Size discrimination of hollow hemispheres by echolocation in a nectar feeding bat

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Summary

Nectar feeding bats use echolocation to find their flowers in the dense growth of tropical rainforests, and such flowers have evolved acoustic features that make their echo more conspicuous to their pollinators. To shed light on the sensory and cognitive basis of echoacoustic object recognition we conducted a size discrimination experiment with the nectarivorous bat Glossophaga soricina and compared the bats’ behavioural performance with the echoic features of the training objects.

We chose a simple geometric form, the hollow hemisphere, as the training object because of its resemblance to the bell-shaped concave form of many bat flowers, as well as its special acoustic qualities. The hemispheres showed a characteristic echo pattern, which was constant over a wide range of angles of sound incidence. We found systematic size-dependent changes in the echo’s temporal and spectral pattern as well as in amplitude.

Bats were simultaneously confronted with seven different sizes of hollow hemispheres presented from their concave sides. Visits to one particular size were rewarded with sugar water, while we recorded the frequency of visits to the unrewarded hemispheres. We found that: (1) bats learned to discriminate between hemispheres of different size with ease; (2) the minimum size difference for discrimination was a constant percentage of the hemisphere’s size (Weber fraction: approximately 16% of the radius); (3) the comparison of behavioural data and impulse response measurements of the objects’ echoes yielded discrimination thresholds for mean intensity differences (1.3 dB), the temporal pattern (3–22 μs) and the change of spectral notch frequency (approximately 16%). We discuss the advantages of discrimination in the frequency and/or time domain.

Key words: flower-visiting bat, echoes of hollow hemispheres, object discrimination by echolocation, Weber–Fechner law.

Introduction

Nectarivorous bats spend much of their nightly activity and energy expenditure in finding and exploiting nectar-bearing flowers. Their excellent spatial memory helps them revisit known nectar sources (Thiele and Winter, 2001). To acquire new sources, the bats use olfactory (von Helversen et al., 2000), visual (Suthers et al., 1969; von Helversen and Winter, 2003; Winter et al., 2003) and echoacoustic features (von Helversen et al., 2003; von Helversen and von Helversen, 1999) offered by the flowers to attract bats and use them as pollen vectors. Close to the flower, echoacoustic features seem to play the major role in guiding the bats to the nectar chamber (von Helversen and von Helversen, 2003).

A serious problem for the echoacoustic perception of single flowers in a rainforest is that flower echoes are acoustically buried in echo clutter produced by the surrounding vegetation. In contrast, aerial hawking insectivorous bats have fewer problems with disturbing background echoes and any echo indicating an object of adequate size will most likely be a flying prey insect (Schnitzler and Henson, 1980).

Insectivorous bats hunting close to vegetation are affected by echo clutter in the same way as nectarivorous bats. They employ extremely short (Schnitzler and Henson, 1980) and broadband (Siemers and Schnitzler, 2004) signals, because such signals facilitate separation of objects from background. To circumvent problems caused by echo clutter, some bats rely on additional prey-specific information. Many gleaning bats, for example, listen passively for sounds generated by their prey (Kalko and Schnitzler, 1998). Rhinolophid bats use the Doppler shift in echoes caused by wing motions of flying prey (Neuweiler, 1990; Schnitzler et al., 2003). Chiropterophilous flowers do not stand out by motion or by sounds they produce themselves, but have evolved floral shapes generating conspicuous and characteristic echoacoustic features that help bats to discriminate between nectar-bearing flowers and the surrounding vegetation. In the chiropterophilous vine Mucuna holtonii the vexillum of the flower is echoacoustically conspicuous for the bat (von Helversen and von Helversen, 1999), because it broadcasts its echo back to the bat over a wide range of sound incidence angles. Therefore its echo is audible over many calls for a bat passing by; in contrast a flat leaf will only ‘twinkle’ when...
Many chiropterophilous plants have concave bell-shaped flowers. Such concave flowers show temporal and spectral echo characteristics, which could be acoustically conspicuous for bats (von Helversen et al., 2003). Nectar feeding bats can easily be trained in the laboratory to discriminate between different artificial concave forms of the same frontal diameter based on echolocation alone, and they are also able to correctly classify such forms independent of their size (von Helversen, 2004).

But which are the echo features that enable a bat to discriminate between concave forms? In general, echo features that provide information about the size and the 3D structure of a target are the intensity, the temporal structure and the spectral pattern of the echo (e.g. Ostwald et al., 1988; Schmidt, 1988; Schmidt, 1992; Schnitzler and Henson, 1980; Simmons et al., 1974). Hitherto the objects used for object recognition tasks were such that their echo heavily changed with the angle of sound incidence (Bradbury, 1970; Simmons et al., 1974; Simmons and Vernon, 1971), which renders it difficult to determine the decisive echo feature. We used the simplest possible concave form, the hollow hemisphere, because of its extraordinary acoustic properties. Its echoes are nearly constant over a wide range of angles of sound incidence (von Helversen et al., 2003), and echo intensity as well as spectral and temporal echo characteristics scale with hemisphere radius in a predictable but differing manner (von Helversen, 2004).

In the present study we determine the ability of a glossophagine bat to distinguish between different sized hollow hemispheres by echolocation. We used nine individuals of the flower-visiting bat Glossophaga soricina (Phyllostomidae), a species well suited for training and object recognition tasks. We also measured the ‘echoes’ (i.e. impulse responses) of the hollow hemispheres, extracted the three relevant acoustic features (amplitude, temporal and spectral features), and compared them with the bats’ performance. From this comparison we aimed to identify the acoustic feature used by the bats for size discrimination.

Materials and methods

Training experiments

Experimental paradigm

The experiments followed a multiple forced choice paradigm. In contrast to a two-alternative forced choice paradigm, this allowed us to test more than two alternatives at the same time. We presented seven alternatives simultaneously to the bats. All data were collected in a continuous combined training and test paradigm.

Experimental set-up

The experiments were conducted in a circular flight cage of 3.5 m diameter and a height of 2.5 m. A training apparatus was positioned in the centre of the cage. This apparatus consisted of a central column holding electronics, nectar reservoirs and valves. From this column 16 spokes protruded in two horizontal planes. A feeder was mounted at the end of each spoke (see Fig. 1). To avoid position learning, the central column with the spokes was slowly turned clockwise or counterclockwise with angular velocities of up to 360° min⁻¹ during all experiments. Turning direction changed in a pseudorandom sequence of rotation angles with smooth deceleration and acceleration. The feeders were short PVC tubes of diameter 25 mm. They contained an infrared light barrier and were connected to a sugar water reservoir via silicone tubing. Training objects were fixed directly above each feeder. Each interruption of a light barrier was recorded by the computer, and in the case of a correct visit, the computer triggered the valve to release a small reward of sugar water (17–20 μl). In order to prevent repetitive visits a second visit to the same feeder within 20 s was recorded but not rewarded. The reward was 17% sugar solution of a mixture of sucrose, glucose and fructose (1:1.5:1.5) (w/w). Sugar water is scentless.

Stimulus objects

Training objects were different sized hollow hemispheres of acrylic glass. They were displayed directly above the feeder with their concave surface pointing outwards. We used 14 different sizes of hollow hemispheres of radii between 6 mm and 58.5 mm (see Fig. 2). From this pool we chose five different sets of hemispheres, each with seven different hemisphere sizes, for experiments.

Experimental design

The eight feeders of each spoke wheel carried a set of seven...
different sizes of hollow hemispheres – thus one intermediate size was present twice. One of these two identical hemispheres provided a reward (rewarded positive stimuli) while the other did not (unrewarded positive stimuli). The six other sizes (some smaller, some larger) were also presented without reward (unrewarded neutral stimuli). At the second wheel of spokes the same set of hollow hemispheres was presented analogously but in a different order. The order of the stimuli on both wheels of spokes was changed every night. Thus the bat could in total choose between 16 stimuli: two rewarded positive stimuli (one in the upper, another in the lower spoke wheel), two unrewarded positive stimuli and two times six (12) unrewarded neutral stimuli of different sizes. Unrewarded visits were not punished. To exclude the use of any possible alternative cue or strategy, we evaluated only the visits at the 14 (two times seven) unrewarded feeders as a measure of the bats’ ability to discriminate between the different sizes.

Training and testing

Bats were allowed to fly freely in the flight cage and could access each feeder with equal ease. As soon as a bat was accustomed to the training apparatus and accepted the feeders as food source, one hollow hemisphere was mounted on top of each of the 16 feeders. During the first, and sometimes also the second, night of training, a reward was accessible at each of the four feeders that displayed the hollow hemisphere with the positive radius. The following night we started the tests with only two rewarded feeders as described above. During all training and test periods the room was in total darkness such that the bats had to rely on echolocation alone to orient and find the feeders.

Data analysis

We analysed our data in two steps. First, all successive visits to the same feeder within a 20 s period were regarded as one single visit. In a second step the whole series of consecutive visits was split into blocks of 100 unrewarded visits. We excluded 100-visit-blocks when the number of visits to the rewarded positive hemisphere exceeded the visits to the unrewarded positive hemisphere by more than a factor of 1.5, as this indicated that bats temporally adopted an unknown deviant strategy to find the rewarded feeder. For each block the numbers of unrewarded visits to each size of hollow hemispheres were counted. Then we calculated the relative frequency of visits with respect to the number of visits to the unrewarded positive stimulus, which was set to 100% (see Fig. 3). Statistical analysis was performed using SPSS 11.0 (SPSS, Chicago, IL, USA).

Bats

During our experiments we used nine individual males of the flower-visiting bat Glossophaga soricina Pallas 1766. Animals were taken from a colony at the University of Erlangen that had been kept in captivity for more than 20 years. The origin of the breeding group was northern Venezuela.

The downward frequency modulated (FM) echolocation calls of G. soricina show two harmonics covering frequencies of approximately 50 kHz to 140 kHz (first harmonic 56–96 kHz, second harmonic 87–137 kHz). Call durations are between 1 and 2 ms. The auditory threshold curve of this species reaches from 15 to 130 kHz (maximum sensitivity between 60 kHz to 110 kHz, best frequency around 80 kHz) (J. Lopez, Y. Winter and O. von Helversen, manuscript in preparation).

Impulse response measurements

The impulse response function (IR) fully characterizes the transmission properties of any linear system. In an echoacoustic context, one might think of the IR as the echo of an indefinitely short click. Actual echoes of natural calls can be derived from the impulse response by convolution with the calls. We used the impulse responses for our analysis.

The acoustic measurements were conducted in an anechoic chamber. To irradiate the objects we used a custom-built condenser speaker with a membrane diameter of 15 mm, and a 1/4” condenser microphone without protecting grid (G.R.A.S. 40BF with preamplifier 26AB and power module 12AA; Holte, Denmark). The speaker and the microphone were fixed in parallel at the end of a holder. To mimic the dimension of a bat’s head, the distance between the centre of the microphone and the loudspeaker membrane was set to 18 mm. This
“artificial bat head” was mounted 20 cm or 40 cm above a bench and pointed in the direction of the object to be irradiated. Objects were fixed at the same height on a turntable by means of a piece of wire. By moving their position on the bench the distance between the object and ‘artificial bat head’ could be changed. The measurements were taken from distances of 20 cm or 40 cm, respectively. First, the opening of the hollow hemisphere was directed exactly towards the artificial bat head. We defined this orientation of the hollow hemisphere as 0°. Then the turntable bearing the hollow hemisphere was turned around the vertical axis in steps of 2° or 10° from −90° to +90°. The frequency response of the loudspeaker and the microphone allowed measurements from 20 kHz to 140 kHz.

The objects were irradiated with a continuously replayed MLS (maximum length sequence) signal, which was generated by a custom-built sound generator. Replaying and recording were sample-synchronous at a sampling rate of 500 kHz. The microphone signal was digitized with 12-bit resolution and recorded by a custom made hard disc recorder (Institut für Technische Elektronik, Universität Erlangen, Germany).

As the impulse response is not directly accessible from the recordings, we had to process our recording with the original MLS in a ‘Fast Hadamard Transformation’ (FHT). From the impulse response the frequency response (spectrum) was calculated, using a Fast Fourier Transformation (FFT; window size 1024 samples; rectangular window). The actual spectra of the loudspeaker frequency characteristic, were calculated as the (complex) difference spectrum between the spectra of the loudspeaker and the impulse response. To acquire the frequency response of the loudspeaker, we replaced the object with an acrylic glass plate directed perpendicularly to the angle of sound incidence. Thus, we obtained the same impulse response as if we had placed the microphone on the acoustic axis facing the loudspeaker at twice the distance from the object (i.e. 40 cm) (for details, see von Helversen et al., 2003).

We analysed the impulse responses with regard to three features: the relative amplitude, the temporal structure and the spectral pattern. To derive relative amplitude (Fig. 4A, Fig. 5C) of each individual impulse response we first integrated its spectrum (Pa/Hz) over a frequency range of 20 kHz to 140 kHz and then normalized this to the maximum such value. As a measure of temporal structure we used the duration of the pause between first and second reflection (gap1–2) of the impulse response. It was defined as the duration between the maximum of the first peak and the maximum of the second peak (Fig. 5A). To describe the spectral pattern of the impulse response we determined the frequency of the notches, which were defined as the local minima in the corresponding frequency area (Fig. 6).

Some geometrical considerations

For sound with a wavelength that is small compared to the diameter of a hollow hemisphere, geometrical optics may serve as approximation. If a parallel sound wave impinges on a hollow hemisphere, there are only certain pathways the sound can travel within the hemisphere to be reflected back exactly into the direction of incidence (Fig. 5D). The more often the sound is reflected, the longer the path the sound has to travel within the hemisphere. As shown in Fig. 5D, the path length d will be:

\[ d = 2n \times \sin \left( \frac{90°}{n} \right) r, \tag{1} \]

where \( n \) is number of reflections.

Assuming a velocity of sound in air of 340 m s\(^{-1}\) (or 0.34 mm us\(^{-1}\)) and \( d \) in mm, the time \( t \) necessary to pass the hemisphere will be \( t = d \times 1/0.34 \) (\( \mu s \)). For \( n = 1 \) the travelling path length within the hemisphere will be \( d = 2r \) and for \( n = \infty \) it will be \( d = \pi r \); the maximum duration of the impulse response will thus be \( t_{\text{max}} = (\pi - 2) r \times 1/0.34 \) (\( \mu s \)). The time gap (\( \mu s \)) between reflection number \( n_1 \) and \( n_2 \) will be:

\[ \text{gap}_{n_1-n_2} = \left[ 2n_1 \times \sin \left( \frac{90°}{n_1} \right) - 2n_2 \times \sin \left( \frac{90°}{n_2} \right) \right] r \left( \frac{1}{0.34} \right). \tag{2} \]

Results

Training experiments

Nine bats were trained to discriminate between different sized hollow hemispheres. All bats learned to find the positive stimuli with ease. In the second or in the third night most of the bats made significantly more visits to the unrewarded positive stimuli than to the other unrewarded neutral stimuli. Fig. 3A shows the frequencies of visits plotted over the radius of the hemispheres. Each curve represents the frequencies of visits to one particular set of hemisphere sizes and can originate from up to four individuals. This is exemplified by the fourth curve from the left (diamonds, data for one bat), which shows results for a set with a positive stimulus of 38.5 mm radius and four smaller and two larger neutral hemispheres. This curve represents 2900 unrewarded visits. 1211 of these were made to the unrewarded positive stimulus (\( r = 38.5 \) mm) and the remaining 1689 visits were to unrewarded neutral stimuli of different sizes with the following frequencies: \( r = 19 \) mm, 48 visits; 24 mm, 92 visits; 29 mm, 281 visits; 33.5 mm, 569 visits; 48.5 mm, 488 visits; 58.5 mm, 211 visits.

We pooled the numbers of visits of all individuals that were tested with the same set and normalized the frequency of visits to the unrewarded positive hemisphere to 100%. Comparing the five curves in Fig. 3, it is noticeable that all sets elicited the same general preference pattern: the closer a hollow hemisphere’s radius was to the radius of the positive hemisphere, the more frequently it was visited (see Fig. 3A).

To get a measure for the breadth of the curves, the intercept points of the individual curves with the 75% level were determined. This resulted in two \( \Delta r \) measurements, one to the smaller radius and one to the larger. \( \Delta r \) plotted over the smaller radius increased with the radius of the hollow hemisphere. We found a mean Weber fraction of \( \Delta r / r = 0.16 \pm 0.06 \), the linear...
regression was $\Delta r=0.13r+0.48$ ($F_{1,16}=19.65$, $R^2=0.55$, $P=0.0004$), when forced through the origin the regression equation was $\Delta r=0.15r$ ($F_{1,17}=181.62$, $R^2=0.91$, $P<0.0001$; please note that these values cannot be compared to values for models that include an intercept).

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**Fig. 3.** Size discrimination in the training experiments. (A) Relative frequency of unrewarded visits to hollow hemispheres of different sizes, for training experiments with five different positive sizes ($r=9$, 19, 29, 38.5 and 48.5 mm) and a total of nine bats. The frequencies were calculated and averaged for groups of 100 consecutive unrewarded visits each. The frequency of visits to the unrewarded positive size was set to 100%. Values are means ± s.e.m. The broken line marks the 75% level. Data for up to four individuals were pooled (filled circles: one bat, $n=2000$; filled squares: two bats; $n=1300$, 2000; filled triangles: four bats, $n=300$, 800, 2300, 3100; filled diamonds: one bat, $n=2900$; open squares: one bat, $n=1100$). (B) $\Delta r$ for 75% discrimination as a function of the radius $r$. $\Delta r$ was measured between the training $r$ and the intercept with the 75% discrimination level, and is always plotted over the smaller value of $r$. The solid black line gives the linear regression ($F_{1,16}=19.65$, $R^2=0.55$, $P=0.0004$), the broken black line gives the linear regression when passing through the origin ($F_{1,17}=181.62$, $R^2=0.91$, $P<0.0001$). The 95% confidence intervals are indicated by black dotted lines.

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**Echoes of hollow hemispheres**

Fig. 4 shows relative amplitude, impulse response and frequency spectrum of the impulse response for a hemisphere of 25 mm radius as a function of angle of sound incidence. Within a wide range of angles of sound incidence (approximately $-70^\circ$ to $+70^\circ$) the impulse response of each hemisphere was nearly constant with respect to its spectral and temporal pattern (Fig. 4B,C). The relative amplitude was steadily high for incidence angles between $-45^\circ$ and $+45^\circ$ (Fig. 4A).

We measured the impulse response functions of 16 different sized hollow hemispheres, the 14 sizes used in the training experiments and two additional ones. It is noticeable that all three echo parameters depend on the radius $r$ of the hemisphere (see Figs 5, 6): the relative amplitude of the object’s impulse response is linearly dependent on $r$, because the reflected power linearly scales with target surface and both scale with $r^2$ (Fig. 5C).

Fig. 5A depicts one hemisphere’s impulse response taken from an angle of $10^\circ$. The first two small peaks in the impulse response originate from the edges of the hemisphere. Their position changes with the angle of incidence (labelled as ‘edge’ in Fig. 4B and Fig. 5A; 1000–1300 µs). The next large solitary peak corresponds to the first reflection in Fig. 5D. The subsequent gap is followed by many peaks with gradually decreasing amplitude corresponding to the second to $n$th reflection (see Fig. 5D).

The most striking feature of the impulse response functions is the time gap between the first and the second reflection. The duration of this gap complies with the time the sound needs to cover the path length difference between first and second reflection (gap1–2; see Fig. 5B,D). Its duration increased linearly with the radius (Fig. 5B), and is in agreement with the expectation from Fig. 5D and Eqn 2.

Every feature in the time domain (temporal pattern) has its mathematical equivalent in the frequency domain (spectral pattern) and vice versa. Through interference, multiple reflections with different path length and thus different time delays cause reinforcement and cancellation, resulting in a complex spectral composition. Fig. 4C depicts the spectral directional pattern, i.e. the spectrum of the impulse response as a function of angle of sound incidence. It shows distinct horizontal ridges and valleys corresponding to notches, which are at the same frequencies for all angles of sound incidence. The hemisphere with a radius of 25 mm had its lowest notch at about 45 kHz (Fig. 4C). This was also the most prominent notch in the spectrum. Proceeding to higher frequencies, more or less regularly spaced further notches arose that were separated by flat peaks, giving the plots their characteristic banded pattern.

The larger the radius of a hollow hemisphere, the more notches were present in the spectral pattern (Fig. 6). We determined the frequency of the most prominent notches in the spectrum and found that single notches could be traced throughout the range of different sized hollow hemispheres. The frequency of individual notches was inversely proportional
to the hemisphere radius, yet with different proportionality factors (Fig. 6G). For every notch:

\[ v_{\text{notch}} = a_{\text{notch}} \times \frac{1}{r}, \]  
\[ r_{0} \]

where \( a_{\text{notch}} \) is a constant coefficient, characteristic for every particular notch (see Fig. 6G legend). In other words, notch wavelength was linearly proportional to hemisphere radius – a result that can be derived from geometry, compare Fig. 5D. This is true not only for single notches but for the whole spectrum. Thus, the spectral distribution \( s(v) \) of a larger hemisphere is a compressed version of a smaller hemisphere’s one. In a first approximation, the function \( s(v) \) is constant for all hemispheres and changes only by an expansion factor inversely proportional to the factor by which the radius of the hemisphere is altered:

\[ s(v) = s_{c} \left( \frac{r_{0}}{r} \right)^{v}. \]  
\[ s_{c} \]

(see Fig. 6). On a logarithmic scale, according to Eqn 3, this becomes:

\[ \log v_{\text{notch}} = \log a_{\text{notch}} - \log r. \]  
\[ \log v \]

This means that on a logarithmic frequency scale, a change in radius will shift each notch by a constant factor of \(-\log r\). In other words, spectra plotted over \( \log v \) are identical, but shifted by \(-\log r\) (see Fig. 6A–F).

**Discussion**

The behavioural data indicate a general rule that can be deduced from Fig. 3: the larger the size of a hollow hemisphere, the larger the absolute size difference necessary for correct discrimination. 75% discrimination was reached on average with a relative radius difference of 16%. This finding corresponds with the Weber–Fechner law, which applies to many perceptual tasks. But what perceptual quality allowed discrimination of the size of hollow hemispheres? We analysed three parameters of the hollow hemispheres’ impulse responses: intensity, time structure and spectral pattern, and deduced the difference thresholds for every feature. To obtain the difference threshold in intensity, gap1–2 duration and frequency \( \nu \), we used the 75% discrimination level as an indicator of the just-discriminable radius difference and then derived the respective difference threshold by interpolation (Fig. 7).

Despite the fact that time structure and spectral pattern are linked to each other, we first discuss all three parameters...
separately to estimate what performance the bats had to accomplish, given that they based their discrimination ability solely on one of the three echo features. Thus we must bear in mind that the bat’s echolocation call is typically 1–2 ms long and covers the frequency band 50–140 kHz. Therefore the echoes that we measured and analysed are not identical to the echoes received by the bat. In particular it is still controversial if and with what detail bats can deduce the echo’s impulse response, which we analysed to derive the time structure. Such problems will be addressed in the following discussion.

**Intensity of the impulse response**

The difference in sound pressure level between the just-discriminable hemispheres in our experiment was at a mean of 1.3 dB (see Fig. 7A). Just-detectable level differences between two pure tones are at 4–6 dB in the mouse, 1–2 dB in macaques and 0.5–1 dB in humans (for a review, see Fay, 1992). The level discrimination threshold for noise in humans seems to be slightly higher, ranging around 1–4 dB (Zwicker and Feldtkeller, 1967). Several authors have published values for intensity discrimination by echolocation in bats. A 17% surface area difference threshold was found for triangles, giving a corresponding intensity difference of 1.5–3 dB (Simmons and Vernon, 1971); however, temporal and/or spectral cues may also have been used by the bats in these experiments, but these were not discussed. The same is true for experiments with *Noctilio leporinus* (1–2 dB) (Suthers, 1965) or for experiments with *Rhinolophus ferrumequinum*, which were trained to discriminate spheres of different sizes. In such experiments, thresholds of 2.4–4.4 dB (Airapetianz and Konstantinov, 1974)
Fig. 6. Prominent frequency notches in the echo spectrum (20–140 kHz) of different sized hollow hemispheres. (G) Notch frequencies displayed as a function of the reciprocal value of the radius. The shaded area indicates the frequency range of the echolocation call of Glossophaga soricina. (A–F) Spectral directional patterns and spectra (averaged over 13 single spectra from –60° to +60°) of six hollow hemispheres of different sizes. Note that the frequency scale is logarithmic. The arrows indicate the frequency notches. For tone gradation key in steps of 6 dB, see Fig. 4C.
Size discrimination by echolocation and 2.8–3.2 dB (Fleissner, 1974), were measured. These values are in a similar range but slightly higher than the 1.3 dB (Fig. 7A) needed by the bats in the present study, given they had based their decision solely on intensity differences.

It thus seems possible that the bats used intensity differences for size discrimination of hollow hemispheres, but one needs to consider that a level difference of 1.3 dB is comparatively small, taking into account that echo intensity is strongly dependent on the bat’s distance to the target. Intensity-based discrimination would thus require highly accurate distance-intensity-compensation. This might not pose a major problem for a bat, however.

**Temporal pattern**

The just-noticeable difference of the most obvious time domain pattern, the gap1–2, ranged between 3–22 µs; the gap1–2 itself ranged from 12 to 148 µs. The time resolution, measured as the threshold of recognizing two ‘pips’ as two separated ‘pips’, was about 100–200 µs in Megaderma lyra (Weissenbacher et al., 2002). Neurophysiological studies revealed a cochlear integration time of about ~300–400 µs for Eptesicus fuscus (Simmons et al., 1989). It is thus highly unlikely that time gaps in the low µs range are resolved exclusively in the time domain.

**Temporal pattern and spectral domain**

The limited temporal resolution led to the conclusion that bats generally evaluate echoes in the frequency domain when time differences of less than 100 µs in overlapping echoes are offered (Beuter, 1980; Simmons et al., 1974). Nevertheless, behavioural experiments showed that Eptesicus fuscus perceives electronically generated echoes of two front targets in terms of two distinct reflections, and this with a resolution of up to 2 µs (Simmons, 1989; Simmons et al., 1998). The discrepancy between the limited temporal resolution found in other studies and these results are explained by a mechanism that combines perception in the time and spectral domain.

Through interference, a two-front echo with a given gap in the time domain corresponds to notches at particular frequencies in the spectral domain. Spectral notches are particularly expedient for resolving small changes in time gaps, because changes in two-front spacing that are too small to be resolved in the time domain correspond to drastic and more easily accessible changes in notch frequency. It was therefore suggested that bats perceive two front echoes in the spectral domain and then translate the spectral notch pattern into a full time domain representation of the actual range profile (Simmons et al., 1990). The spectrogram correlation and transformation (SCAT) model (Saillant et al., 1993) explains the transformation of spectral information into time information. Assuming this mechanism, gap1–2 duration may well have played a decisive role for the discrimination of different sized hollow hemispheres.

**Spectral pattern**

Hollow hemispheres reflect echoes with a characteristic spectral composition that is clearly size-dependent. From Eqn 4
it becomes clear that the just-noticeable change of the spectrum can be measured by the relative change, expressed as $\Delta f / f$, of any particular peak or notch of the spectrum. We chose the lowest notch (see 1. notch in Fig. 6G), as this notch is least blurred by noise and easiest to measure. Each higher notch would have the same result, however. The importance of the fact that $\Delta f / f$ is constant for all notches, irrespective of the absolute notch frequency, becomes apparent when one considers that the bandwidth of the echolocation call is limited (50–140 kHz). A bat can only evaluate spectral changes when they are within the frequency range of the bats’ echolocation call (Mogdans and Schnitzler, 1990). Yet, a certain notch being within the spectral range of the call at one hemisphere size might at another size be out of it and thus unavailable. Minimal noticeable change expressed as $\Delta f / f$ is a reliable and comparable measure as long as at least one notch occurs within the echo’s frequency range.

From Eqn 5 it can be deduced that:

$$\frac{\Delta f}{f} = \frac{\Delta f}{r}.$$  

The average $\Delta f / f$ detected by the bats was thus 16% (7–21%, one outlier at 40%; see Fig. 7C). This is not much larger than the values (6–13%) obtained for *Megaderma lyra* (Schmidt, 1992) in experiments with ‘two-front phantom targets’ with delays of 7.8 and 20.7 $\mu$s.

How does the observed discrimination ability relate to cochlear morphology? Cochlear frequency maps of humans, many mammals and unspecialised FM bats (Greenwood, 1990; Vater and Siefer, 1995) show an exponential frequency distribution along the cochlea. We have shown above that the spectra of different hemispheres, when plotted on a logarithmic frequency scale, are at a first approximation identical and only shifted by $-\log r$ (see Eqn 5). This means that the spectral echo pattern (peaks and notches) projected onto the cochlea is about the same for all hemisphere sizes, but its position shifts along the cochlea for a constant distance depending on hemisphere size change (Eqn 5; Fig. 6A–F). Thus every notch or peak will be shifted by the same number of hair cells on the basilar membrane. This also might be a mechanism facilitating generalization of form independent of size (von Helversen, 2004). As discrimination ability is believed to depend on cochlear distance, our finding of a constant $\Delta f / f$ supports the spectral basis of size discrimination.

An adequate measure for frequency discrimination in broadband signals is the critical bandwidth, as it takes masking and integration in the cochlea into account (e.g. Greenwood, 1961). The critical bandwidth is a function of the centre frequency and is presumed to represent equal distances on the basilar membrane. Typical values for the critical bandwidth (CB, expressed as percent of the mean frequency) and the corresponding critical distance (CD) on the basilar membrane are: CB 17% (CD 1.2 mm) for humans, 21% (1.1 mm) for the macaque, about 23% (1.1 mm) for the cat and 40% (1.5 mm) for the chinchilla (for a review, see Fay, 1992). This is in the same order of magnitude as our mean of 16%. For *G. soricina*, equation 6 in Fay (Fay, 1992) would yield a CD estimate of 0.46 mm [assumed CB: 16%, cochlear length: 14 mm, derived from Pye (Pye, 1980) and highest audible frequency $F_{\text{max}}$: 130 kHz (J. Lopez, Y. Winter and O. von Helversen, manuscript in preparation)]. This is between the values mentioned above for non-echolocating mammals and the only available CD value for a bat [*Rhinolophus*: 6%; 0.2 mm; outside of the acoustic fovea (Long, 1977)]. Thus the observed discrimination ability might well be a consequence of the mechanical filtering properties of the inner ear.

The magnitudes of differences in intensity, in gap $\Delta t$ duration and spectral pattern all agree reasonably well with known mammalian performance. With our experimental approach we are not able to decide whether discrimination was achieved in the time or in the spectral domain. Of course echolocating bats will profit from evaluating all acoustic information available to them, including temporal/spectral and intensity differences. In support of a spectral basis for the observed discrimination ability it is nevertheless important to note that frequency mapping and filtering properties of the mammalian cochlea can explain the finding of a constant $\Delta f / f$ in general and a value of about 16% in this species in particular.

This article is dedicated to Dagmar von Helversen, who initiated this work before her all too early death. Her fervour to work, her amazing inventiveness and her enthusiasm was an inspiration to us. We acknowledge gratefully the help of Neville Fletcher who gave constructive suggestions on theoretical considerations of the hemisphere’s echoes. We are thankful to York Winter for support with soft- and hardware to run the set up. Also we thank Nick Kodratieff helping us to keep the wheel turning and are grateful to Hans Opel who helped us to produce some of the hemispheres. We are also thankful to two anonymous referees for their extensive and helpful reviews.

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