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## Object classification by echolocation in nectar feeding bats: size-independent generalization of shape

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**Abstract** The nectar-feeding bat *Glossophaga* can be trained to discriminate two hollow forms, a hollow hemisphere and a paraboloid with the same diameter and depth, in total darkness. During training a saturation level of about 85–90% correct choices or more can be reached within 50–100 visits. To investigate generalization abilities, the bats were tested with pairs of the same shape but of different size. Although no reward was offered, they preferred the hollow sphere (30 mm and 50 mm diameter, but not 18 mm) over the corresponding paraboloids. Thus, the bats were able to generalize some features of the rewarded form and detect them in forms of the same shape but different size. This transposition is remarkable, since the bats could not use absolute spectral characters, but had to pay attention to size-independent features common to hollow hemispheres. Possible cues are the variation of echoes in dependence of different angles of calling direction (constant in spheres, changing with position in paraboloids) and/or the “timbre” of the echoes, i.e. their spectral pattern independent of their absolute pitch

**Keywords** Echo-acoustic object recognition · Generalisation · *Glossophaga* · Size-independence · Spectral structure

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This is the last manuscript that Dagmar von Helversen was able to complete before her death on July 20, 2003. We cherish the memory of a great scientist and a loving and beloved human being. All correspondence relating to this paper should be addressed to: Otto von Helversen, Zoologisches Institut der Universität, Staudtstr. 5, 91058 Erlangen, Germany (e-mail: helver@biologie.uni-erlangen.de)

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### Introduction

Glossophagine bats find new nectar sources not only by the special odor of chiropterophilous flowers but also by recognizing the specific shape and texture of the flowers by echolocation (von Helversen and von Helversen 1999; von Helversen and von Helversen 2003). This implies that the bats are able to solve the general problem of sensory perception, i.e., to recognize objects on different occasions and under different conditions. This recognition must take place in spite of large variations in the spike trains produced by the receptor cells that arise, for example, from different sizes of objects, different backgrounds, different distances, or different angles of approach. Recognition must therefore involve constancy mechanisms and generalization capacities, also known from other sensory systems. Here I present discrimination experiments on nectar-feeding bats aimed at testing whether similar capacities exist in the recognition of shapes by means of echolocation.

To investigate whether a bat is capable to generalize echoes or sequences of echoes, *Glossophaga soricina* was trained to discriminate between a pair of hollow forms, a hemisphere and a paraboloid, with the same opening radius and depth. After the bat had attained a discrimination level of more than 85% for the training pair, in a test situation without reward the bat was offered a choice between another pair of hemisphere and paraboloid but now in a different size. If bats were able to recognize the form as such, one would expect the bat to prefer the shape, which was rewarded in the training phase irrespective of its absolute size.

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### Materials and methods

#### Animals

The experiments were run with two *G. soricina* males from a colony introduced from Venezuela and held and

bred in the Zoological Institute in Erlangen since more than 20 years.

### Training and tests

Training and tests were run in a two-alternative forced choice paradigm. A single bat was housed in an U-shaped cage, the two parts of it were about 5 m long and separated by a plastic wall. At both ends two pairs of feeders were mounted. A feeder consisted of a PVC ring housing a small infrared photoelectric barrier and a tube for delivering sugar water solution. Above the feeder one of two forms could be presented. These forms were mounted at the two ends of an aluminum-rod, which could be switched between two positions by a motor: either the rewarded or the unrewarded form was positioned exactly above the feeder. At the same time the second feeder, 47 cm away, presented the opposite form. Thus, the approaching bat had to decide whether to visit the right or left feeder. A photoelectric signal was registered by a computer when the bat, hovering in front of the feeder, interrupted the light beam with its snout. This triggered a valve to release a small reward (about 20  $\mu$ l of 17% sugar water containing sucrose:fructose:glucose 1:1:1) when the bat had chosen the correct form. A reward of this size is well within the range of nectar sugar concentration and nectar amount that may be gained in the natural situation (O. von Helversen, personal communication).

The bat had to fly to the other end of the U-shaped tunnel in order to get the next reward. By rewarding only the first visit in a compartment the bat was forced to alternate between the feeders at the two ends of the U-tunnel. By doing so, the bat had to approach the pair of feeders from the front and could not simply switch between the two feeders within one compartment. Whether the positive form was presented at the right or left position in a given compartment was determined by a pseudo-random sequence (with the same stimulus never occurring more than three times at the same position in a row). The changes were triggered when the bat visited one of the feeders in the other compartment. Thus, it was guaranteed that the bat was in the neighboring compartment when the motor changed the forms, and that the bat reentering the compartment was confronted with the next constellation. This training was the basic treatment. Light-on (day) to light-off (night) was programmed as 12:12 h. Experiments were run only during the 12 h of darkness and the bat performed about 600 to more than 1,800 visits during this period.

When the percentage of correct choices was higher than 80–90%, the tests were started. In one compartment the training shapes were replaced by a pair of a different size and any reward was stopped in this compartment, while in the other compartment the normal training with reward was continued. This kept the bat active, since otherwise, with no food available,

the bat would have reduced flight activity immediately. Thus, due to the forced alternation between the compartments a sufficient number of decisions per time could be obtained (40–60  $\text{h}^{-1}$ ). Test or training phase was frequently changed between the compartments.

After the tests, control experiments were run in which the bats were trained to either discriminate the different sizes of the spheres or the two forms of each pair.

### Hollow forms and echo recordings

Four different sizes of hollow hemispheres and paraboloids were used, each paraboloid having the same diameter and depth as the corresponding sphere: diameter 18, 30, 36, and 50 mm. The hollow forms were made of 0.5-mm-thick, stiff polyethylene, which was warmed up and pulled over a brass negative by a vacuum pump (Vacformat, Deve). The brass negatives were produced by a computer controlled milling machine.

For the echo-recordings the hollow forms were glued to a stiff thin wire which was mounted on top of a turntable. The front view was adjusted to face the speaker and the microphone, and the echoes were recorded in steps of 2° in the horizontal plane. Microphone and speaker were as close together as possible (the distance between the centers of the speaker and the microphone was 18 mm). We used the MLS method (“maximum length method”, which reduces noise in echo measurements; for further details see von Helversen et al. 2003).

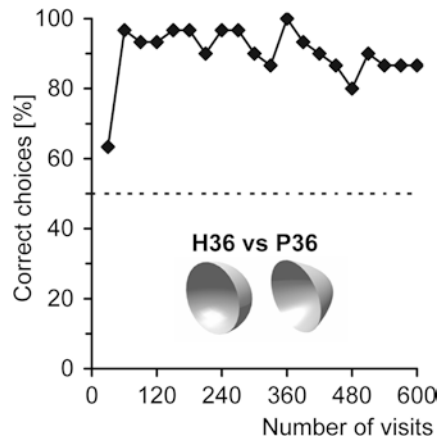
For every direction the spectrum was calculated from the impulse function. As the spectra change with direction of incidence, when plotting spectra against angle of incidence a pattern is obtained that may well be regarded as an “acoustic fingerprint” of an object (von Helversen et al. 2003). Impulse functions and derived spectra are independent of call structure and thus describe the properties of the object. *Glossophaga* uses echolocation calls of distinct duration (mostly ca. 1 ms) and frequency range (140–60 kHz). The echoes they would perceive can be calculated by the convolution of the call function with the impulse function of the echo. For further details see von Helversen et al. (2003).

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## Results

### Discrimination of hemisphere and paraboloid

The initial basic training was the discrimination of a rewarded hollow sphere (diameter 36 mm) versus an unrewarded paraboloid of the same diameter and depth (see insets in Fig. 1). This task was easily learned by the bats as soon as they were familiar with the training procedure (see Materials and methods). As shown in Fig. 1, in which the percentage of correct choices during



**Fig. 1** Learning curve of *Glossophaga soricina*, individual A2, trained to discriminate a hollow sphere (S+) from a paraboloid of the same diameter and depth. The mean value of correct choices is plotted for every 30 decisions over the first night

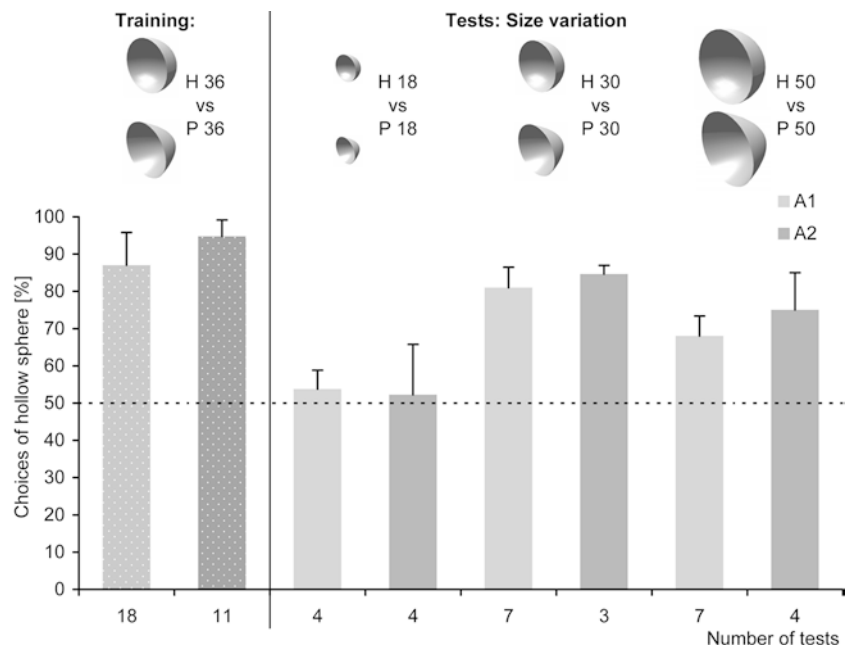
the first night of training is plotted, a saturation level of 85–95% was already reached after about 60 visits.

#### Tests with shapes of different sizes

In order to answer the question of whether a bat is able to generalize some features of the complex echo sequences, tests were performed in which the bat was offered a pair of the same shape, sphere and paraboloid, but differing in size from the training pair (test sizes: 18, 30 and 50 mm diameter).

The results from two animals tested with three pairs of objects are presented in Fig. 2 (light and dark grey bars). Both animals clearly preferred the hollow sphere of the 30-mm and 50-mm pair, but not of the 18-mm pair. At this size, sphere and paraboloid were chosen in about 50% of the visits.

**Fig. 2** Frequency of visits of two individual *G. soricina* (A1 and A2, light and dark grey columns) to the hollow hemisphere of three differently sized pairs of spheres and paraboloids. The two columns at the left side represent the frequency of correct choices of the rewarded sphere (36 mm diameter), averaged for the time of all test sessions performed at the same time in the other compartment. At the right side, the frequency of visits at the (unrewarded) hemisphere is shown compared to a same sized paraboloid (diameter indicated above forms). Numbers of tests are indicated below columns, SD is indicated by a vertical bar; number of visits per test 30–150



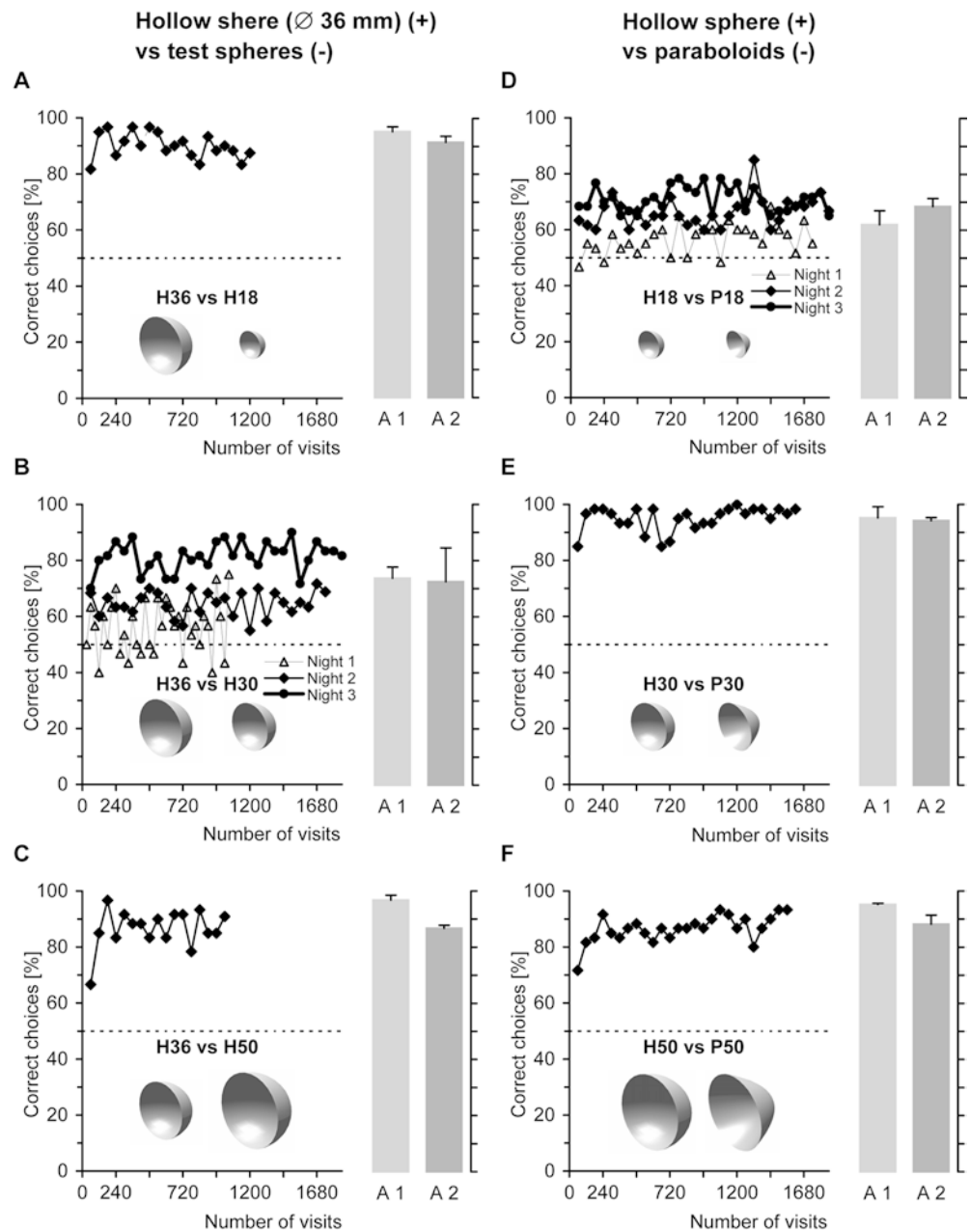
#### Control experiments

An obvious explanation of this result could be that the bats simply could not discriminate a sphere of 30 mm or 50 mm from the 36-mm training sphere, so that there was no necessity for a transfer of the learned pattern in the case of the 30-mm and 50-mm-diameter spheres. In the test with 18 mm diameter, however, the bats either might not be able to discriminate the sphere and the corresponding paraboloid and/or both objects might be perceptually equally distant from the 36 mm hollow sphere so that some kind of trading resulted in a 50:50 choice.

To exclude the possibility that the animals could not discriminate between spheres differing in size, I tested to what degree the bats were able to discriminate hollow spheres. This was done in three experiments, in which the bats were now trained to discriminate between the 36-mm sphere (rewarded) and either an 18-, a 30-, or a 50-mm sphere (unrewarded). The velocity of learning and the saturation level of the respective learning curves were used as a measure of similarity between these shapes (Fig. 3A–C). While the spheres of 18 mm and 50 mm diameter were easily discriminated from the 36-mm sphere within the first night, discrimination of the 30-mm and 36-mm spheres was weak in the beginning, but gradually improved to about 90% correct choices in the third night as well. Thus, the three spheres were perceived as different to the training sphere, but the important point for the argument here is that the bats could discriminate spheres of all tested sizes from the 36-mm sphere.

Next I tested the respective “similarities” between spheres and paraboloids of the pairs shown in Fig. 2 with the sphere being the rewarded form. In the 30-mm and 50-mm pair the hollow sphere and the corresponding paraboloid were easily discriminated from the very

**Fig. 3A–F** Learning curves of individual A2, and mean percentage of correct choices for both animals at the training sphere versus the spheres used in the tests of Fig. 2 (*left panel*) and among the forms of each test pair (*right panel*). The interruption in A indicates a test phase. Three nights of training are plotted in the two cases with slow learning (**B, D**). For comparison, the columns represent means of the first two nights of training only



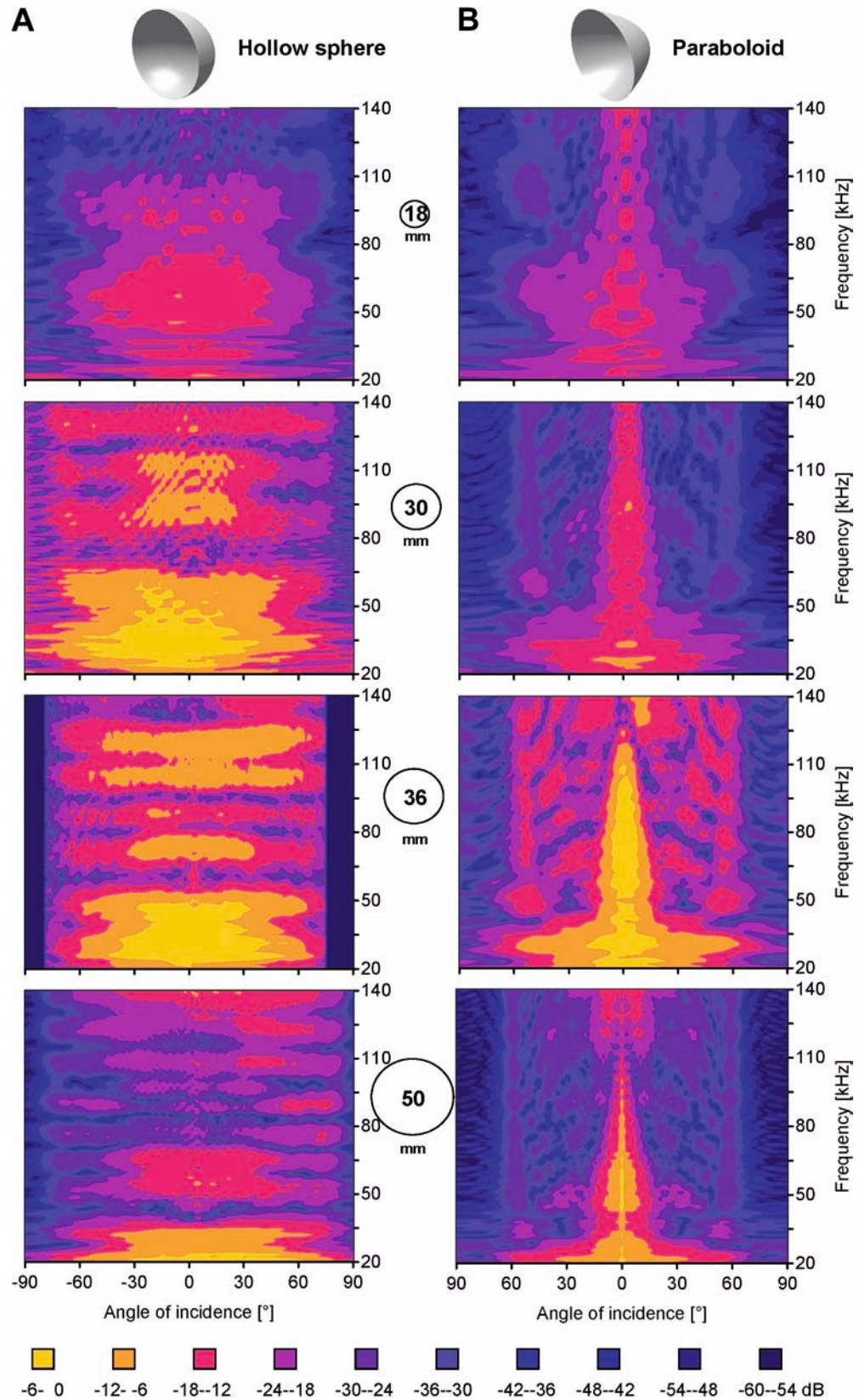
beginning of the training (Fig. 3E, F), but not in the small pair (Fig. 3D), which was hardly discriminated during the first night, and led to only ca. 70% correct choices even after three nights of training. The learning curves thus indicate that it was a much harder task to discriminate the small shapes.

#### Echoes

A better understanding of the described results should be possible when looking at the echoes, which are reflected by the various forms. In Fig. 4 spectral directional patterns of the training and test figures are

presented for one plane, which is representative for all planes since rotary bodies were used. The spectral composition of the hollow spheres changed depending on the diameter, characterizing the objects by their unique spectral composition, especially for the frequency window of the bat's call, which is in the range of 140–60 kHz (cf. for example, 0° in hollow spheres in Fig. 4). With increasing diameter the number of notches increased due to multiple pathway reflection. In particular, because of the constant radius of curvature, the bands of notches remain constant for any incidence angle of the echolocation call, which corresponds to the extinction bands parallel to the abscissa in the diagram.

**Fig. 4** Spectral directional patterns of hollow hemispheres (A) and paraboloids (B)



Accordingly, in the paraboloids the lines of notches have a declining course with increasing incidence angle of the middle axis. Note, however, that for the smallest

size the echoes of sphere and paraboloid look much more alike than for the larger shapes, which reflects the difficulty in discriminating this pair (Figs. 2, 3).

## Discussion

Discrimination of hollow forms in training experiments: which cues may be used?

Earlier experiments (von Helversen et al. 2002) and those presented here show that *Glossophaga* learned to discriminate between various hollow hemispheres and paraboloids without difficulty, even in total darkness and therefore only depending on echolocation. The forms were of the same material and texture, thus recognition was indeed based on shape alone.

As suggested in earlier studies on recognition of texture and shape (Bradbury 1970; Simmons et al. 1974; Haber-setzer and Vogler 1989; Schmidt 1992, 1995a; von Helversen and von Helversen 2003) the spectral composition seems to be the most important cue for discrimination. The directional spectral echo patterns are highly characteristic (Fig. 4), while other features such as intensity and duration of echoes were similar within training pairs because of the same depth and diameter. However, single echo spectra of the different forms may be very similar, making it unlikely for bats to rely on them. Rather, the sequence of spectra during approach and the relation of spectral cues and exact position of the bat seem to contain enough information to explain the high certainty of discrimination (Moss and Surlykke 2001; von Helversen and von Helversen 2003). The idea, that the sequence of spectral echo patterns may be learned is in congruence with the observation that the bats needed more than one night to discriminate the two 18 mm forms, while they easily learned to discriminate the two other pairs, which differ much more in their spectral pattern than the 18-mm forms (Fig. 4). Hollow forms, and in particular rotary hollow forms, with characteristic echoes due to multiple pathway interference, seem well suited to test out the auditory capacities of spectral resolution in these bats.

### Generalization of form

The bats did not only discriminate easily between the hollow sphere and the paraboloid during training but they even preferred unknown spheres over same-sized paraboloids (30 mm and 50 mm) in unrewarded test situations. Hence bats are obviously able to extract some general features of echo sequences inherent to hollow spheres, such as notches at the same frequencies independent of the spatial relation of the calling bat relative to the object, and they are able to transpose these general features to an object of the same shape but of different size. These features cannot include the *absolute* spectral composition, since the absolute pitch of frequency bands strongly depends on the size of the object (see Fig. 4), but may reflect something like the “timbre” of the echo, the relative spectral structure independent of absolute pitch.

The transposition to forms of different size and therefore different pitch is remarkable since the memory

for absolute pitch was found to dominate recognition in the bat *Megaderma lyra* (Schmidt 1995b) and other non-human vertebrates (Hulse and Cynx 1985; D’Amato 1988; May et al 1989).

In the complex situation of the experiments reported here the bats had learned the spatial/spectral composition of sphere echoes, and could transfer this pattern to test forms, which were never rewarded and thus excluded any further learning. Experimental observations in a bird, the European starling, suggest how this transfer could be achieved (Braaten and Hulse 1991). Starlings have demonstrated a perceptual constancy for relational spectral structures that could provide a basis for the generalization across forms of different size. These birds readily transfer a learned discrimination between signals of different timbre (e.g., as can be created by adding different harmonics to the same fundamental) to novel fundamental frequencies. This also could be observed in bullfinches, which had learned to copy melodies (Güttinger et al. 2002). The echo spectra of the hollow spheres of different size show similar relative amplitudes of specific harmonics, but the fundamental is shifted up and down in frequency with a decrease or increase in the size of the hollow sphere, respectively. Thus, their timbre is similar although their pitch changes. If bats would exhibit the same perceptual constancy for relational spectral structures as birds, they could use this capability to generalize across the forms of different size.

Such a discrimination is possible independent of the angle of incidence for the hollow sphere since the spectra do not change with the angle. In the case of other forms that exhibit a change in the echo spectrum with the angle of sound incidence, an additional ability of integrating perception over a series of echoes would be needed. A serial integration of acoustic signals, such as humans use in the recognition of melodies, has also been demonstrated in the starling and the bullfinch (e.g., Hulse and Cynx 1986, Hulse et al. 1990, Braaten et al 1990, Güttinger et al. 2002) and in mammals (e.g., Wright et al. 2000, Ralston and Herman 1995). This serial integration has been shown to be generalized (with some limitations) to other fundamental frequencies. If the bats would exhibit a similar ability, this would allow also the recognition of even more complex forms.

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