

## The absence of spatial echo suppression in the echolocating bats *Megaderma lyra* and *Phyllostomus discolor*

Maike Schuchmann, Matthias Hübner and Lutz Wiegrebe\*

Department Biologie II, Universität München, Großhadernerstrasse 2, 82152 Planegg-Martinsried, Germany

\*Author for correspondence (e-mail: lutzw@lmu.de)

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### Summary

Acoustic orientation most often takes place in echoic environments. The mammalian auditory system shows a variety of specializations to suppress misleading spatial information mediated by echoes. Psychophysically these specializations are summarized as the precedence effect. This study investigates how echolocating bats deal with multiple reflections of their sonar emissions from different spatial positions.

In a two-alternative, forced choice paradigm, a study was made of the extent to which the echolocating bats *Megaderma lyra* and *Phyllostomus discolor* spontaneously suppress the spatial information of a second reflection of their sonar emission. The delay between the first and the second reflection ranged between 0 and 12.8 ms.

In general, *M. lyra* (five individuals) and *P. discolor* (two individuals) did not suppress the spatial information of the

second reflection of their sonar emission, whatever the delay. Only one *M. lyra* showed significant suppression for delays between 0.8 and 3.2 ms. However, this suppression could not be confirmed in an exact repetition of the experiment.

The current data indicate that although bats may be able to suppress the spatial information of a second reflection, this is not their default mode of auditory processing. The reason for this exceptional absence of spatial echo suppression may lie in the shorter time constants of cochlear processing in the ultrasonic frequency range and the strong influence of cognitive components associated with the 'precedence effect'.

Key words: echolocation, precedence effect, sound localization, bat, *Megaderma lyra*, *Phyllostomus discolor*.

### Introduction

Echoes are a fundamental feature of acoustic environments. In most natural settings, a sound propagates in several directions and is reflected by nearby surfaces. The sound travels to a listener's ears not only along a direct path, but also indirectly, as echoes arriving a short time after the direct sound. Each of these echoes carries its own set of localization cues and provides misleading information about the sound source's position. In order to avoid localization errors the auditory system must resolve which cues belong to the sound source. A psychophysical phenomenon relevant to sound localization in reverberant environments is commonly known as the 'precedence effect' (Wallach et al., 1949).

Accurate sound localization is possible for most animals because the spatial information cues from the direct and shortest path from sound source to listener carries greater perceptual weight than the spatial information in the echoes. Only the directional information of the sound that reaches the ear first dominates the perceived position of a sound source. The spatial information of the echoes is suppressed.

A common behavioural paradigm used to examine the precedence effect is to simulate a direct sound source ('lead')

and a single echo ('lag') with two loudspeakers in an anechoic chamber. The speakers are placed in the left and right hemi field equidistant to the listener, each presenting identical sounds offset in time such that the lagging sound is delayed relative to the leading sound. This 'lead-lag paradigm' allows for the investigation of the mechanisms used by listeners to resolve spatial information for sounds in reverberant environments.

The precedence effect is characterized by three distinct but related phenomena. (1) When the delay between leading and lagging click is zero or close to zero (within 1 ms), the listener will hear one fused auditory event between the two loudspeakers ('summing localization'; Litovsky et al., 1999; Blauert, 1997). (2) For lead-lag delays between about 1 and 5 ms, the sound and its echo remain perceptually fused, but the perceived position of this fused sound image is dominated by the position of the lead. This is referred to as 'localization dominance'. (3) With a further delay, both lead and lag become audible as separate sound events. This delay is referred to as 'echo threshold'. Echo-threshold values can vary tremendously (2–50 ms). The delay range depends on both signal duration and complexity. The lead-lag delays are much shorter for brief stimuli such as clicks (around 6 ms) than for longer duration

stimuli such as noise and ongoing complex stimuli such as running speech. Until now, behavioural evidence for precedence has been found in several animals at lead–lag delays that are similar to those reported in humans (see Discussion).

Echolocating bats are confronted with a very complex echo-acoustic situation. They always have to deal with lots of echoes, many of them being echoes of their own echolocation calls. At first sight, the ability of the bats to orient through the auditory analysis of echoes of their vocal emissions is in contrast to the precedence effect. It is just the spatial information in echoes that enables the localization of objects in the dark. Bats rely heavily on the evaluation of these echoes for orientation and hunting.

Each echo includes information about the properties of the environment, but this information can be misleading: an ensounded target object reflects an echolocation call not only directly back to the bat's ears, but also in other directions. There, the echo can be reflected by another object, e.g. a water surface or a wall. This second reflection constitutes a higher-order echo, which includes misleading spatial information of the target object. The perceptual suppression of this misleading information would facilitate the echo-acoustic localization of the target object.

However, the higher-order echoes provide information about other objects in the vicinity of the target object. Thus, it may be beneficial for a bat not to suppress the perception of the higher-order echo because the latter provides information about the distance between the target object and the other object.

The current experiments were designed to investigate whether, and to what extent, the echolocating bats *Megaderma lyra* and *Phyllostomus discolor* exhibit localization dominance behaviour consistent with the precedence effect in the processing of reflections of their echolocation calls.

## Materials and methods

### Animals

#### *Megaderma lyra*

*Megaderma lyra* Geoffroy 1810, the false vampire bat, is an old world tropical gleaner bat. It detects its prey both via echolocation (Schmidt et al., 2000) and based on prey-generated rustling noises (Neuweiler, 2000). Its echolocation calls are short, multi-harmonic frequency sweeps. An exemplary echolocation call is shown in Fig. 1.

Five adult *M. lyra* took part in the training (one female, four males). The animals were kept together in a 12 m<sup>2</sup> room with free access to water. In this room, they were only fed on days without training sessions, i.e. only for 2 days after the 12-day periods of training. They were fed with mice during the training breaks. During the training period they were only fed with mealworms for reward.

#### *Phyllostomus discolor*

*Phyllostomus discolor* Wagner 1843, the lesser spear-nosed bat, is a new world tropical bat. It feeds on fruit and small insects. Its echolocation calls are also short, multi-harmonic

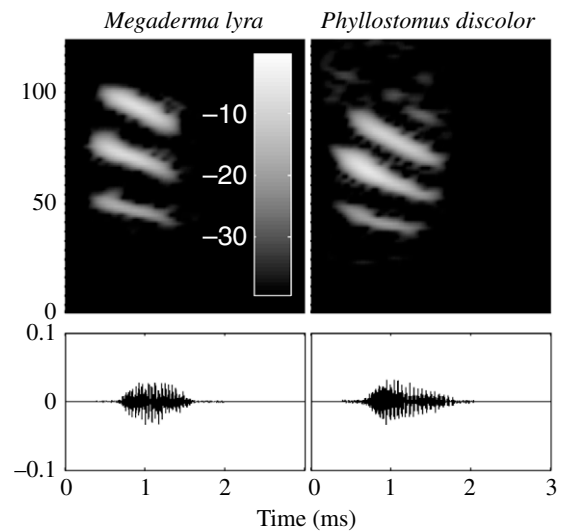


Fig. 1. Characteristic samples of a *Megaderma lyra* echolocation call (left) and a *Phyllostomus discolor* call (right). The upper panels show the spectrograms (the shaded bar shows the magnitude in dB); the lower panels show the oscillograms. *M. lyra* emits brief (0.5–1.5 ms), broadband, multi-harmonic echolocation calls. The fundamental frequency is frequency modulated from about 26 to 19 kHz. The strongest harmonics are the 3rd, 4th or 5th. *P. discolor* also emits brief (<3 ms), broadband, multi-harmonic echolocation calls covering the frequency range between 40 and 90 kHz. The fundamental frequency is modulated from about 23.5 to 16 kHz.

frequency sweeps but slightly longer than *M. lyra* calls and with a stronger dominance of lower harmonics. An exemplary echolocation call is shown in Fig. 1.

Two adult *P. discolor* (both female) took part in the training. The animals were housed together in a box (80 cm×40 cm×50 cm) with free access to water. In this box, they were only fed on days without training sessions, i.e. only for 2 days after a 5-day training period. They were fed with mealworms during the training breaks. During the training period, they were fed with banana pulp for reward.

### Experimental design

First and second reflection of echolocation calls were simulated in a lead–lag paradigm. In this paradigm, two ultrasonic speakers were placed at the same distance and angle in each hemi field to the bats' starting position. The bats were trained in a two-alternative, forced choice experiment. In an initial training period, only one of the two speakers emitted a reflection of the bats' ultrasonic emission to train the bats to move to the speaker emitting the reflection to get a food reward ('lead-only trials'). The presenting speaker alternated randomly. When the bats were able to solve this task with a stable performance of >85% correct choices over 5–6 training days, test trials were randomly interspersed between these lead-only trials with a probability of 25%, such that two of eight trials were test trials. In these test trials, both speakers emitted a reflection but the reflection from one speaker had an additional delay of 0 ms and 0.1 ms up to 12.8 ms in doublings ('lead–lag

trials'). The lead–lag delays were presented randomly across lead–lag trials. As in the lead-only trials, the speaker emitting the leading reflection in the lead–lag trials varied randomly. In these trials the bats were free to choose any speaker to receive a food reward, i.e. the spontaneous performance of the bats was assessed. Thirty lead–lag trials were collected for each of the nine lead–lag delays, therefore each bat completed 270 lead–lag trials interspersed between 810 lead-only trials. The performance was calculated as decisions for the side of the leading reflection in percent as a function of the lead–lag delay.

In the lead–lag trials, the following behaviour would be expected: the bats were trained to move to the side of the speaker where they perceived a reflection of their emission. If the bats experience summing localization (one fused auditory event between the two speakers) with a lead–lag delay of 0 ms, they could not show any side preference, thus the performance level would be around 50%. With increasing lead–lag delay, the bats would be expected to prefer the side of the leading speaker. If the bats perceive localization dominance, meaning the leading reflection dominates the perceptive position of the auditory event, they would significantly (performance >75% for 30 trials; Miller, 1996) move to the side of the leading reflection. Reaching the echo threshold, the bats would perceive two separate sounds in distinct positions and would again choose one of the sides randomly.

#### Experimental layout

##### *Megaderma lyra*

The experiments, conducted with flying *M. lyra*, took place in a weakly illuminated, echo-attenuated chamber (3.5 m×2.2 m×2.2 m). As in former studies (Weissenbacher and Wiegrebe, 2003; Wiegrebe and Schmidt, 1996) the layout consisted of a starting perch on one side of the room and two ultrasonic speakers, one in the left and one in the right hemi field. Each speaker was associated with a feeding dish. The distance from the loudspeakers to the bat's head was 1.2 m. The angle between the speakers and the bat's head was 45°. The experimental layout is shown in Fig. 2A,B.

To pick up the bats' sonar emissions, a 6.35 mm microphone (Brüel & Kjaer, 4135, Naerum, Denmark) was installed 0.12 m in front of the bat's head. The emissions were amplified (B&K 2636), band-pass filtered (10–99 kHz, Krohn Hite 3342, Brockton, Massachusetts, USA) and digitized by a data acquisition board (Microstar DAP 5200, Bellevue, Washington, USA) at a sampling rate of 250 kHz. On this board, the emissions were digitally delayed and played back over either one channel (lead-only trials) or over two channels (lead–lag trials). These signals were attenuated (custom passive attenuation network), amplified (Rotel RB 976 MK II, Worthing, UK) and presented *via* ultrasonic speakers (Matsushita EAS 10 TH 800D, Osaka, Japan) at an overall attenuation of 30 dB re. emission level. The playback delay of the lead was always 4.5 ms including the acoustic travel times. The frequency response of all components, including speakers, was flat within ±5 dB between 5 and 100 kHz. On the side of the room opposite to the perch, the experimenter was seated,

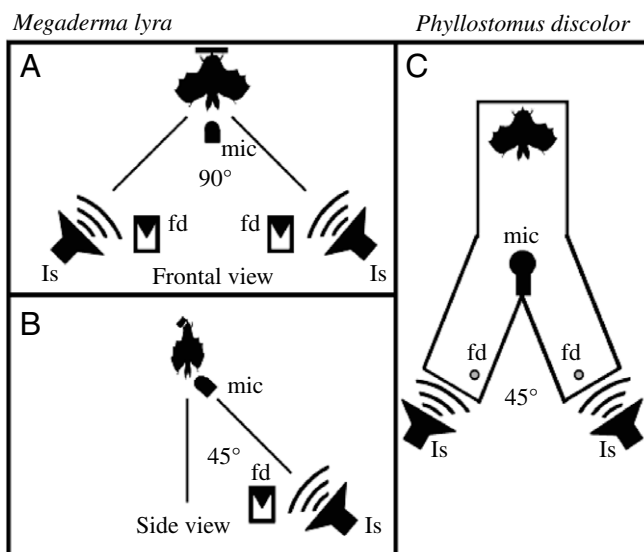


Fig. 2. Experimental designs for *Megaderma lyra* (A,B) and *Phyllostomus discolor* (C). The layout consisted of a starting perch and two ultrasonic speakers (Is), each of which was associated with a feeding dish (fd) next to the speakers. The angle between the speakers in the *M. lyra* experiments was 90°. This angle was positioned at an elevation of 45° (B). A microphone (mic) was placed in front of the bat's head to pick up its ultrasonic emissions. The *P. discolor* layout was a Y-shaped maze (45×30 cm; wire mesh); the angle between the two legs was 45°. The inner width of each leg was 10 cm.

controlling the experimental procedure and the data storage with a touch screen (WES TS, ELT121C-7SWA-1, Nidderau-Heldenbergen, Germany). The experimental program was written in Matlab 5.3.

##### *Phyllostomus discolor*

The experiments, conducted with crawling *P. discolor*, took place in a horizontal Y-shaped maze in an echo-attenuated chamber. A starting perch was located at the bottom of the leg of the Y, and a feeder was mounted at the end of each upper leg. The angle between the legs was 45°. An ultrasonic speaker (Matsushita EAS 10 TH 800D) was placed in a distance of 15 cm in front of each upper leg (see Fig. 2C). Further, a 6.35 mm microphone (B&K 4135) was located in the middle of the maze to pick up the bats' sonar emissions. The stimulation apparatus was identical to that used with *M. lyra*.

The experimenter was seated outside the chamber, controlling the experimental procedure via a computer interface and an infrared camera.

These slightly different experimental layouts were used to suit the animals' exploration behaviour under laboratory conditions: whereas *P. discolor* prefers to crawl to a food source, *M. lyra* always prefers to fly.

## Results

In a two-alternative forced-choice task, the bats were successfully trained *via* lead-only trials to move towards the

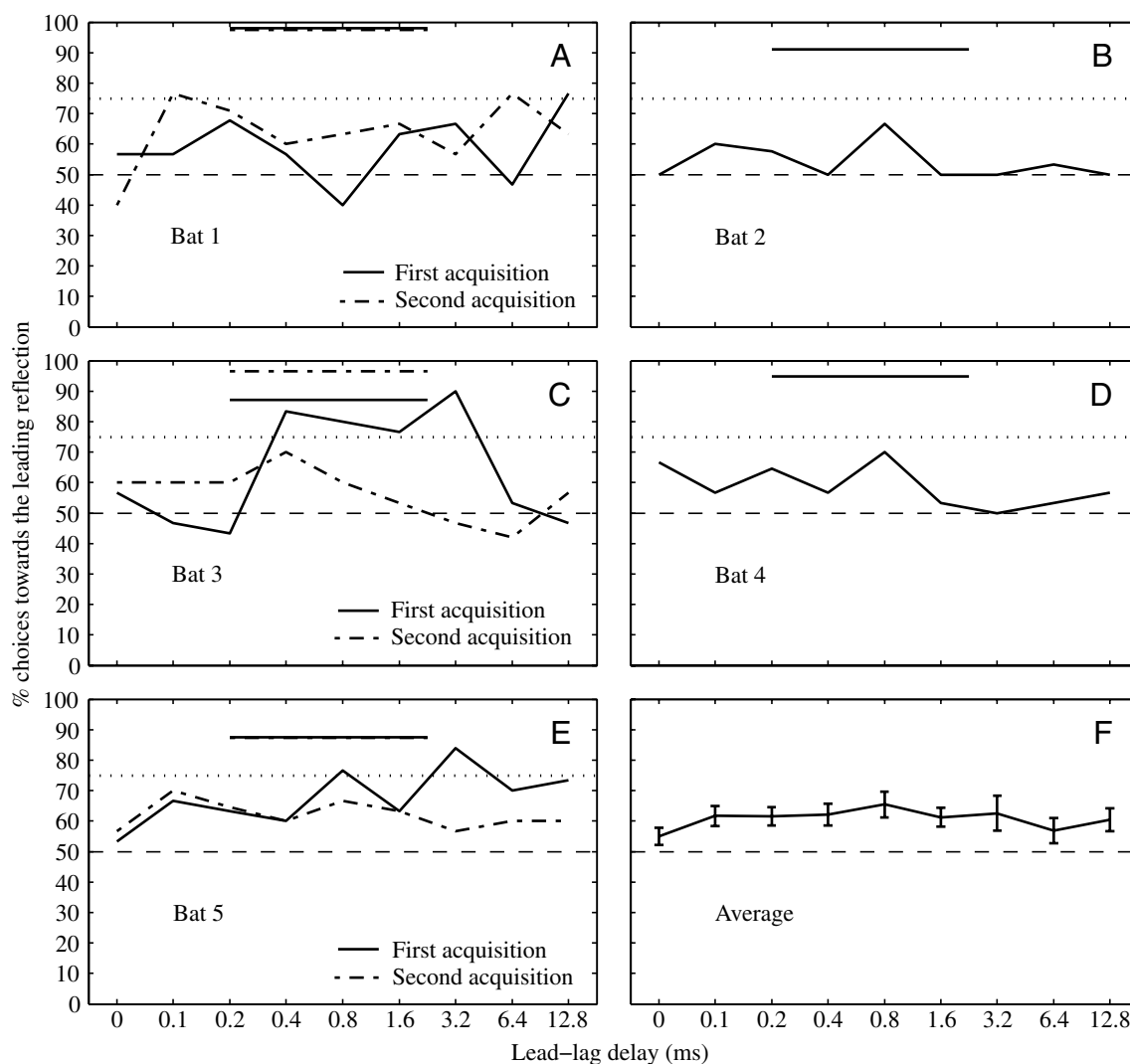


Fig. 3. Echo suppression in the echolocating bat *Megaderma lyra*. The figure shows the percentage decisions towards the first of two reflections plotted against the lead–lag delay. Chance performance is represented by the horizontal broken line at 50%; significant performance is represented by the dotted line at 75%. The bats' performance in the lead-only trials is shown by the short horizontal lines. A–E show data for individuals; F shows the mean performance of all bats. The two data plots in A,C,E show a first (solid line) and second (broken line) data acquisition of these bats. Only one of five *M. lyra* individuals spontaneously showed significant preference (>75%) for the first of two reflections (C; first acquisition).

speaker from which the single reflection was presented. After this training period, the performance in these lead-only trials was always above 85% correct. The data reported below were obtained while the bats maintained this good performance for the lead-only trials. The data are based on a total of about 12 000 trials obtained from seven animals.

The spontaneous decisions of the five *M. lyra* individuals in the interspersed lead–lag trials as a function of the lead–lag delay are given in Fig. 3: individual data are plotted in A–E, average data are shown in F. Based on 30 trials per condition, significant performance is reached at about 75% correct. In general, the bats did not significantly prefer the leading reflection of their sonar emission over the lagging reflection. While the first acquisition of Bat 3 (Fig. 3C) indicates a significant preference for the leading reflection for lead–lag delays between 0.4 and 3.2 ms, a second acquisition could not

confirm this finding. The average data show that there is only a weak trend towards a preference for the first reflection.

Data for the two *P. discolor* individuals are shown in Fig. 4. Again, both individuals do not significantly prefer the first reflection over the second.

### Discussion

The current experiments show that both bat species, *M. lyra* and *P. discolor*, do generally not reveal localization dominance when confronted with a pair of reflections of their sonar emissions. Only one *M. lyra* individual spontaneously showed localization dominance in a first data acquisition period but failed to do so in a repetition of the experiment. Note that in both these acquisition periods, the animal's performance in the lead-only trial was above 90% correct at



all times. Thus, the data from both acquisition periods are valid.

The general absence of localization dominance in the current data is quite different from the findings in all other species tested so far. Summing localization similar to humans has been found in cats (Populin and Yin, 1998). Tested on clicks in a lead-lag paradigm, cats showed localization dominance for delays between 0.5 and 2 ms (Cranford, 1982). Fur seals show the precedence effect in a similar time range as humans (for clicks from around 1 ms up to 6 ms; for tonal pulses up to 11 ms; Babushkina and Poliakov, 2001). Other studies found similar values for rats (Kelly, 1974) and crickets (Wytenbach and Hoy, 1993). It appears that these animals experience localization dominance at nearly the same delays as human listeners do. Also birds such as budgerigars and owls reveal localization dominance in a manner similar to humans (Dent and Dooling, 2004, 2003a, 2003b; Keller and Takahashi, 1996a; Keller and Takahashi, 1996b).

Why do most of the echolocating bats tested in the current experiments show no localization dominance when confronted with two reflections of their own echolocation calls?

Hartung and Trahiotis (2001) showed that the integration times of the peripheral auditory filters may play an important role in echo suppression. They showed that the ringing of auditory filters in response to the lead-lag stimulation generates changes in the central auditory representation of interaural time differences, which can quantitatively predict a large variety of psychophysical findings related to the precedence effect.

In the frequency region which dominates the precedence effect in human listeners (around 750 Hz; Tollin and Henning, 1999), the ringing times of auditory filters are in the range of several milliseconds. This is in good agreement with the time range of localization dominance. For ultrasonic hearing bats, the ringing times are very short because the auditory filters are very broad. Weissenbacher et al. (2002) and Wiegrebe and

Schmidt (1996) showed that the ringing time of *M. lyra* auditory filters does not exceed about 200  $\mu$ s. Thus, if auditory-filter ringing were the main physiological basis of localization dominance, it cannot be expected that localization dominance is seen in bats while they are echolocating. Note that both the sonar emissions and consequently the reflections do not provide significant acoustic energy below about 40 kHz (cf. Fig. 1).

A possible neural correlate of spatial echo suppression has been described in the ascending auditory pathway of cats and rabbits. In these studies, neurons were found, the responses of which to a lag stimulus, depending on the delay between lead and lag, were substantially reduced compared to a single stimulus (Fitzpatrick et al., 1999; Litovsky et al., 1999; Tollin et al., 2004).

A case for the possible neural correlate of a precedence effect in bats comes from physiological studies in two microchiropteran bat species (Burger and Pollak, 2001; Pollak et al., 2002). They found a persistent inhibition in the dorsal nucleus of the lateral lemniscus (DNLL) of the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*) and the mustached bat (*Pteronotus parnellii*). This inhibition is evoked by short duration stimuli to the ipsilateral (inhibitory) ear and can persist up to 60 ms after stimulus offset. Thus, delayed stimulation of the contralateral (excitatory) ear is suppressed in the DNLL response.

Portfors and Wenstrup (1999) studied delay-sensitive inferior-colliculus neurons in *P. parnellii*. Apart from a relatively large population that showed a facilitatory response to stimulus combinations resembling a pulse-echo pair, the authors also described a small population of neurons with an inhibited response to pulse-echo pairs. It is conceivable that this population may be involved in the auditory processing of higher-order echoes.

High-level, cognitive processes might also influence the precedence effect (Blauert et al., 1989; Clifton et al., 1994; McCall et al., 1998; Freyman et al., 1991; Damaschke et al., 2005). These studies suggest that echo processing may depend on the listeners' prior listening experience and the resulting expectations about the sound-source position and the room acoustics. Also Rakerd and Hartmann (1985) proposed that localization of sound is a dynamic, interactive process that has inputs from higher cognitive levels.

In our experimental paradigm, the bats were confronted with reflections of their own ultrasonic emissions. Bats orient through the auditory analysis of reflections of their own vocal emission. Conceivably, bats need all the information contained in these reflections both for an auditory assessment of space and for localizing objects in this space. For this reason they do not suppress the spatial information contained in these reflections. It cannot be excluded that bats are able to suppress the spatial information of their own ultrasonic emission (as also shown in Fig. 3C); but it may be dependent on the acoustic situation the bats are confronted with. They may be able to recruit localization dominance when it is beneficial for them. Such a facultative adoption of localization dominance may underlie the different patterns of results obtained from *M. lyra* individual 3 (cf.

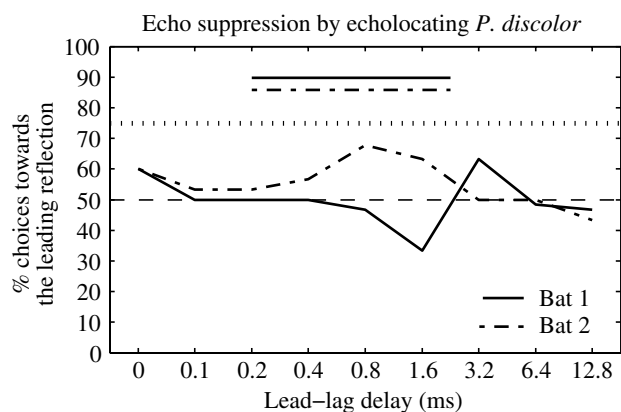


Fig. 4. Echo suppression in the echolocating bat *Phyllostomus discolor*. The figure shows the decision towards the first of two reflections plotted against the lead-lag delay. Data are shown in the same format as in Fig. 3. The two data plots represent data from the two *P. discolor* individuals. None of these showed significant spontaneous preference for the first of two reflections.

Fig. 3C). While in the first acquisition, the animal chose to adopt localization dominance, in the replication of the experiment, about six months later, it chose to switch its strategy.

It is possible that this recruitment of localization dominance is also stimulus-dependent. Some bats live in reverberant caves where they congregate in large colonies. There is a lot of social interaction between the animals, accompanied by a rich repertoire of communication calls. Thus, bats not only have to cope with echoes of their own vocal emissions but also with echoes of communication calls from conspecifics. In this acoustic situation, localization dominance would facilitate the perception of the origin of communication signals from other bats and would ease social interaction. So, while the suppressing of spatial information of higher-order echoes of their own echolocation calls may cause a loss of information, a suppression of misleading spatial information in echoes of social calls might be quite beneficial for a bat. Experiments are in progress to investigate passive-acoustic localization dominance in bats similar to that observed in humans and animals.

Also hunting strategies could influence how echolocating bats deal with multiple, spatially divergent reflections. Both bat species tested here are non aerial hawkers. Instead they are very good at detecting and identifying edible prey in acoustically complex environments with many, close reflections arising from nearby objects. It is conceivable that bats hunting for flying insects in an open space may recruit a different auditory strategy to deal with multiple, spatially divergent reflections of their ultrasonic emissions.

In summary, the current data show that the two bat species studied here did not reveal spontaneous localization dominance when they were trained to lateralize reflections of their ultrasonic sonar emissions. This finding can be explained based on the different peripheral auditory processing in the far ultrasonic frequency range and a possible strong influence of cognitive processes on the precedence effect. A singular contrary data set suggests that echolocating bats may be able to recruit localization dominance facultatively in an echo-acoustic situation in which localization dominance is beneficial for them.

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## References

- Babushkina, E. S. and Poliakov, M. A.** (2001). Lokalizatsiya summy akusticheskikh signalov severnym morskim kotikom v vozduшной srede. [Localization of a sum of acoustic signals in air by the northern fur seal]. *Biofizika* **46**, 557-562.
- Blauert, J.** (1997). *Spatial Hearing: The Psychophysics of Human Sound Localization*. Revised edn. Cambridge, MA, USA: MIT Press.
- Blauert, J., Canevet, G. and Voinier, T.** (1989). The precedence effect – no evidence for an active release process found. *J. Acoust. Soc. Am.* **85**, 2581-2586.
- Burger, R. M. and Pollak, G. D.** (2001). Reversible inactivation of the dorsal nucleus of the lateral lemniscus reveals its role in the processing of multiple sound sources in the inferior colliculus of bats. *J. Neurosci.* **21**, 4830-4843.
- Clifton, R. K., Freyman, R. L., Litovsky, R. Y. and McCall, D.** (1994). Listeners expectations about echoes can raise or lower echo threshold. *J. Acoust. Soc. Am.* **95**, 1525-1533.
- Cranford, J. L.** (1982). Localization of paired sound sources in cats – effects of variable arrival times. *J. Acoust. Soc. Am.* **72**, 1309-1311.
- Damaschke, J., Riedel, H. and Kollmeier, B.** (2005). Neural correlates of the precedence effect in auditory evoked potentials. *Hear. Res.* **205**, 157-171.
- Dent, M. L. and Dooling, R. J.** (2003a). Investigations of the precedence effect in budgerigars: Effects of stimulus type, intensity, duration, and location. *J. Acoust. Soc. Am.* **113**, 2146-2158.
- Dent, M. L. and Dooling, R. J.** (2003b). Investigations of the precedence effect in budgerigars: The perceived location of auditory images. *J. Acoust. Soc. Am.* **113**, 2159-2169.
- Dent, M. L. and Dooling, R. J.** (2004). The precedence effect in three species of birds (*Melopsittacus undulatus*, *Serinus canaria*, and *Taeniopygia guttata*). *J. Comp. Psychol.* **118**, 325-331.
- Fitzpatrick, D. C., Kuwada, S., Kim, D. O., Parham, K. and Batra, R.** (1999). Responses of neurons to click-pairs as simulated echoes: auditory nerve to auditory cortex. *J. Acoust. Soc. Am.* **106**, 3460-3472.
- Freyman, R. L., Clifton, R. K. and Litovsky, R. Y.** (1991). Dynamic processes in the precedence effect. *J. Acoust. Soc. Am.* **90**, 874-884.
- Hartung, K. and Trahiotis, C.** (2001). Peripheral auditory processing and investigations of the 'precedence effect' which utilize successive transient stimuli. *J. Acoust. Soc. Am.* **110**, 1505-1513.
- Keller, C. H. and Takahashi, T. T.** (1996a). Binaural cross-correlation predicts the responses of neurons in the owl's auditory space map under conditions simulating summing localization. *J. Neurosci.* **16**, 4300-4309.
- Keller, C. H. and Takahashi, T. T.** (1996b). Responses to simulated echoes by neurons in the barn owl's auditory space map. *J. Comp. Physiol. A* **178**, 499-512.
- Kelly, J. B.** (1974). Localization of paired sound sources in rat – small time differences. *J. Acoust. Soc. Am.* **55**, 1277-1284.
- Litovsky, R. Y., Colburn, H. S., Yost, W. A. and Guzman, S. J.** (1999). The precedence effect. *J. Acoust. Soc. Am.* **106**, 1633-1654.
- McCall, D. D., Freyman, R. L. and Clifton, R. K.** (1998). Sudden changes in spectrum of an echo cause a breakdown of the precedence effect. *Percept. Psychophys.* **60**, 593-601.
- Miller, J.** (1996). The sampling distribution of  $d'$ . *Percept. Psychophys.* **58**, 65-72.
- Neuweiler, G.** (2000). *The Biology of Bats*. New York: Oxford University Press.
- Pollak, G. D., Burger, R. M., Park, T. J., Klug, A. and Bauer, E. E.** (2002). Roles of inhibition for transforming binaural properties in the brainstem auditory system. *Hear. Res.* **168**, 60-78.
- Populin, L. C. and Yin, T. C. T.** (1998). Behavioral studies of sound localization in the cat. *J. Neurosci.* **18**, 2147-2160.
- Portfors, C. V. and Wenstrup, J. J.** (1999). Delay-tuned neurons in the inferior colliculus of the mustached bat: implications for analyses of target distance. *J. Neurophysiol.* **82**, 1326-1338.
- Rakerd, B. and Hartmann, W. M.** (1985). Localization of sound in rooms. II. The effects of a single reflecting surface. *J. Acoust. Soc. Am.* **78**, 524-533.
- 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.
- Tollin, D. J. and Henning, G. B.** (1999). Some aspects of the lateralization of echoed sound in man. II. The role of the stimulus spectrum. *J. Acoust. Soc. Am.* **105**, 838-849.
- Tollin, D. J., Populin, L. C. and Yin, T. C. T.** (2004). Neural correlates of the precedence effect in the inferior colliculus of behaving cats. *J. Neurophysiol.* **92**, 3286-3297.
- Wallach, H., Newman, E. B. and Rosenzweig, M. R.** (1949). The precedence effect in sound localization. *Am. J. Psychol.* **62**, 315-336.
- Weissenbacher, P. and Wiegrebe, L.** (2003). Classification of virtual objects in the echolocating bat, *Megaderma lyra*. *Behav. Neurosci.* **117**, 833-839.
- Weissenbacher, P., Wiegrebe, L. and Kossel, M.** (2002). The effect of preceding sonar emission on temporal integration in the bat, *Megaderma lyra*. *J. Comp. Physiol. A* **188**, 147-155.
- Wiegrebe, L. and Schmidt, S.** (1996). Temporal integration in the echolocating bat, *Megaderma lyra*. *Hear. Res.* **102**, 35-42.
- Wytenbach, R. A. and Hoy, R. R.** (1993). Demonstration of the precedence effect in an insect. *J. Acoust. Soc. Am.* **94**, 777-784.