

# Lack of generalization of object discrimination between spatial contexts by a bat

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## Summary

**Discrimination and generalization are important elements of cognition in the daily lives of animals. Nectar-feeding bats detect flowers by olfaction and probably vision, but also use echolocation and echo-perception of flowers in immediate target surroundings. The echo received from an interference-rich flower corolla is a function of a bat's own relative position in space. This raises the question how easily a free-flying bat will generalize an echo stimulus from a learning situation to a new spatial context where differences in relative flight approach trajectories may lead to an unfamiliar spectral composition of the self-generated echoes. We trained free-flying *Glossophaga soricina* in echoacoustic discrimination in a two-alternative forced-choice (2-AFC) paradigm at location A. We then tested at location B for spontaneous transfer of discrimination ability. Bats did not spontaneously transfer the discrimination ability acquired at A to location B. This lack of spontaneous generalization may have been caused by factors of the underlying learning mechanisms. 2-AFC tasks may not be representative of the natural foraging behaviour of flower-**

**visiting bats. In contrast to insect-eating bats that constantly evaluate the environment to detect unpredictable prey, the spatial stability of flowers may allow flower visitors to rely on spatial memory to guide foraging. The 2-AFC task requires the disregard (learned irrelevance) of salient spatial location cues that are different at each new location. In *Glossophaga*, a conjunction between spatial context and 2-AFC discrimination learning may have inhibited the transfer of learned irrelevance of spatial location in the 2-AFC task to new spatial locations. Alternatively, the bats may have learnt the second discrimination task completely anew, and were faster only because of an acquired learning set. We suggest a dissociation between 2-AFC task acquisition and novel object discrimination learning to resolve the issue.**

Key words: generalization, object discrimination, learning set, cognition, echo location, two-alternative forced-choice, context specific learning, spatial, bat.

## Introduction

Several hundred species of neotropical plants attract echolocating bats (Phyllostomidae) as nectar-feeders and pollinators to their flowers at night (Dobat, 1985). This is mediated by floral odours that are highly attractive to bats (Knudsen and Tollsten, 1995; Bestmann et al., 1999; von Helversen et al., 2000). The combined occurrence of UV-sensitivity in flower bats (Winter et al., 2003) and UV-reflectivity of bat flower corollas (Biedinger and Barthlott, 1993) also indicates a function of vision in flower detection (Winter et al., 2005). A bat may visit the same flower many times per night and such revisits are then mainly guided by spatial memory (Thiele and Winter, 2005; Winter and Stich, 2005).

The importance of echolocation to detect and discriminate flowers is probably restricted to orientation in the immediate

target surroundings. In the rainforest vine *Mucuna holtonii*, for example, a uniquely formed petal (the vexillum) acts as an echoacoustic mirror and 'nectar-guide', which is necessary to successfully attract bat pollinators to single flowers (von Helversen and von Helversen, 1999; von Helversen and von Helversen, 2003). Other bat-pollinated flowers are bell-shaped or of other echoacoustically conspicuous form (for details, see von Helversen et al., 2003). Since these features differ with respect to the echoes of leaves or other objects from surrounding vegetation it has been speculated that such echoes may facilitate flower detection (von Helversen et al., 2003).

The echo signal or stimulus a bat receives from a given flower target is a function of this bat's own position in space and angle of echo call generation. Since bats approach targets from flight rather than from a stationary decision platform they ensonify ('view') hitherto unknown objects from unpredictable

directions. In this situation, the echo signals resemble so-called physical colours ('metallic colours') in the visual domain that change their appearance with the angle of object illumination and perception. This is caused by spectral interference.

In the laboratory, flower bats (*Glossophaginae*) readily learn to discriminate echoacoustic stimuli (von Helversen and von Helversen, 2003; von Helversen, 2004; Thiele and Winter, 2005). *Glossophaga soricina* is also capable of size-independent generalization of hollow forms that differ in curvature (e.g. hemisphere vs paraboloid) when training and test stimuli are presented at the same location (von Helversen, 2004). But will a bat recognize flower shape cues learnt at one spatial location, when confronted with such flowers at a different spatial location with a potential change in appearance?

This recognition task is treated as a problem of stimulus constancy in the classical perception literature. But it may also be regarded as a problem of stimulus generalization (Ghirlanda and Enquist, 2003). The same geometric object serving as the signal source may generate echoes that vary in complex ways if ensounded ('viewed') from different directions, as compared to stimulus training. While the physical similarity between objects will likely include familiar components, which would be a basis for generalization, the change in echo parameters will not necessarily occur along a simple sensory gradient and thus could be difficult for the animals to classify.

We examined the following question: do free-flying bats, conditioned in a two-choice task to a positive echoacoustic object stimulus (S+), transfer their stimulus response to a new spatial location? We tested this experimentally by conditioning flower bats at one location to differentiate between a positive (S+) and negative (S-) echoacoustic stimulus. After learning this task bats were confronted with the same discrimination task at a second location. If at the second location they utilized their knowledge of S+ previously acquired, then they should distinguish between S+ and S- immediately, which should be reflected in the proportion of choices for S+. If, on the other hand, they did not transfer their knowledge between spatial locations then there should be no initial preference for the S+ stimulus at the second location.

## Materials and methods

### *Animals and apparatus*

Nine adult, male *Glossophaga soricina* Pallas 1766 bats, raised in captivity, participated in this experiment. During the behavioural experiments, bats were housed in individual computer-controlled flight cages measuring 1.5 m × 0.7 m in area and 2.2 m in height, each equipped with two computer-controlled feeders, a hanging place attached to a balance, video camera and a motorized door. Cages were within an experimental room with a floor area of about 40 m<sup>2</sup> and a height of around 4 m; the 12 h:12 h light:dark cycle was maintained by automatic timers with the dark phase starting at 14:00 h. During general maintenance the animals received 17% honey water (w/w), partly supplemented with Nektar Plus (Nekton Products, Pforzheim, Germany) and Nutricomp (Braun,

Melsungen, Germany), also ground flower pollen, banana and live flies (*Musca domestica* L.). During experiments bats received rewards consisting of 9.6 µl of sugar solution (18% mass/mass, fructose, glucose and sucrose in equal parts) for visiting feeders. In addition, each animal was given daily 200 mg of Nektar Plus and 300 mg of Nutricomp in 1 ml of water, plus ground flower pollen.

Experimental feeders were computer-controlled, equipped with photosensors at the front to detect the visit of a bat and connected to a stepper-motor syringe pump for reward delivery. Feeders were also equipped with a motorized swivel arm for automatic presentation and exchange of echoacoustic stimuli (see Winter and Stich, 2005). We employed the two different geometrical objects shown in Fig. 1: a perforated hollow sphere (training golf ball) as the positive object and a triple mirror (three-sided corner reflector) as the negative object – two very different stimuli with regard to their echoacoustic reflective properties [see fig. 1(Thiele and Winter, 2005)]. Previous experiments had shown that *Glossophaga* can discriminate these stimuli by echolocation (Thiele and Winter, 2005).

The swivel arm of a feeder carried both the positive and negative object at its opposing ends. The arm's orientation determined which object was presented to the front (Fig. 1). Within a pair one feeder presented the positive (S+), the other the negative stimulus (S-) determined by a random procedure, with a maximum of three consecutive presentations of S+ on the same side. After each choice by a bat, both swivel arms rotated by 90° and then either continued the rotation (change of presented stimulus) or turned back again (previous stimulus presented). This ensured that swivel arm motors did not provide predictive acoustic cues.

Individual feeders within a pair were arranged horizontally, separated by 25 cm and placed about 20 cm in front of a plastic wall. During phase II of the experiments, individual bats had alternating access to two identical pairs of feeders, each programmed as a two-alternative forced-choice paradigm. The

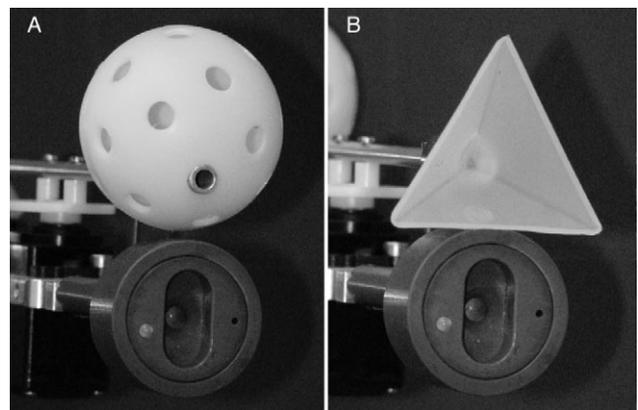


Fig. 1. Feeders with their echoacoustic stimuli. (A) perforated hollow sphere (S+, rewarding positive stimulus) and (B) three-sided corner reflector or 'triple mirror' (S-, non-rewarding negative stimulus).

first pair of feeders was within the individual cage, the second pair of feeders was within the experimental room. Room feeders were part of a larger feeder array (8×8), whose 62 other feeders were concealed behind a large plastic sheet during the experiment described here. Bats showed no interest in the covered feeders.

To exchange a bat between the cage feeder pair and external feeder pair, the bat was automatically released from its cage, then searched for nectar at the external feeder pair within the experimental room, and was locked in its cage again after the end of a trial at the room feeder pair (see below). Details and illustrations of this automated experimental set-up are given elsewhere (Winter and Stich, 2005).

#### *Pretraining*

All individuals were already familiar with the automatic feeders and were habituated to the individual cages used in the experiment. We used two groups of animals that differed in their previous experience with 2-AFC echoacoustic discrimination. The six animals in one group (naïve group) had participated in an experiment using the automated feeders, both in the cages and in the larger experimental room, about 4 months earlier; however, without echoacoustic discrimination training (Winter and Stich, 2005) (K.P.S. and Y.W., unpublished). The three bats in the other group (experienced group) had taken part in an experiment immediately prior to the one described here, in which they had learned to differentiate between rewarding and non-rewarding feeders on the basis of echoacoustic characteristics in a 2-AFC paradigm (Y.W. and D. Tafur, unpublished data). In this earlier echoacoustic discrimination experiment a similar type of feeder was used, but the specific echoacoustic stimuli employed differed from those in the present study.

#### *Experimental procedure*

##### *Experimental phase I*

All animals started the experiment in their cages where they learned to discriminate between the S+ and S− stimulus pair. We used the perforated sphere as S+ and the triple mirror as S− (Fig. 1). The bats required 1–3 nights and several hundred to 8000 choices until they had learnt this discrimination task.

##### *Experimental phase II*

Phase II began immediately after phase I. The animals continued with the discrimination task from phase I while in their cages. In addition, each individual left its cage to the feeder pair in the experimental room for up to five times per night and for time intervals of about 40 min each. The animals were divided into three groups with three individuals each. All three individuals from one group performed their individual experiments in parallel but only a single bat was released into the experimental room at the same time. Overall, each bat spent about one third of its 12 h night time with the room feeder pair and two thirds with its cage feeder pair. A bat left its cage voluntarily to enter the room when its electronic cage door opened, after cage feeders had been turned off and

experimental room feeders turned on. A bat returned from the room to its cage when the procedure was reversed after the end of a trial. Details of this procedure allowing series of trials with multiple individuals without the presence of the experimenter are described elsewhere (Winter and Stich, 2005). Animals quickly adopted the procedure and we had no problems running three individuals in parallel. Experimental phase II began with the first trial at the room feeder pair (see below) and lasted until the end of the experiment. Experimental phase II lasted 3–4 nights.

#### *Definitions*

##### *Experimental phases I and II*

See above.

##### *Room feeder trial*

A trial began with the first visit to one of the two room feeders and ended after a total of 200 visits or after 40 min, whichever occurred first.

##### *Cage feeder trial*

During phase II, each uninterrupted period that a bat was in its cage was considered a cage trial. Since the experiments were conducted with three animals simultaneously with only one single individual released into the experimental room at a time, a cage feeder trial lasted roughly twice as long as a trial at the room feeder pair, i.e. about 80 min, and contained a correspondingly larger number of visits.

##### *Percent correct choices*

Correct choices were visits to the S+ feeder (perforated sphere, Fig. 1). Therefore, ‘percent correct choices’ equals the number of correct choices divided by all choices. During phase I, percentages were determined for blocks of 100 choices. During phase II, one percentage value was determined for single trials, i.e. for 60–200 choices each.

#### *Data analysis*

Statistical analysis of the animals’ performance was carried out using generalised linear models (GLM, SAS Procedure Genmod). Since the percentage of correct choices was calculated from binomial data (correct or incorrect), we transformed data with a logit link function. The quotient ‘correct choices/all choices’ was taken as the dependent variable. Individuals were treated as repeated subjects. We corrected models for overdispersion (SAS dscale option).

#### **Results**

The total number of behavioural choices obtained in this study was 118072. Of these, 45302 choices occurred during phase I and 72770 choices during phase II (22767 at room feeders, 49818 at cage feeders). Of 143 trials at room feeders in phase II, 46 ended with the 200th visit (32%) and 97 with the end of the 40 min time period, and the average number of choices per trial was 155. Between individual room feeder trials

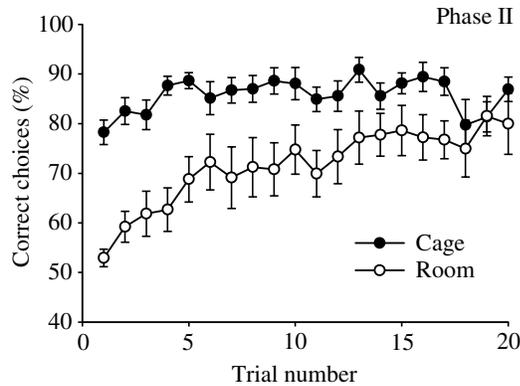


Fig. 2. Choice performance during experimental phase II at the two spatially and temporally separated sets of 2-AFC feeders. Individual trials strictly alternated between 'cage' and 'room'. Values are means  $\pm$  s.e.m. ( $N=9$ ). Data are based on 66323 decisions (room 22767, cage 43556). Trials were conducted over 3 or 4 days. All individuals completed 10 trials in both cage and room but only 3 completed 20 trials. Individual trials averaged 155 decisions at the room feeder pair and 324 in the cage.

during phase II the animals spent about 80 min in their cages, making on average 324 choices at cage feeders.

#### Generalization?

The aim of the study was to discover whether the bats would transfer S+ performance to a new location (here the experimental room), and immediately perform the echoacoustic discrimination task learned in the cage with the same level of competence. During the 20 trials of experimental phase II, performance in the cage was on average 85% correct choices (Fig. 2), clearly exceeding the 50% random choice level. However, performance during the very first 40 min trial at the room feeder pair was only around 50%, significantly below concurrent performance in the cages (GLM, location,  $Z=7.11$ ,  $P<0.0001$ ; Fig. 2). This means that the animals did not select the positive stimulus at the room feeders, even though it was well known to them from phase I and the cage trials, where they chose this same positive stimulus correctly.

#### Influence of previous experience on acquisition of discrimination performance

We had two experimental groups of animals: the naïve group ( $N=6$ ) and the experienced group ( $N=3$ ). Both groups were exposed to two treatments, here termed experimental phases I and II. We analysed the data over the first 1000 choices under each condition within a single generalized linear model comparing groups and conditions. As a general effect, correct performance increased with the number of trials an individual had made (GLM trial, Wald  $\chi^2=5.87$ , d.f.=1,  $P<0.02$ ). This increase in performance, however, differed between experimental groups (GLM trial $\times$ group, Wald  $\chi^2=8.10$ , d.f.=3,  $P<0.05$ ), an effect that we further examined by *post-hoc* comparisons using contrasts. In experimental phase I, bats from the experienced group increased

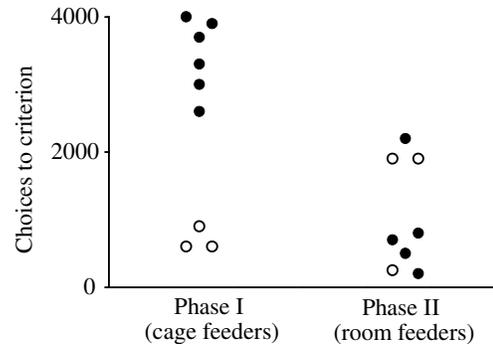


Fig. 3. Number of decisions until a performance of 70% correct choices was reached. Single circles correspond to individual bats. Black symbols: animals without prior experience from an earlier experiment; open symbols: animals with prior experience in 2-AFC echo-acoustic object discrimination from an earlier experiment. One of the six individuals without prior experience needed more than 4000 decisions to reach 70% in phase II and was not included in the figure.

performance significantly faster than individuals from the naïve group (Fig. 3, Fig. 4A; GLM trial $\times$ group, Wald  $\chi^2=160.14$ , d.f.=1,  $P<0.0001$ ). On the other hand, groups did not differ in their initial correct choice level (GLM intercept group effect, Wald  $\chi^2=0.71$ , d.f.=1,  $P=0.40$ ). During phase II, the naïve group increased performance at the room feeder pair faster than during the previous phase I at the cage feeders (GLM, Wald  $\chi^2=10.7$ , d.f.=1,  $P=0.001$ ). However, during this phase II there was no difference any more between the two groups naïve and experienced (Fig. 4B, GLM, Wald  $\chi^2=0.03$ , d.f.=1,  $P=0.86$ ). Since the discrimination task was identical at both locations it follows that prior experience appears to accelerate the initial acquisition of the task. Groups 'naïve' and 'experienced' did not differ in performance during phase II at the second location, since by then individuals from both groups were experienced with the 2-AFC paradigm. There was also a trend for the experienced group to learn more slowly during phase II at the room feeders than during phase I (GLM, Wald  $\chi^2$ ,  $P=0.052$ ).

#### Discussion

##### No evidence for echoacoustic generalization to new 2-AFC location

We investigated whether flower-visiting bats in free flight would transfer their behavioural response towards a positively conditioned echoacoustic stimulus within an S+/S- pair from a training location to a new location with an identical stimulus pair. Our experiments provide no evidence for such spontaneous echoacoustic generalization between spatial contexts. After the completion of task acquisition during phase I of the experiment, nine bats performed at 78% correct choices at the original pair of cage feeders at the beginning of phase II (Fig. 2). At the same time they chose S+ only at 50% chance level at a novel location (room feeder pair). Despite the unexpected outcome, this is a robust result derived from the

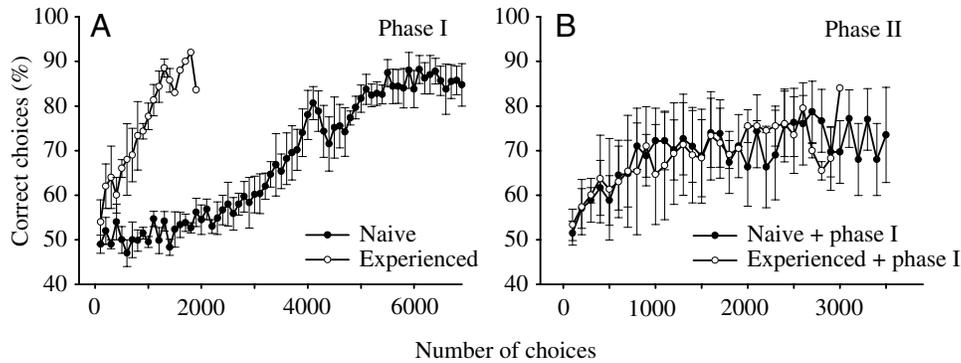


Fig. 4. Performance during experimental phase I (A, cage feeders) and experimental phase II (B, here only room feeders). Data are shown separately for individuals with prior experience (white circles,  $N=3$ ) and without prior experience (black circles,  $N=6$ ). Values are means  $\pm$  s.e.m. of individual percentages based on 100 visits. Different individuals needed unequal numbers of choices to acquire the task; this causes the discontinuity of the line in 4A (naïve).

performance of nine individuals tested in three consecutive groups.

We found this result astonishing. Among bat-pollinated plant species, at least the legume *Mucuna holtonii* utilises differences in the echoacoustic signature of its flowers to attract bats at the right time. When nectar is available, a petal, the vexillum, is raised acting as an echoacoustic triple mirror. *Mucuna holtonii* flowers without a functioning vexillum are hardly ever visited by nectarivorous bats (von Helversen and von Helversen, 1999; von Helversen and von Helversen, 2003). In this natural setting, glossophagine bats therefore clearly use the echoacoustic configuration of flowers – as one would expect – without learning this signature for every flower; in other words, they generalize. Yet why was this not apparent in the experiment presented here? Possible explanations are discussed below.

#### Relevance of echoacoustic generalization

A question at the outset is whether the learning of echoacoustic generalization is likely to be important to nectar-feeding bats under natural conditions. Numerous behavioural studies from echolocation research have examined the psychophysics of echoacoustic stimulus discrimination in bats (Neuweiler, 2000). Nevertheless, comparative information on learning ability between members from different trophic groups is not available. Flower-visiting glossophagines belong to the so-called ‘whispering bats’ that emit only faint or highly directional echolocation calls (Neuweiler, 2000). Reduced development of echolocation goes along with the increased importance of olfaction for flower detection, a very different sensory modality. The origin of an olfactory cue is more difficult to localise than an echoacoustic or visual stimulus. On the other hand, the composition or ‘shape’ of an olfactory stimulus is maintained independent of the angle into which it propagates or from which it is perceived. This stability in signal structure should facilitate the recognition of a floral bouquet from a computational point of view and make such stimuli highly useful for plant species identification. It would be interesting to know how bats would respond to olfactory stimuli in our experiments.

Despite the importance of olfaction, echolocation is definitely used to orient at flowers such as *Mucuna* or at feeders in the laboratory, at least within the regional scale of the immediate target surroundings (von Helversen et al., 2003; von

Helversen and von Helversen, 2003; Thiele and Winter, 2005). The echolocation calls of Glossophagines are high-pitched and brief, which allows for a good resolution of small structures (von Helversen and von Helversen, 2003) although probably only from short distance. *Glossophaga* is able to generalize between different sizes of hollow forms differing in curvature in a situation where training and test stimuli are presented at the same location (von Helversen, 2004). Similarly, artificial reflectors placed on flowers in the natural environment are discriminated by bats. Initially artificial reflectors suppress flower visitation rates, but over time (within 2 nights) naturally foraging bats learn to accept them (von Helversen and von Helversen, 2003). Thus the ability to recognize and distinguish echoacoustic objects associated with flowers is evident and relevant also in an ecological context for flower visiting bats.

#### Spatial context: 2-AFC conflict with spatial memory

*Glossophaga* bats in previous laboratory experiments remembered both the spatial location of a feeder and its echoacoustic characteristics (Thiele and Winter, 2005). However, when returning to a profitable feeder the animals oriented primarily by the spatial cue even if this was in conflict with object information, i.e. the feeder or flower specific echoacoustic appearance. Thiele and Winter also observed in the course of an echoacoustic 2-AFC discrimination task that a highly trained *Glossophaga* (over 90% correct choices) began to develop a location preference after only eight consecutive presentations of the positive object at the same side (Thiele and Winter, 2005). These two findings indicate a strong preference of *Glossophaga* to orient based on spatial memory rather than by object-cue guidance.

Spatial context specific learning may have interfered with the learning task of the present experiment. During phase II of our experiments, bats were confronted with two 2-AFC setups at different locations: the known setup in the cage, and the novel setup in the room. The nature of the discriminative stimulus pair and also the reward contingency of the 2-AFC paradigm were the same in both locations. We expected bats to have acquired the general factors of the 2-AFC paradigm and thus only be confronted with the generalization problem of recognizing and discriminating S+ and S– stimuli at a new location and possibly from a different flight approach trajectory. This assumption may have fallen short of fully

recognizing the learning requirements posed for the bats. Since flower bats use location as a main food predicting stimulus, experimental bats here were confronted with a new set of spatial stimuli at the new location, in addition to a new 2-AFC feeder pair. In a 2-AFC task both left and right positions are rewarded half of the time. If the bats used location as the dominant cue in this experiment, they might initially associate a 2-AFC setup as two distinct spatial locations, each of which irregularly provides food. Eventually, bats must ignore spatial location as a predictor of food and instead restrict attention to the positive object stimulus. In the present study, bats needed several thousand choices (Fig. 4A, naïve) before they learned to ignore spatial location as a predictor of rewards (learned irrelevance). Since flower-visiting bats may be naturally predisposed to experience spatial location cues as salient, learning the 2-AFC paradigm may have been particularly difficult for *Glossophaga*.

With these considerations in mind, the lack of transferring the disregard of spatial location within a 2-AFC paradigm to other positions within a room may not be so surprising after all if we consider the training in the lab *versus* in nature. In the lab, the training takes place in one context, the home cage. There is then no transfer of object discrimination to a new context, although there is a savings effect, in that the naïve group learned faster during the second time than during the first. In nature, the flowers are found in many locations, and discrimination training is thus distributed over many contexts. The number of instances should promote learning and generalization of the relevant 'concept' (the S+ object). There is much evidence from learning studies. Pigeons that learn one single instance of 'matching to sample' do not generalize task performance to other cues. But given many instances of training, transfer to new cases is good (Wright, 1997; Kendrick and Wright, 1990).

#### *Niche-specific cognitive strategies?*

Concerning the importance of location for orientation during foraging and the ease with which location as a cue is ignored, flower visiting and insect eating bats may differ. Insect eaters need to evaluate the environment constantly (mainly by echolocation) to detect spatially unpredictable prey. In contrast, flower visitors may rely on the spatial stability of flowering plants and return to known locations instead of constantly searching by echolocation: most flowers remain available at least for a single night and rarely alter their echo acoustic signature. On a more general level this suggests that the spatial and temporal distribution of food may be significantly associated with a species' cognitive architecture or its ability to learn different kinds of tasks. For bats this implies that different cues (e.g. spatial, visual, echo acoustic, olfactory etc.) may vary in importance for different trophic groups. Within the trophically diverse leaf-nosed bats (Phyllostomidae), for example, we would predict that some of the insect-eating and flower-visiting bats operate at opposite ends of a continuum of food predictability ranging from the stochastic occurrence of single insects to the stationary locations of flowers. Fruit-eating bats may be at some intermediate position. While a fruiting

plant can offer resources over an extended time span, which makes its location worth memorizing, a single fruit is collected only once. In contrast, a flower with continuous nectar secretion may be revisited 20 or 30 times during a single night (Winter and von Helversen, 2001). This hypothesis of cognitive specialisation to trophic niche dimensions finds support in neuroanatomical correlates. Brain regions associated with spatial learning such as the hippocampus are largest in frugivorous and flower visiting bats (Baron et al., 1986; Hutcheon et al., 2002; Safi and Dechmann, 2005).

#### *The effect of previous experience on two-choice discrimination*

The different prior experience of the two experimental groups allows the examination of learning performance at the level of a learning set. Both groups of bats learnt at the same rate the second 2-AFC task during phase II of the experiment (Fig. 3, Fig. 4B). In contrast, experienced bats appeared to learn faster than naïve bats during phase I (cage, Fig. 3, Fig. 4A). Apparently, prior learning experience made learning easier. This supports the idea of the appearance of a learning set, a general disposition acquired by learning to solve similar problems (Shettleworth, 1998). An operationally defined learning set can reflect the operation of many different psychological processes: habituation to the testing procedures, attention to the relevant stimulus dimensions, learning of the response-reinforcement contingencies, and so on (Zeldin and Olton, 1986; Macphail, 1982). In other words this could be described as learning how to learn. In this way changes or improvements in the method of approaching a problem or material to be learned can arise, allowing more rapid or better learning (Shettleworth, 1998).

In discrimination tasks, animals not only learn the differentiation characteristics relevant to the task but also diverse other characteristics of the environment before they have discovered the relevant ones. Such experience ought to help them solve the next task with novel stimuli faster, since attention can immediately be directed to the relevant characteristics (Shettleworth, 1998). If a task is presented in a novel environment, however, then this could hamper performance in an otherwise familiar task. Such could have been the case in our study. Bats made initially random visits to novel stimuli in a known environment during phase I, which is the typical situation for any classical learning experiment. In addition, they also made initially random visits to known stimuli in a novel environmental context (room feeder pair, phase II). The individuals with prior experience actually had a tendency to learn more slowly at the room feeder pair than in the cages (Fig. 4). Having to master a novel environmental context could be the reason for such slower learning.

#### *Conclusions*

An initial conjunction of spatial context and discrimination learning may have hindered transfer of object discrimination to a new spatial location. Alternatively, the bats may have learnt the discrimination task at the room feeder pair completely

anew, and were faster only because of a learning set. In a new set of experiments to distinguish between these possible explanations, object discrimination learning on the one hand and 2-AFC acquisition at multiple locations on the other hand would have to be dissociated. This could be achieved by first having bats learn the 2-AFC paradigm at multiple sites, then presenting a new stimulus pair at some of those sites, and finally confronting them with this already known, new stimulus pair at the remaining sites where 2-AFC performance has already been acquired.

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