex difference between the spectra of the metal plate and the object. The distance of 20 cm between object and 'artificial bat head' was chosen because then the spectrum indicates the echo amplitude at a reference distance of 10 cm related to the incident amplitude measured at the place of the object. This complies with the definition of 'target strength' as given (e.g. by Møhl, 1988) and therefore the calibrated spectra can be called 'spectral target strength'. Calculations were performed with the programs MONKEY FOREST (Audio & Acoustics Consulting, Aachen, Germany) and MATLAB 6.5 (The MathWorks, Inc., Natick, MA, USA).

We turned the turntable to obtain the objects' echoes from different directions in a horizontal plane in steps of up to 1°. For each direction, signals picked up by the two microphones were recorded successively. Echoes from a range of ±60° around frontal orientation were recorded in 2° steps. For the flower, angles between ±5° were measured at 1° resolution in addition, to get a higher resolution of the small-scale acoustic echo pattern in this angular range (see below).

#### Objects

Echo measurements were obtained for two objects: first, a metal cube with a side length of 10 mm and second, a bat-pollinated flower collected in a Costa Rican lowland rainforest and measured immediately, i.e. under normal turgor. We chose flowers of *Vriesea gladioliflora*, a bromeliad growing in the canopy of tropical rainforests in Central and South America. The monaural acoustic properties of these flowers have been described (von Helversen et al., 2003).

#### Reconstruction of object features from binaural disparities in glint delays

Complex echoes consist of several basic echoes, so-called glints, originating from different reflective substructures in the complex object. The temporal delay pattern of glints reflects the spatial patterns of reflective substructures in the object (Simmons and Chen, 1989). We analysed the binaural differences in glint delays to calculate the position of the glint-bearing structure in a horizontal plane. As a measure of the glint delays we used the times of ascending zero crossings in the target's IRF. Only zero crossings above a minimum steepness were included. In order to localize the underlying substructure the glint needed to be present in the IRFs of both ears. From each pair of corresponding glint delays the substructure's position was triangulated based on the microphone distance of 14 mm and for a speed of sound of 340 m s<sup>-1</sup>.

#### Results

##### Binaural spectral disparities generated by a metal cube

Fig. 2 depicts impulse response function (IRF) spectra picked up by the two microphones at a distance of 20 cm from a metal

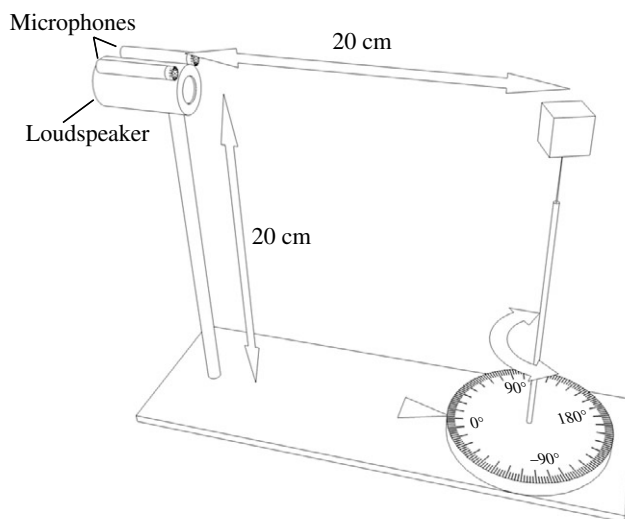


Fig. 1. Schematic drawing of the recording setup with the artificial bat head, consisting of one loudspeaker and two microphones and a turntable with a holder. The object presented is a metal cube.

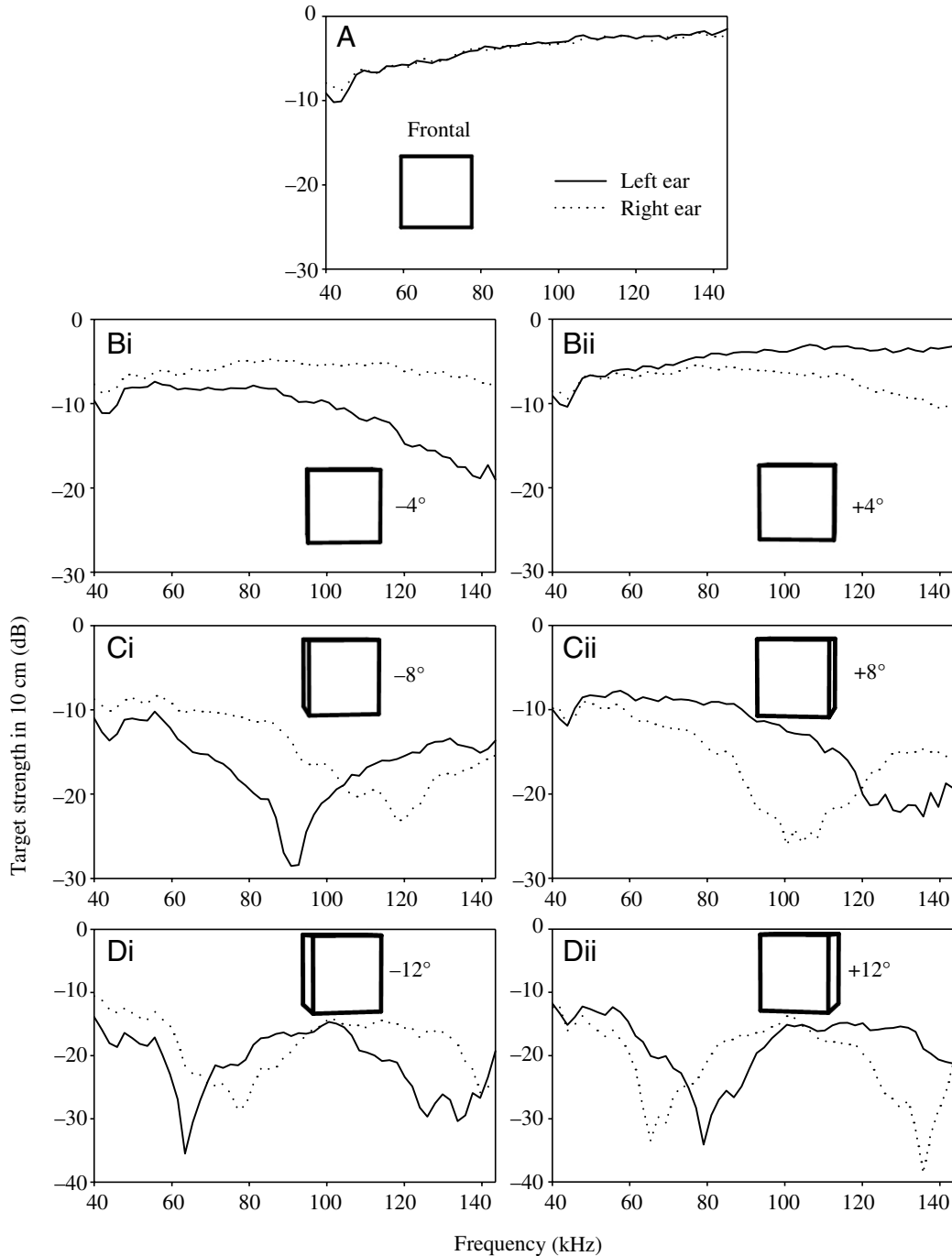


Fig. 2. Left and right ear cube echo spectra for bat to cube angles from frontal (A,  $0^\circ$ ) and from  $-12^\circ$  to  $12^\circ$  (B–D). FFT size: 1024, rectangular window. Insets: schematic of cube in respective turning angle.

cube. The horizontal angle between mouth, cube and ear was  $2^\circ 1'$ . When one side of the cube was perpendicularly facing the bat's head, both ears picked up almost exactly the same echo, with no spectral notches (Fig. 2A,  $0^\circ$ ). Turning the cube to the left and right side ( $4^\circ$  steps, see text and inset in Fig. 2B–D) resulted in a gradual change in the echo spectrum, with one spectral notch visible at  $-8^\circ$  and  $+8^\circ$  and two notches at  $-12^\circ$  and  $+12^\circ$ . Equal turns to left and right resulted in almost mirrored left and right spectra (compare Fig. 2Bi–Di and Bii–Dii).

Fig. 3 shows interaural intensity disparities (IIDs) at different frequencies in the IRF spectra for angles between the

bat and the front of the cube from  $-10^\circ$  to  $+10^\circ$  in  $2^\circ$  steps. IIDs in frontal direction ( $0^\circ$ ) were at 0 dB, and IID was positively correlated with bat to cube front angle at all frequencies. IID increased faster with angle at high frequencies than at low frequencies. The  $-2^\circ$  to  $+2^\circ$  difference was approx. 1 dB at 50 kHz and increased to about 7 dB at 130 kHz. The angular region over which IID increased monotonically was larger at low frequencies ( $>20^\circ$  at 50 kHz and 70 kHz) than at high frequencies ( $10^\circ$  at 130 kHz). Equivalent IID vs angle functions were found for all intermediate frequencies from 40 kHz to 140 kHz.

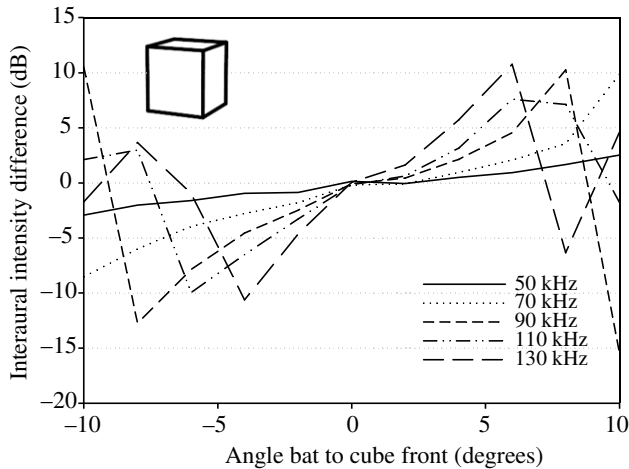


Fig. 3. Interaural intensity differences of echoes of a metal cube as a function of the angle between bat and the cube's front for frequencies from 50 to 130 kHz.

#### Binaural amplitude differences of a bat-pollinated flower's echoes

Fig. 4 shows the relative overall rms amplitude of the IRFs of *V. gladioliflora* as a function of angle between bat and flower axis over the range from  $-5^\circ$  to  $+5^\circ$ , which is the relevant range for the approaching bat to find the entrance to the nectar chamber.  $0^\circ$  (frontal) indicates that the plane defined by the front of the corolla ridge was perpendicular to the head to flower axis. In this frontal direction amplitude was the same at both ears. Amplitude was highest at slightly different angles of  $-1^\circ$  and  $+1^\circ$ , respectively. Both curves are similar, but not identical and seem to be separated by  $2^\circ$ . Interaural disparity in overall amplitude, i.e. the difference between the two curves, would suffice for lateralization over the complete range of angles, but it would be an unambiguous indicator of bat to flower axis angle only between  $-1^\circ$  and  $+1^\circ$ .

#### Binaural spectral disparities of a bat-pollinated flower's echoes

Fig. 5 presents spectra of the same IRFs as a function of angle between bat and flower axis. Spectra span 40–145 kHz i.e. the complete spectral bandwidth of the echolocation signals of their main pollinators [Phyllostomidae; Glossophaginae (von Helversen and Winter, 2003)]. At the frontal angle of  $0^\circ$ , spectra picked up by both ears were very similar up to 90 kHz (Fig. 5A). The differences at higher frequencies presumably result from the fact that the flowers of *V. gladioliflora* are not completely bilateral symmetric.

With increasing absolute angle the spectra changed markedly. Such changes were at least partially bilaterally symmetric (Fig. 5). At  $-1^\circ$  the left ear received a higher level, whereas at  $+1^\circ$  the right ear leads in a nearly opposite pattern (Fig. 5B; 40–90 kHz). A similar symmetry is found at  $+2^\circ$  vs  $-2^\circ$  and  $+3^\circ$  vs  $-3^\circ$  (Fig. 5C,D). However, here the leading ear is switching at about 80–90 kHz for  $+2^\circ$  vs  $-2^\circ$  and at about 70 kHz for  $+3^\circ$  vs  $-3^\circ$ . This is in agreement with the changes

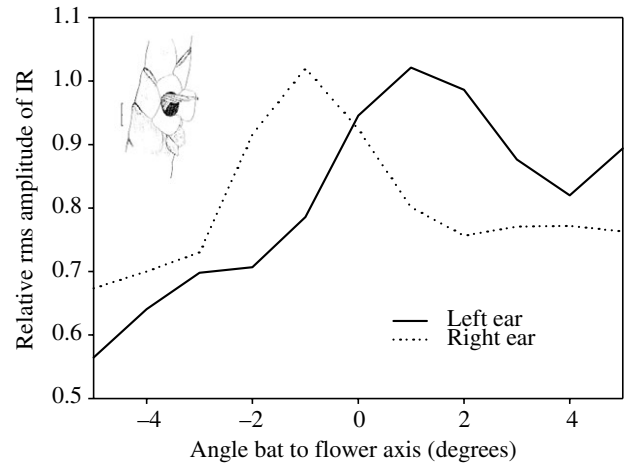


Fig. 4. Overall relative root mean square (rms) amplitude of IRFs of *V. gladioliflora* as function of the angle between bat and flower axis for left and right ear.

in overall amplitude as presented in Fig. 4. Also note that at opposite angles many spectral notches occur at similar frequencies in both ears (compare e.g. Fig. 4D;  $-3^\circ$  vs  $+3^\circ$ ).

Fig. 6 shows spectral IIDs for some frequencies between 40 and 90 kHz. At each frequency IID was 0 dB at about  $0^\circ$  with an increase to higher and a decrease to lower angles. At 40 kHz a monotonically increasing slope is present from  $-4^\circ$  to  $+5^\circ$  that spans about 20 dB in total. Thus, the bat to flower axis angle is encoded in the spectral IID at 40 kHz over a range of  $9^\circ$ . As in the cube (compare with Fig. 3), the steepness of the corresponding slope increased with frequency, and the angular range of monotonic rise shortened. At 90 kHz the IID increases monotonically only between  $-2^\circ$  to  $2^\circ$  but covers 17 dB. This basic pattern was found also at all intermediate frequencies between 40 and 90 kHz, but not above 100 kHz.

#### Binaural disparities of the impulse response of a bat-pollinated flower

Fig. 7 shows top views of the IRF as a function of bat to flower axis angle. Medium grey encodes an IRF amplitude of 0. Darker shades of grey stand for negative and lighter shades for positive amplitude. For comparison see the same IRFs plotted separately in Fig. 8 and Fig. 9. Fig. 7A gives a wide-angle view spanning  $-60^\circ$  to  $+60^\circ$  and covering the full duration of the IRFs of the left ear. The most noticeable feature in this panel are the two curves that cross at about  $0^\circ$  and are labelled right and left ridge of the corolla, respectively. The corolla of *V. gladioliflora* is bell-shaped, with a circular cross section and consists of three merged petals. It is embedded in a straight, stem-like inflorescence with only one flower open at a time. The apical parts of the three petals are separated and bend backwards, thereby forming a torus-like corolla ridge (see sketch in Fig. 6). All parts of this torus that are perpendicular to the direction of sound incidence will reflect sound and thus produce glints that superimpose. When the corolla is ensounded perpendicularly (from  $0^\circ$ ), the corolla



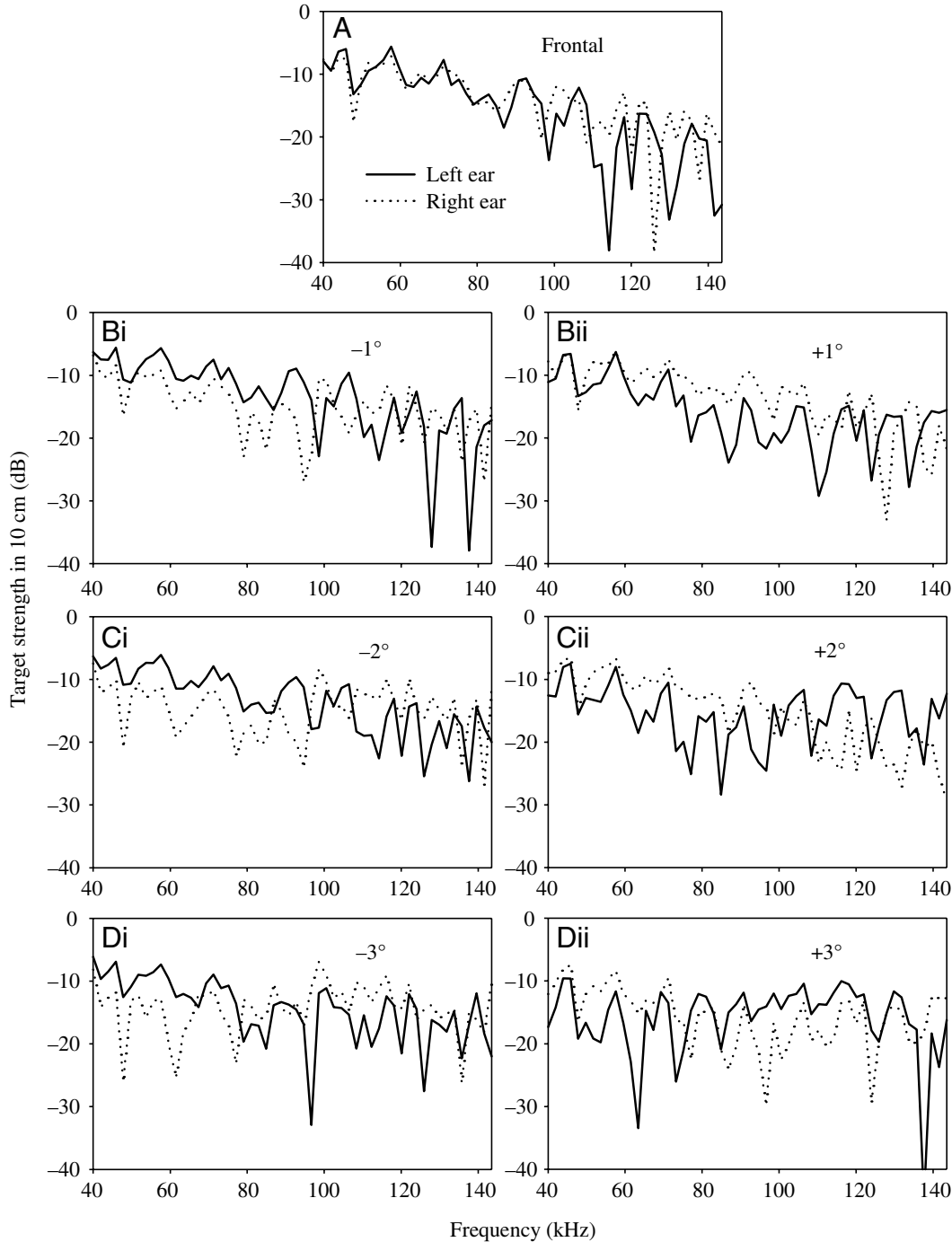


Fig. 5. Left and right ear *V. gladioliflora* echo spectra for bat to flower axis angles frontal (A, 0°) and from -3° to 3° (B–D). Frontal orientation, i.e. 0°, indicates that the plane of the front of the flower's corolla is oriented perpendicularly towards the bat head. The horizontal angle between mouth, flower and ear was 2°.

ridge reflects sound along its complete circumference, thereby producing one large glint. As a result the IRF amplitude at this frontal direction is highest (see Figs 7 and 9 at about 0°). When the flower is turned, only the left and right parts of the torus still present a surface perpendicular to the impinging sound and thus only these two parts generate two separate glints. The remaining top and bottom parts of the corollar ridge cannot produce glints, as they do not expose a surface perpendicular to the direction of sound incidence (in fact a faint such glint is visible that cuts through the centre of the crossing of the two main glints in Fig. 7A, but it fades soon as the flower is turned).

As the angle increases one side of the corollar ridge will get closer to the bat head while the other side moves backward, which brings forth the x-shaped crossing. Thus, the temporal separation between the two glints increases. At small angles the two left and right glints still merge into one prolonged glint (see e.g. Fig. 7Bi, left ear at +2° and +3°). At the left ear they become visible as two separate glints at angles above +4° and below -2° (Figs 7 and 9). The systematic changes in glint delay as the flower is turned are reflected in the curved appearance of the corresponding glint delays in Fig. 7.

Likewise, Fig. 7Bi,ii show the same IRFs for the left and

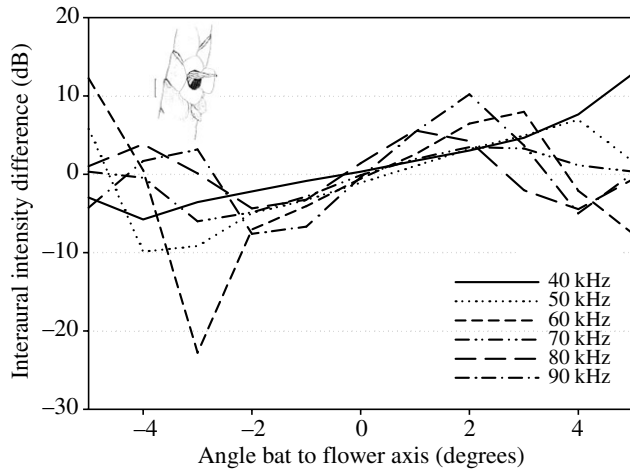


Fig. 6. Interaural intensity differences of echos of *V. gladioliflora* as a function of the angle between bat and flower axis for six frequencies from 40 to 90 kHz. Frontal orientation, i.e. 0°, indicates that the plane of the front of the flower's corolla is oriented perpendicularly towards the bat head.

right ear, respectively, separately, but for a reduced frontal range of  $-5^\circ$  to  $+5^\circ$ . The delay range was reduced to better reveal temporal detail of the two corollar ridge glints. The crossing of the glint delays and their merging at the frontal direction are clearly visible. The obvious difference between both ears is that the angle of crossing lies at  $-1^\circ$  at the right ear and at  $+1^\circ$  at the left ear.

To test whether these binaural differences in the IRF encode spatial information characterising the flower, we segregated the IRFs into separate glints. Fig. 8 exemplifies this with the two IRFs recorded from a lateral angle of  $5^\circ$ . The binaural IRF difference is remarkable. Both IRFs show two separate glints, corresponding to the left and right side of the corollar ridge respectively. The circles and drop lines in Fig. 8 indicate the zero crossing delays that serve as a measure of glint delay. The additional x-axis shows the distances between bat head and the glint-producing structures corresponding to these delays.

Fig. 9 depicts the changes in IRF over bat to flower axis angles ranging from  $-5^\circ$  to  $+5^\circ$  in  $1^\circ$  steps. IRFs in Fig. 9A,C are the same as in Fig. 8, but over a somewhat longer part of the IRF and also including glints from structures inside the concave corolla. Symbols mark corresponding ascending zero crossings as a measure of corresponding glint delays. Binaural glint delay difference ranged between  $-2.3 \mu\text{s}$  and  $+2.4 \mu\text{s}$  for the first glint and was  $-2.9 \mu\text{s}$  at  $-5^\circ$  and  $+3.0 \mu\text{s}$  at  $+5^\circ$  for the second glint. Fig. 9B shows a schematic top view horizontal section through a *V. gladioliflora* corolla at the corresponding turning angles. Superimposed are the locations of the objects behind the glints marked in Fig. 9A,C. The angular pattern of glint localisations reveals that spatial information about the flower is indeed present in the binaural IRF disparity: the first glint is always correctly localised at the point of the corolla that is closest to the bat. It is particularly interesting, how the first glint gradually moves from one side to the other along the front

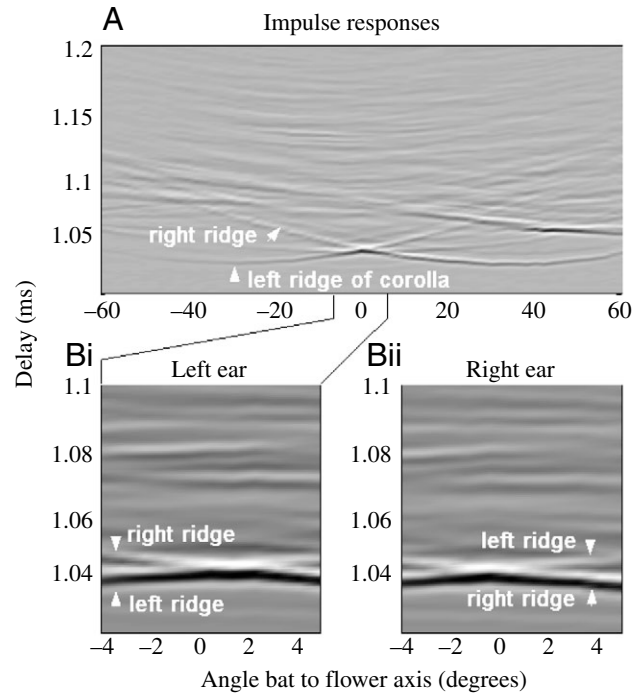


Fig. 7. Impulse response functions of *V. gladioliflora* as a function of the angle between bat and the flower axis. (A) Left ear wide angle from  $-60^\circ$  to  $60^\circ$  in steps of  $2^\circ$ . (B.i,ii) Left and right ear, respectively, from  $-5^\circ$  to  $5^\circ$  in steps of  $1^\circ$ . Medium grey stands for zero IRF amplitude. Higher amplitudes have lighter and lower values darker shades of grey. Compare Fig. 9C,A, which show the same IRFs as in B. Ridges of the corolla are designated left and right, as seen by the approaching bat. At  $0^\circ$  the plane of the front of the flower's corolla is oriented perpendicularly towards the bat head.

of the corolla when the flower is turned through the frontal orientation of  $0^\circ$ . The second glint from the more distant side of the corolla is absent because it merges with the first glint, in all but the largest angles, i.e.  $-5^\circ$  and  $+5^\circ$ . At these angles the second glint source is localized, according to expectations, at the opposite side of the corollar ridge. This means that binaural glint delay differences do indeed encode first the distance between the two sides of the corolla, i.e. its diameter, and second also the angle at which the corolla is tilted.

Further glints from structures inside the corolla are much smaller in amplitude than the ridge glints. Such glints are, with very few exceptions, localized within the corolla. They might originate from the staminal column, but are very likely the product of several superimposed glints of different floral structures and/or separate reflection pathways, which might explain why some are localized outside the schematic corolla.

## Discussion

We searched for object-specific information contained in the echoes received by the two ears of a bat irrespective of whether the bat may be able to extract this information, and found marked binaural disparities in overall amplitude, in echo

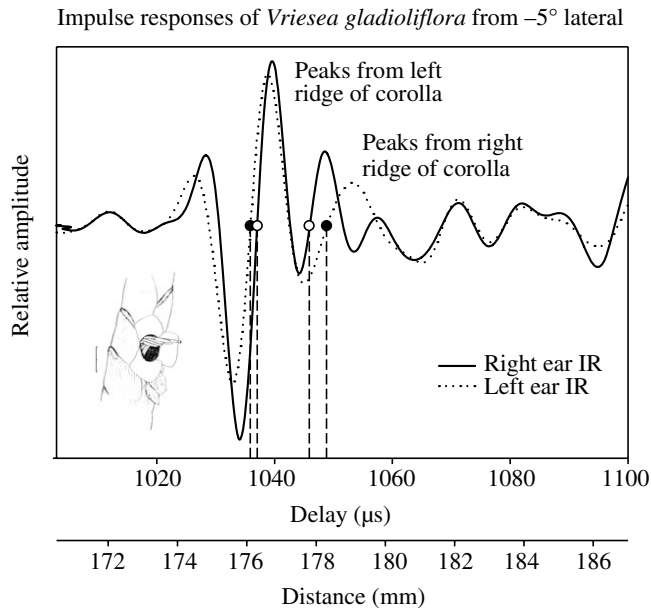


Fig. 8. First part of the left and right ear's impulse responses of a *V. gladioliflora* at a bat to flower axis angle of  $-5^\circ$ , showing the two initial peaks (i.e. glints). Circles mark the ascending zero crossings that serve as measures for the echo glints from the left ridge (first peaks) and the right ridge (second peaks) of the flower's corolla. Ridges of the corolla are designated left and right, as seen by the approaching bat. Drop lines indicate echo delay and the corresponding distances (second x-axis) between the respective ear and the reflective parts of the corollar ridge.

spectrum and the time course of the IRF. In the present study, we therefore asked whether such binaural disparities encode (a) the position of the flower, (b) the orientation of the corolla with respect to the approaching bat and (c) the size and shape of the flower. All this information is important to the nectar-feeding bat because it has to localise the flower accurately, approach it in flight from the correct angle and identify the right manner and place to reach the nectar chamber. Finally, we discuss whether bats might be able to extract this acoustic information in all necessary detail.

#### Binaural disparities encoding object position

The sonar head and the experimental setup were designed to exclude any direction-specific binaural echo disparities: the object was right in front of the microphones such that no intra-aural differences in arrival time (ITDs) arose. Additionally, microphones had no pinna-like structures and show a broad directionality, such that directional spectral filtering can be assumed to be weak. Because the microphones were identical and arranged symmetrically with respect to the target, such weak filtering would be identical in both ears. Thus, any echo disparity between the ears cannot be due to direction-specific frequency filtering and is purely gestalt specific.

The actual approach flight of a bat is similar to our setup in several respects. Once the bat has initiated its approach, it will direct its head towards the flower, thereby avoiding any

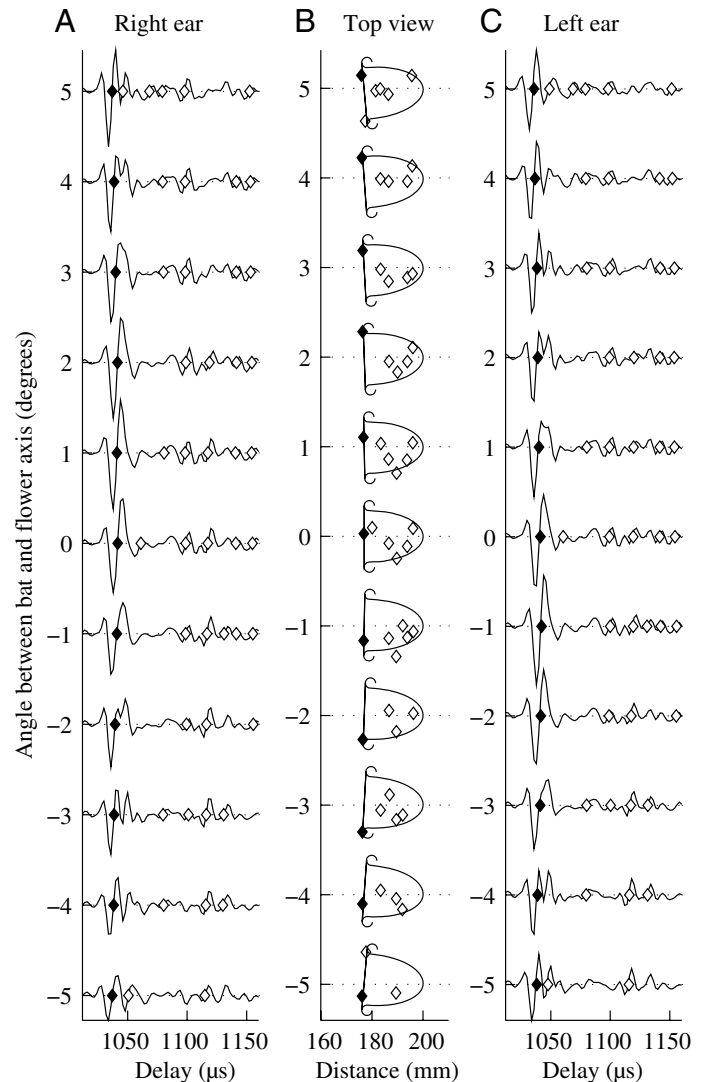


Fig. 9. Reconstruction of horizontal 2D flower structures from impulse responses of *V. gladioliflora* for eleven different angles between bat and flower axis from  $-5^\circ$  to  $5^\circ$ . (A) Impulse responses picked up by right ear. (C) Impulse responses picked up by left ear. Symbols indicate positions of pairs of steeply ascending zero crossings, which serve as a measure of separate glints. Filled symbols: first glint. (B) Top view of a schematic horizontal section through a *V. gladioliflora* flower turned by the respective bat to flower angle. Symbols indicate glint positions calculated using zero crossing time pairs and the artificial bat head's geometry. Note how the first glint position always coincides with the closest part of the corolla and moves from one side to the other.

direction-specific ITDs. Bats do have pinnae though, and direction-specific frequency filtering will occur. Yet, the two pinnae can be regarded as identical mirror images of each other and the frequency filtering will thus ideally be identical for an object right in front of the bat. Even though the echoes picked up by the two ears will contain spectral directional information, binaural differences would therefore only be gestalt specific.



*Binaural disparities encoding angle between bat and cube front*

Many animals can evaluate excitation differences at the two ears to localise a sound source [some examples: humans (Blauert, 1997); barn owl (Konishi, 2003), grasshopper (Michelsen and Rohrseitz, 1995)]. Figs 2 and 5 reveal that the power spectra of the objects' echoes show a characteristic distribution of maxima and minima that shifts as a function of the angle between bat and object axis. This results in a direction-specific spectral intra-aural intensity difference (IID) pattern (Figs 3 and 6). For the cube, spectral IID increased over a range of more than  $\pm 10^\circ$  at the lowest frequency (40–50 kHz) that is present in the nectar-feeding bat's calls (Fig. 3). Likewise, such information is still available at the highest frequencies of 130 kHz, but over a restricted range of angles. Assuming that bats have a threshold of 1 dB for spectral IIDs, they would be able to discriminate  $4^\circ$  at 60 kHz. Yet, above 120 kHz an angular change of  $4^\circ$  resulted in 5 dB IID, which translates into  $0.8^\circ$  mean angular resolution for cube orientation. 0 dB spectral IID reliably indicates an angle of  $0^\circ$  at all frequencies. Thus, binaural spectral disparities are an accurate measure of the orientation of the metal cube that is available over a large range of angles.

*Binaural spectral disparities encoding angle between bat and flower axis*

In the chiropterophilous flower, the binaural difference in overall echo amplitude (Fig. 4) and the spectral IID (Fig. 6) both convey information that might be used by a bat to judge the orientation of the floral corolla. Yet, such information is not equally available in both. Overall IID would reliably encode flower orientation only between  $-1^\circ$  and  $+1^\circ$  (Fig. 4). This is too narrow to guide the approach flight except perhaps at close range, during the very last phase of the approach. The angular availability of orientation information is much wider in spectral IID: at 40 kHz IID increases monotonically by 20 dB from  $-4^\circ$  and  $+5^\circ$ . At higher frequencies ( $\leq 100$  kHz) the angular range decreases, but the rate at which IID changes with flower orientation increases (Fig. 5). Assuming a spectral IID threshold of 1 dB, this would allow the bat to judge the orientation of the flower with a resolution well below  $1^\circ$  from the distance of 20 cm.

*Binaural temporal disparities encoding flower orientation and dimensions*

A complex object's echo impulse response function (IRF) shows several glints with delays corresponding to the distances of structures in the object generating them. So the glint pattern is an indicator of the depth profile of the complex object behind the echo (Simmons and Chen, 1989), and the relevance of binaural disparities in glint patterns for object recognition has been discussed (Simmons et al., 1995b). We report that IRFs picked up by the two ears can indeed differ considerably in a bat-pollinated flower (Fig. 8). Binaural delay disparity of the first glint was in the range of  $\pm 2.3^\circ$  between  $-5^\circ$  and  $+5^\circ$ . Through triangulation this can reveal the actual horizontal

position of the closest part of the flower's corolla (Fig. 9B, first symbol from the left in each plot). At absolute angles above  $5^\circ$  the two glints from both sides of the corolla were separated in time in the IRFs of both ears (Figs 7 and 9). Fig. 7A shows that the two glints are available in the IRFs from about  $-32^\circ$  to  $+26^\circ$  in *V. gladioliflora*. The glint separation time rises from  $9 \mu\text{s}$  at  $+5^\circ$  to  $58 \mu\text{s}$  at  $+26^\circ$  and from  $8 \mu\text{s}$  at  $-4^\circ$  to  $80 \mu\text{s}$  at  $-32^\circ$  at the left ear. Even with monaural hearing, double glint separation time would thus be a useful source of information about floral orientation available over a wide range of angles. However, this is only a relative measure of flower orientation, which also depends on the opening width of the flower. In contrast, the binaural disparity in the two glints' delays allows direct independent triangulation of the two respective horizontal points of reflection at the left and right part of the corolla (Fig. 9B at  $-5^\circ$  and  $+5^\circ$ ). The distance between these two points can provide information about the width of the opening of the corolla and the angle between the points can be a reliable indicator of the flower orientation. A triangulation based on the glint patterns in Fig. 7A confirms that the orientation of the flower can be inferred from the relative position of the two glints with high accuracy (measured angle =  $1.08 \times$  actual angle). Thus, glint structure in the IRF potentially is a valuable indicator of flower orientation and size that is present over a wide range of different approach directions.

Taken together, our results suggest that the orientation of *V. gladioliflora* flowers is available from spectral IIDs at angles from  $-4^\circ$  to  $+4^\circ$  where the two glints are merged in the IRFs. Both corollar glints are separated in the IRFs at adjacent angles from  $-5^\circ$  down to  $-34^\circ$  and from  $+5^\circ$  up to  $+26^\circ$ . Over this angular range, double glint separation time is a relative measure of flower orientation, and triangulation based on binaural glint delay disparities would provide an excellent direct measure of flower orientation but also of the diameter of the corolla.

*Binaural disparities during target approach*

In Fig. 4 an amplitude peak was found at horizontal angles of  $-1^\circ$  and  $+1^\circ$  respectively, while the horizontal angle between each ear, the flower and the centre of sound emission was  $2^\circ 1'$ . Thus the highest amplitude was recorded under reflection conditions, i.e. when the angle of inclination and the angle of reflection at the flower were both at the same value of  $1^\circ$ . The same angular separation of  $-1^\circ$  and  $+1^\circ$ , respectively, was found in the position of the x-shaped crossing of two corollar glint delays in the IRF patterns of the two ears (Fig. 7Bi, Bii). One ear receives the same IRF pattern as the other ear that is shifted by  $2^\circ$ . This shows that the observed binaural disparities can be explained by the different locations of the ears in the complex echo field generated by the flower.

However, these angular relations are only valid for the particular distance between bat and flower during our measurement, which was 20 cm. At larger distances the angle mouth–flower–ear will decrease and all binaural disparities will become accordingly smaller. In the laboratory, nectar-feeding bats initiate their approach sequence at a distance of about 1 m

(M. W. Holderied and A. Volz, manuscript in preparation). During the course of this approach the bat will start with comparably small binaural disparities and poor information about floral angle. As it gets closer the angular resolution will improve. The angular resolution achievable with spectral IIDs from a distance of 20 cm was well below 1°. It is unlikely that sub-degree angular resolution of flower orientation has any adaptive value *per se*, primarily because the nectar chamber is accessible from a larger range of different approach angles. The observed strong angular patterning of the spatial echo field will, however, be advantageous at greater distances when the IIDs get correspondingly smaller. On geometric grounds a resolution of 0.5° at 20 cm corresponds to 1° at 40 cm and 2.5° at 1 m. This way, a reasonable representation of floral orientation at large distances would be achieved, which will ease flight trajectory planning from a distance.

#### *Floral shapes and echo traits*

Some bat-pollinated plants have reportedly evolved acoustic floral traits that meet the informational needs of their echolocating pollinators (von Helversen et al., 2003; von Helversen and von Helversen, 1999; von Helversen and von Helversen, 2003). As a result of this plant-pollinator co-evolution on an echoacoustic scale, it seems reasonable to hypothesise that a spatial echo pattern of the flower has evolved to make object-specific information available through binaural disparities that would be observable with a bat's head as receiver.

Overall and spectral IIDs, which according to our results do carry object orientation information, depend on how narrow the angular echo pattern is (see Fig. 4). A narrow frontal peak brings forth good angular resolution. All bat-pollinated bell-shaped flowers investigated so far indeed show an angular echo pattern with such a peak in the frontal direction (von Helversen et al., 2003). A likely explanation for the origin of this peaked angular pattern is that at frontal directions the full corollar ridge is ensonified perpendicularly, thus contributing to one composite high-amplitude glint. This frontal glint is of highest amplitude, because in any other orientation only two lateral parts of the ridge are perpendicular to the direction of sound incidence and thus reflect glints (see Fig. 9). To some degree glints from inside the concave corolla itself might further sharpen this angular peak.

The second echo feature that carries object-specific information is the temporal pattern of the two glints of the corollar ridge, which results in the x-shaped glint crossing pattern in the angular IRF plot (Fig. 7). All bell-shaped chiropterophilous flowers show such a characteristic x-shaped glint structure (von Helversen et al., 2003). So both cues that bear binaural directional information – overall and spectral IIDs as well as corollar glint delays – originate from the stiff and prominent torus-like frontal ridge of the corolla (see inset in Fig. 6) (von Helversen et al., 2003; Dobat, 1985). The noticeable rigid ridge of all larger bell-shaped chiropterophilous flowers may function as a mechanical grasping support for the visiting bats that sometimes land on

the corolla rather than hover in front of it. Our results indicate that this ridge might additionally serve as indicator of object orientation. The fact that this ridge often has a rounded cross-section cannot be explained by mechanical constraints alone. Yet, a rounded cross-section presents a small surface area reflecting sound perpendicularly over a wide range of different angles of sound incidence. The presence of the prominent x-shaped double glint delay pattern in Fig. 7 over such a wide angle is thus a direct consequence of this rounded cross-section. Non-rounded cross-sections would not generate glints of high amplitude over an equivalently broad range of angles (e.g. artificial hollow hemispheres) (von Helversen, 2004).

The representation of two separate glints originating from opposite regions of the corollar ridge is present for a wide range of relative bat to flower axis positions. But these parts of the corolla do not always have to be in a horizontal plane. On geometric grounds, those two opposite regions of the corolla will be present in the IRF with separate glints that are in the plane defined by the bat-to-flower axis and the floral axis. During lateral approach, glints will originate from the left and right parts of the corolla. In contrast, a bat approaching from below the floral axis will receive glints from the top and bottom parts of the corolla. In case bats prefer two lateral glints over two on top of each other, they might approach from a lateral position relative to the floral axis.

#### *Extraction of object-specific information from echoes by bats*

So far we have only shown that object-specific information is available through binaural disparities in different aspects of the IRFs. However, extracting such information holds several severe challenges for the hearing system of a bat.

The importance of the object-specific spectral composition of echoes has been a subject of discussion for a long time (e.g. Simmons and Chen, 1989) and its relevance has been shown in choice experiments (Mogdans and Schnitzler, 1990; Schmidt, 1988; Schmidt, 1992). The first problem in extracting object-specific information arises because the spectrum of the echo reaching the eardrum will not only show peaks and notches that are object-specific, but also others that are generated by the directional filtering of the head and pinna. *Phyllostomus discolor*, a bat species in the same family (Phyllostomidae) as most nectar-feeding bats, shows direction-specific spectral IIDs of up to 42 dB (Firzlaff and Schuller, 2003). Behavioural experiments with an insectivorous bat confirmed ambiguities introduced by direction-specific spectral notches (Simmons et al., 2002). In order to extract object-specific information, those spectral features that are part of the directional filtering would need to be identified and actively disregarded. Matsuo et al. present a model mechanism that might be involved in the separation of object-specific and direction-specific information (Matsuo et al., 2001). During flower approach this task is eased in several ways: highest direction-specific spectral IIDs only occur for lateral angles of sound incidence. During approach the flower is in front all the time and its echoes will thus not experience such pronounced filtering. Additionally, from experience the bat might know the

characteristics of the highly important spectral filter for frontal directions quite well, such that all additional notches can be identified as object-specific. Finally and most importantly, echoes from a flower right in front will experience exactly the same directional filtering at both ears, given both pinnae are exact mirror images. As a result any binaural disparities will not represent directional but only object-specific information. This makes binaural disparities particularly useful for the extraction of object-specific information.

The second problem regards the object-specific information contained in the delays between the first two glints in the IRFs. Bats do not have direct access to the IRF of an echo as such, with its temporal resolution in the  $\mu\text{s}$  range. In contrast, typical approach echolocation calls of nectar-feeding bats last approximately 500  $\mu\text{s}$  to 2000  $\mu\text{s}$ . Clutter interference experiments showed that the integration time for echo separation is about 350  $\mu\text{s}$  (Simmons et al., 1998), which is more than the maximum duration of the IRF of *V. gladioliflora* echoes. It has been a subject of discussion whether and by which auditory computational processes bats can use the interference patterns of the overlapping glint echoes of a complex target to derive the object's range profile with a temporal acuity and resolution comparable to the IRFs (Simmons, 1989; Saillant et al., 1993; Peremans and Hallam, 1998). Behavioural experiments with double-glint phantom targets support the idea that *E. fuscus* can indeed separately perceive the range of two echoes that overlap by as little as 2–3  $\mu\text{s}$  (Simmons et al., 1998). In *V. gladioliflora* monaural double-glint separation times ranged from 8  $\mu\text{s}$  at  $-4^\circ$  to 80  $\mu\text{s}$  at  $-32^\circ$  (Figs 7 and 8). With 3  $\mu\text{s}$  resolution, bats would be able to resolve the orientation of the corolla with  $1.2^\circ$  resolution if they based their perception on the double glint separation time experienced by one ear only. The experiments supporting the 2–3  $\mu\text{s}$  resolution has, however, been performed with double glints. Additional glints, like in the flower's echoes, might complicate deduction of temporal detail.

A connected but independent task for the bat would be to assess the binaural difference in the onset times of the first glint with sufficient accuracy to determine the direction to the closest part of the corolla. Binaural first glint delay differences ranged between  $-3$  and  $3 \mu\text{s}$  at angles between  $-5^\circ$  and  $+5^\circ$ . The relevant performance measure for this task is the temporal resolution of directional hearing based on ITDs. In this respect non-echolocating mammals such as humans achieve remarkable lateralization resolution with broadband noise or click signals of only a few microseconds (2–50  $\mu\text{s}$ ) (see Blauert, 1997). Assuming an interaural delay resolution of even 2  $\mu\text{s}$ , directional hearing by triangulation with our bat head would allow resolution of deviations from the frontal direction of just  $3.3^\circ$ . In humans, localization resolution increases with increasing bandwidth and indeed fruit-eating and flower-visiting bats generally use echolocation calls of remarkably broad bandwidth. The actual ability of nectar-feeding bats to resolve ITDs by echolocation, however, still needs to be quantified.

#### *Influence of microphone-loudspeaker arrangement on echoes*

Our measurements showed that the position of the microphone (ear) relative to the sound source (mouth) had a substantial influence on the echo's intensity and spectral composition. For larger angular separations this had already been shown for the echoes of the bat-pollinated vine *Mucuna holtonii* (von Helversen and von Helversen, 1999). Many recent bat-like echo measurement setups (sonar heads) had larger mouth-to-ear distances than real bats [e.g. 6 cm (Müller and Kuc, 2000); 5.6 cm (Siemers et al., 2001); 8 cm (Walker et al., 1998)]. The reason is that ultrasound loudspeakers are often too large in diameter to be able to place the microphone in a natural mouth-to-ear position. One way to overcome this size-dependent bias would be to move the oversized sonar head to a correspondingly greater distance in the echo field, such that the angular relations between mouth, target and ears are the same as in a bat. Yet, this assumes that the complex echo spreads perfectly radially. At distances in the range of the dimensions of the echo-bearing structure the prerequisite of radial spreading might not be met. In this case close-range disparities in the spatial echo field can only be measured correctly with a bat-sized sonar head. If echo measurements aim to quantify the acoustic information available to the bat at close range, the distances between loudspeaker and microphones and between the sonar head and the target need to be adapted to natural conditions. The fact that the two ears of a bat experience binaural object-specific disparities has implications for behavioural experiments on object recognition through replay of phantom targets.

#### References

- Aytekin, M., Grassi, E., Sahota, M. and Moss, C. F. (2004). The bat head-related transfer function reveals binaural cues for sound localization in azimuth and elevation. *J. Acoust. Soc. Am.* **116**, 3594–3605.
- Blauert, J. (1997). *Spatial Hearing*. Cambridge, MA: MIT Press.
- DeAngelis, G. C. (2000). Seeing in three dimensions: the neurophysiology of stereopsis. *Trends Cogn. Sci.* **4**, 80–90.
- Dobat, K. (1985). *Blüten und Fledermäuse (Chiropterophilie)*. Frankfurt: Verlag Waldemar Kramer.
- Firzlaff, U. and Schuller, G. (2003). Spectral directionality of the external ear of the lesser spear-nosed bat, *Phyllostomus discolor*. *Hear. Res.* **185**, 110–122.
- Firzlaff, U. and Schuller, G. (2004). Directionality of hearing in two CF/FM bats, *Pteronotus parnellii* and *Rhinolophus rouxi*. *Hear. Res.* **197**, 74–86.
- Fuzessery, Z. M. (1996). Monaural and binaural spectral cues created by the external ears of the pallid bat. *Hear. Res.* **95**, 1–17.
- Griffin, D. R. (1958). *Listening in the Dark*. New Haven: Yale University Press.
- Grinnell, A. D. and Grinnell, V. S. (1965). Neural correlates of vertical localization by echo-locating bats. *J. Physiol. Lond.* **181**, 830–851.
- Kalko, E. K. V. and Condon, M. A. (1998). Echolocation, olfaction and fruit display: how bats find fruit of flagelliferous cucurbits. *Funct. Ecol.* **12**, 364–372.
- Konishi, M. (2003). Coding of auditory space. *Annu. Rev. Neurosci.* **26**, 31–55.
- Kuc, R. (1997). Biomimetic sonar recognizes objects using binaural information. *J. Acoust. Soc. Am.* **102**, 689–696.
- Kuc, R. (2001). Transforming echoes into pseudo-action potentials for classifying plants. *J. Acoust. Soc. Am.* **110**, 2198–2206.
- Matsuo, I., Tani, J. and Yano, M. (2001). A model of echolocation of multiple targets in 3D space from a single emission. *J. Acoust. Soc. Am.* **110**, 607–624.
- Michelsen, A. and Rohrseitz, K. (1995). Directional sound processing and

- interaural sound transmission in a small and a large grasshopper. *J. Exp. Biol.* **198**, 1817-1827.
- Mogdans, J. and Schnitzler, H.-U.** (1990). Range resolution and the possible use of spectral information in the echolocating bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.* **88**, 754-757.
- Moss, C. F. and Schnitzler, H.-U.** (1995). Behavioral studies of auditory information processing. In *Hearing by Bats* (ed. A. N. Popper and R. R. Fay), pp. 87-145. New York: Springer.
- Möhl, B.** (1988). Target detection by echolocating bats. In *Animal Sonar: Processes and Performance (NATO ASI series A 156)* (ed P. E. Nachtigall and P. W. B. Moore), pp. 435-450. New York: Plenum Press.
- Müller, R. and Kuc, R.** (2000). Foliage echoes: a probe into the ecological acoustics of bat echolocation. *J. Acoust. Soc. Am.* **108**, 836-845.
- Peremans, H. and Hallam, J.** (1998). The spectrogram correlation and transformation receiver, revisited. *J. Acoust. Soc. Am.* **104**, 1101-1110.
- Pollak, G. D.** (1988). Time is traded for intensity in the bat's auditory system. *Hear. Res.* **36**, 107-124.
- Pollak, G. D. and Casseday, J. H.** (1989). *The Neuronal Basis for Echolocation in Bats*. New York: Springer.
- Saillant, P. A., Simmons, J. A., Dear, S. P. and McMullen, T. A.** (1993). A computational model of echo processing and acoustic imaging in frequency-modulated echolocating bats: the spectrogram and transformation receiver. *J. Acoust. Soc. Am.* **94**, 2691-2712.
- Schmidt, S.** (1988). Evidence for a spectral basis of texture perception in bat sonar. *Nature* **331**, 617-619.
- Schmidt, S.** (1992). Perception of structured phantom targets in the echolocating bat, *Megaderma lyra*. *J. Acoust. Soc. Am.* **91**, 2203-2223.
- Schmidt, S., Hanke, S. and Pillat, J.** (2000). The role of echolocation in the hunting of terrestrial prey – new evidence for an underestimated strategy in the gleaning bat, *Megaderma lyra*. *J. Comp. Physiol. A* **186**, 975-988.
- Siemers, B. M., Stütz, P. and Schnitzler, H.-U.** (2001). The acoustic advantage of hunting at low heights above water: behavioural experiments on the European 'trawling' bats *Myotis capaccinii*, *M. dasycneme* and *M. daubentonii*. *J. Exp. Biol.* **204**, 3843-3854.
- Simmons, J. A.** (1989). A view of the world through the bat's ear: the formation of acoustic images in echolocation. *Cognition* **33**, 155-199.
- Simmons, J. A. and Chen, L.** (1989). The acoustic basis for target discrimination by FM echolocating bats. *J. Acoust. Soc. Am.* **86**, 1333-1350.
- Simmons, J. A., Ferragamo, M. J., Saillant, P., Haresign, T., Wotton, J. M., Dear, S. P. and Lee, D. N.** (1995a). Auditory dimensions of acoustic images in echolocation. In *Hearing by Bats* (ed. A. N. Popper and R. R. Fay), pp. 146-190. New York: Springer.
- Simmons, J. A., Saillant, P. A., Wotton, J. M., Haresign, T., Ferragamo, M. J. and Moss, C. F.** (1995b). Composition of biosonar images for target recognition by echolocating bats. *Neural Netw.* **8**, 1239-1261.
- Simmons, J. A., Ferragamo, M. J. and Moss, C. F.** (1998). Echo-delay resolution in sonar images of the big brown bat, *Eptesicus fuscus*. *Proc. Natl. Acad. Sci. USA* **95**, 12647-12652.
- Simmons, J. A., Wotton, J. M., Ferragamo, M. J. and Moss, C. F.** (2002). Transformation of external-ear spectral cues into perceived delays by the big brown bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.* **111**, 2771-2782.
- Simon, R., Holderied, M. W. and von Helversen, O.** (2006). Size discrimination of hollow hemispheres by echolocation in a nectar feeding bat. *J. Exp. Biol.* (in press).
- Urlick, R. J.** (1983). *Principles of Underwater Sound*. New York: McGraw-Hill.
- von der Emde, G. and Schnitzler, H.-U.** (1990). Classification of insects by echolocating greater horseshoe bats. *J. Comp. Physiol. A* **167**, 423-430.
- von Helversen, D.** (2004). Object classification by echolocation in nectar feeding bats: size-independent generalization of shape. *J. Comp. Physiol. A* **190**, 515-521.
- von Helversen, D. and von Helversen, O.** (1999). Acoustic guide in bat-pollinated flower. *Nature* **398**, 759-760.
- von Helversen, D. and von Helversen, O.** (2003). Object recognition by echolocation: a nectar-feeding bat exploiting the flowers of a rain forest vine. *J. Comp. Physiol. A* **189**, 327-336.
- von Helversen, D., Holderied, M. W. and von Helversen, O.** (2003). Echoes of bat-pollinated bell-shaped flowers: conspicuous for nectar-feeding bats? *J. Exp. Biol.* **206**, 1025-1034.
- von Helversen, O. and Winter, Y.** (2003). Glossophagine bats and their flowers. Costs and benefits for plants and pollinators. In *Bat Ecology* (ed. T. Kunz and B. Fenton), pp. 346-397. Chicago: University of Chicago Press.
- Walker, V. A., Peremans, H. and Hallam, J. C. T.** (1998). One tone, two ears, three dimensions: a robotic investigation of pinnae movements used by rhinolophid and hipposiderid bats. *J. Acoust. Soc. Am.* **104**, 569-579.
- Wotton, J. M., Haresign, T. and Simmons, J. A.** (1995). Spatially dependent acoustic cues generated by the external ear of the big brown bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.* **98**, 1423-1445.