

Arjan Boonman · Hans-Ulrich Schnitzler

## Frequency modulation patterns in the echolocation signals of two vespertilionid bats

Received: 18 April 2004 / Revised: 5 August 2004 / Accepted: 12 August 2004 / Published online: 26 November 2004  
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**Abstract** In this study we measure and classify frequency modulation patterns in echolocation signals of two species of bats. By using the derivative of an exponential model fitted to pulses emitted by *Pipistrellus pipistrellus* and *Myotis myotis*, we show that the modulation functions differ fundamentally between the two species and also vary within each species. This variation makes it unlikely that pulse design and the concomitant modulation pattern can be explained by a single common principle as previously suggested.

**Keywords** Bats · Echolocation · Modulation pattern · Signal structure

### Introduction

During evolution the structure of the echolocation signals of bats has been adapted to perform specific echolocation tasks. This resulted in a wide variety of species-specific signal types differing in frequency structure, duration, and sound pressure level (SPL). In addition, signal design varies within each species depending on the echolocation task. Generally, echolocation signals of bats comprise more or less steeply frequency-modulated (FM) components of varying bandwidth or constant frequency (CF) components, or a combination of these (Schnitzler et al. 2003). It is generally accepted that short broadband steep FM components are well suited for accurate target localization but less for the detection of small targets. Additionally, they provide more spectral information and may also have advantages for the classification of different types of vegetation. The longer

narrowband shallow FM components are well suited for the detection of small targets at long distances (Neuweiler 1989; Fenton 1990; Schnitzler and Kalko 1998, 2001; Siemers and Schnitzler 2004). However, all these interpretations of signal adaptations do not include the discussion of the frequency modulation pattern of FM signals. Only a few studies address this issue, e.g., Masters et al. (1991) and Masters and Raver (2000).

Variability of signal design has been a topic of research for a long time. Griffin et al. (1960) already describe task-dependent variations in signal structure. Obrist (1995) discusses the influence of individual, habitat, and conspecifics on signal design and summarizes the relevant literature. The more recent literature on the relevance of signal variability is reviewed in Schnitzler et al. (2003).

Many of the FM signals described so far are characterized not only by large variations in bandwidth and duration but also by a continuous change in sweep-rate (measured in  $\text{kHz ms}^{-1}$ ) from high to low. Such a continuous change in sweep-rate creates the hyperbolic-like frequency time-course found for instance in the echolocation signals of many vespertilionid bats.

This specific modulation pattern prompted radar engineers early on in echolocation research to adapt the hypothesis that the frequency–time course of such FM signals can be approximated by a hyperbolic or linear period modulation and may be an adaptation to prevent Doppler errors (Strother 1961; McCue 1966; Cahlander 1967; Kroszczynski 1969; Glaser 1974). This Doppler hypothesis was supported by Altes and Titlebaum (1970) who have shown that a hyperbolic sweep with a linear period modulation is optimally Doppler tolerant when processed by a cross-correlation receiver. Boonman et al. (2003) described the effect of different signal designs, notably frequency modulation pattern on two different types of Doppler error.

Another approach to understand the frequency modulation patterns of FM signals was taken by Menne (1988a, b), introducing the cochlea hypothesis. He suggested that echolocation pulses have a hyperbolic-like

A. Boonman (✉) · H.-U. Schnitzler  
Tierphysiologie, Zoologisches Institut,  
Universität Tübingen, Auf der Morgenstelle 28,  
72076 Tübingen, Germany  
Tel.: +49-7071-2975351  
Fax: +49-7071-292618  
E-mail: arjan.boonman@uni-tuebingen.de

shape because they are adapted to filter bandwidths in the peripheral hearing system. To achieve the best possible range estimation, the sweep-rate of the echolocation signal and the bandwidth of the excited filter should match. An echolocation signal of which the modulation function is adapted to the bandwidth of the tuning curves would have the advantage that the error of time estimation with a filter bank receiver is minimal. To minimize the ranging error while using a typical “mammalian cochlea”, bats should produce an FM sweep with a modulation pattern that is close to hyperbolic.

Both explanations for the type of modulation pattern found in the echolocation signals of many vespertilionids (Doppler and cochlea hypothesis) assume that a common principle governs signal design in these bats. This seems to be rather unlikely when looking on the large variety of signal structures found among and within these species. However, a rather wide spectrum of signals designs could be explained by a common principle if every signal of the complete signal inventory of a bat would be a temporal “cut-out” of an exponential sweep starting with high and ending with low modulation rate (Fig. 1).

We recorded echolocation signals of two species of vespertilionid bats: the common pipistrelle (*Pipistrellus pipistrellus*) and the mouse-eared bat (*Myotis myotis*). We compared the modulation patterns of the signals within and between the two species to answer the following question: can the modulation functions of the echolocation signals of both species or at least of one of the two species be described by a common principle?

Both investigated bat species produce FM signals in which the steepness of the sweep gets shallower towards the end in most calls. To describe the modulation patterns of the echolocation signal, we therefore fitted an exponential model to the frequency-time functions of sonagrams of both bat species, which has the advantage that it produces linear modulation functions (modulation rate versus frequency). This makes it easier to compare the modulation patterns of different echolocation signals.

We are aware that our approach can only be used for signals which are somehow hyperbolic. Signals with a modulation pattern changing continuously from steep to shallow and then back to steep as found in some bats or the FM-CF-FM signals of horseshoe bats can not be fitted with our method and are therefore not addressed with our approach.

## Materials and methods

### Sound recording equipment

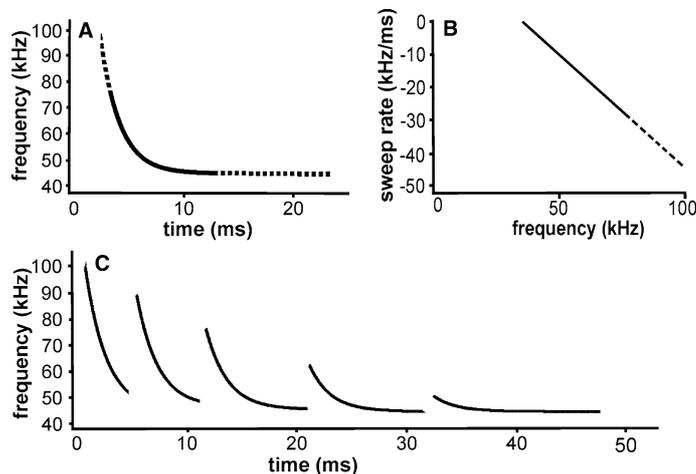
We used a custom made condenser microphone, which was sensitive between 15 and 200 kHz, with a frequency response ( $\pm 3$  dB) between 45 and 165 kHz ( $-10$  dB at 30 kHz), and a maximum dynamic range of 80 dB. Sensitivity was 1 V/Pa at 40 kHz with pre-amplifier. The directionality of the microphone around 60 kHz can be characterized by a  $-10$  dB beamwidth of  $60^\circ$ . The signals were sampled at a rate of 480 kHz, with 16 bits, and stored digitally for subsequent analysis as .wav files on a laptop computer.

### Sound analysis

We used Matlab 6.1 with signal processing and statistics toolbox (the Mathworks, Natick, Mass., USA). Using custom written routines, all pulses above a signal-to-noise ratio of 35 dB were selected from the recorded .wav file. The selected pulses had a signal-to-noise ratio between 35 and 45 dB. We assume that these pulses, which were the loudest of each sequence, were emitted in the direction of the microphone by the bat. The duration of each pulse was defined as the  $-40$  dB duration, relative to the peak level of the pulse, of the analytical envelope of the pulse, obtained by a Hilbert transformation.

The frequency-time structure of each pulse was assessed by using a sliding Hanning-windowed FFT over

**Fig. 1** Bat-like signals generated according to a common principle. A broadband exponential sweep (a) and its modulation function (b) were used to create bat-like signals as cut-outs of the sweep (c). The *solid part* of the curves in a and b describe the signal in the center of c



the course of the pulse, while extracting the frequency of maximum intensity in the first harmonic at every position of the window. From the time point of the peak frequency of the entire pulse, the frequency-time structure of the first harmonic was tracked up, back in time, and down, forward in time, until the start and the end of the pulse, respectively. The start and end of the pulse were defined as the point two-thirds of the FFT length before and after the  $-40$  dB start and endpoints of the pulse, respectively. Since fast sweep-rates need a better time resolution to be adequately tracked than slow sweep-rates, the FFT length was 128 points for pulses shorter than 6 ms, and 256 points for pulses longer than 6 ms. Before the calculation of the peak frequency, the 128-, or 256 point section of the pulse was padded symmetrically with zeros around the pulse up to 512 or 1,024 points, respectively. We used 80% overlap between the unpadded FFT sections. The resulting frequencies were plotted against the time points at which they had occurred, and checked visually on possible anomalies. Bandwidth was calculated as the difference between the first and the last frequency of the frequency-time course.

#### Fitting of frequency-time data

To describe the modulation patterns of echolocation pulses, we used a model that was fitted to the raw frequency-time data to yield descriptive parameters.

We used the following exponential model to fit the frequency time-course, usually consisting of 80–120 data points:

$$F(t) = \frac{[(F_0 - F_1)(aF_1/F_0)^t + (1 - a)F_1]F_0}{F_0 - aF_1} \quad (1)$$

in which  $F(t)$  is the frequency–time course,  $F_1$  defines the lowest frequency of the pulse,  $F_0$  the highest frequency,  $a$  the shape applied to the function, and  $t$  is time. The function can follow concave to convex pulses over a wide range of pulse shapes, and can level out (have an asymptote) at any frequency, which makes the function very suited to model bat echolocation pulses.

We used the built-in “nlinfit” routine of Matlab’s statistics toolbox to fit the above function having three variable parameters, following nonlinear least-squares data fitting by the Gauss-Newton method. The values  $F_0$ ,  $F_1$ , and  $a$  of each fitted function were stored for further calculations. All fitted frequency time-courses were checked visually to avoid artifacts in subsequent calculations.

#### Modulation function

To reduce the complexity of Eq. 1 and extract parameters, which, when plotted, provide a clear overview of possible modulation patterns, we introduced the

“modulation plot”. To this aim, the change in sweep-rate was measured from the fitted function and plotted against frequency (modulation plot, Figs. 1b, 4). This way of plotting a pulse has the convenience of causing a linear function that can be described by only two parameters. The slope of the modulation function indicates the change of the sweep-rate within a pulse with respect to frequency. This change, termed as  $dS$ , is calculated as:

$$dS = \ln\left(a \frac{F_1}{F_0}\right) \quad (2)$$

$dS$  refers to the sweep rate with respect to frequency within a pulse ( $\text{kHz}/(\text{ms} \times \text{kHz}) = \text{ms}^{-1}$ ) (Fig. 5a). A positive value of  $dS$  indicates an increase of the sweep-rate within a pulse, or acceleration. This is reflected in a sonagram by a pulse having a convex shape. A  $dS$  of zero indicates linear frequency modulation, and a negative value indicates a decrease of sweep-rate, or deceleration, which is reflected in a sonagram as a pulse having a concave shape.

The intercept, or constant ( $c$ ) of each line in the modulation plot can be calculated directly from the exponential fit:

$$c = a \frac{F_0 F_1 - F_1^2}{F_0 - a F_1} \ln\left[a \frac{F_1}{F_0}\right] - \ln\left[a \frac{F_1}{F_0}\right] F_1 \quad (3)$$

Equations 2 and 3 were derived by calculating the derivative of Eq. 1 with respect to time. With the value of  $dS$  and  $c$  of a pulse it is possible to calculate the local sweep-rate ( $y$ ), at any frequency ( $f$ ):  $y = dS \times f + c$ . Units of  $y$  in this paper are expressed in  $\text{kHz ms}^{-1}$ ,  $dS$  in  $\text{ms}^{-1}$ , and  $c$  in  $\text{kHz ms}^{-1}$ .

In this study we also tested the possibility that echolocation pulses are adapted to minimize errors due to Doppler shifts. The design of pulses required to achieve this so called Doppler tolerance is hyperbolic, or linear period modulated. Hyperbolic signals are a special class of pulses whose frequency time-course is fixed at a certain start frequency, end frequency, and duration. This is different from exponential pulses whose frequency time-course can be altered freely, independent of these parameters. To test the hypothesis that signals are not only designed according to a common principle but additionally also adapted to achieve Doppler tolerance, we not only fitted each pulse with an exponential model but also assessed the degree of ‘hyperbolicness’ of each pulse by fitting the frequency time-course of each pulse by using the following hyperbolic model:

$$F(t) = \frac{F_0 F_1}{F_1 + (F_0 - F_1)t} \quad (4)$$

To assess the degree of ‘hyperbolicness’ of a pulse, we fitted the raw data with the hyperbolic model (Eq. 4), and subsequently fitted our exponential model again (Eq. 1) to the frequency–time data obtained with Eq. 4. This gave us an exponential fit to the hyperbolically

fitted frequency-time data, in addition to the exponential fit to the raw data. The parameter ‘ $a$ ’ (Eq. 1) resulting from the former fit was then divided by the parameter ‘ $a$ ’ of the fit to the raw data. The ratio of the two ‘ $a$ ’s expressed in percent denotes the similarity in pulse shape to a hyperbolic function. Percentages below 100 indicate that the frequency modulation of the pulse is too linear to be hyperbolic, whereas percentages above 100 indicate that the pulse is ‘curved’ too much to be hyperbolic.

#### Bat-like signals derived from a hypothetical modulation function

Many species of bat, particularly in the family of Vespertilionidae produce FM signals showing large variations in bandwidth and duration and a continuous change in sweep-rate. Often, the sweep-rate decreases within the pulse, which is reflected in a hyperbolic-like, frequency time-course in the sonographic display. The end frequency of these pulses varies little. To understand whether such pulses could be generated according to a general principle we created bat-like pulses with the following rule. Every signal which is a temporal “cut-out” of a broadband exponential sweep (Fig. 1a) has a similar  $dS$  and  $c$ . The plots of the modulation functions of such signals are therefore on the same line (Fig. 1b). With cut-outs of such a sweep we can create bat-like signals ranging from short broadband steep FM to longer narrowband shallow FM if we reduce start frequency and increase duration (Fig. 1c). The model also predicts that the end frequency decreases slightly with increasing signal duration.

The simulated group of signals is rather similar to the signal inventory of many vespertilionid bats. This fact encouraged us to test the possibility that in these bats the signals are generated according to the common principle used in our simulation.

#### Recording protocol

The mouse-eared bats (*M. myotis*) were recorded at two sites while emerging from a known roost in the city of Tübingen, Germany. Individuals were recorded when flying at least 5 m away from the nearest obstacle, over a deep (15 m) gully, which was classified as an ‘open environment’. Other individuals were recorded when approaching and flying through a patch of forest with dense vegetation on all sides. In this situation, the bats sometimes even hit the leaves with their wings. This situation was classified as a ‘dense environment’. Since the bats were commuting to their foraging grounds, it seems unlikely that the same individual was recorded twice.

The common pipistrelle bats (*P. pipistrellus*) were recorded at different sites near Tübingen, Berlin, and Bremen, either as single commuters, or far away from each other to avoid recording of the same individual

twice. In all recording locations *P. pygmaeus* and *P. nathusii* are rare. The recording situations varied from bats flying about 3 m in dense vegetation to flying in open space above water. To reduce the risk of including the pulses of *P. pygmaeus* or *P. nathusii* in our dataset, we rejected pulses with peak frequencies above 50 kHz or below 40 kHz, which resulted in the rejection of one individual in Bremen with a peak frequency of 50–51 kHz. Although we cannot be certain, our dataset is likely to comprise only pulses of *P. pipistrellus*. In the pipistrelle recordings, no separation was made between dense and open environments.

#### Statistical methods

All data were tested for normality (Kolmogorov-Smirnov test) before being subjected to analyses using parametric tests. More than one pulse per individual bat was used in the statistical analyses because one of the aims of the study was to compare pulse parameters intra- and inter-specifically. We used ANOVA, linear regression analysis, and general linear models (GLM) as statistical tools to analyze the data. The degrees of freedom in each test were calculated from the number of individuals used, and not the number of pulses.

Since bats were not known individually in this study, and a variable number of pulses (depending on recording quality) was taken per individual, all test designs are unbalanced.

A problem in investigating the relationship between a parameter, such as  $dS$ , as a function of pulse duration is that the value of  $dS$  may also be affected by the bandwidth of a pulse, which varies in pulses emitted by bats. Since bandwidth and pulse duration can be varied independently by the investigated bat species (all  $R^2 < 0.4$ ), bandwidth should be treated as an unwanted factor whose influence is to be removed statistically. Normally, bandwidth would be taken as a covariate with pulse duration as a factor, but since our error term was the interaction individual×pulse duration (see below) instead of MS error, we could use only pulse duration as a factor. We therefore first calculated the residuals of the dependent variable ( $dS$ , or  $c$ ) obtained from a regression with bandwidth as independent variable. Except for in the single individual pipistrelle bat, bandwidth showed a significant relationship with both  $dS$  and  $c$  in all cases. The residuals of  $dS$  or  $c$  were used as the dependent variable in further analyses.

To test whether the dependent variable exhibited a significant relationship with pulse duration, considering variations in this relationship between individual bats, we used a GLM procedure with pulse duration, individual and the interaction term individual×pulse duration as factors. The factor ‘individual×pulse duration’ tests the assumption of homogeneity of slopes of the dependent variable against pulse duration between different individual bats. We subsequently used hypothesis testing (Wilkinson and Coward 2000), whereby the  $F$

statistic was calculated from the ratio of the mean squares of pulse duration divided by the mean squares of the interaction term. Using hypothesis testing sets to degrees of freedom to the number of individual bats that was analyzed. The disadvantage of this procedure is a high risk of a type II error if the number of individuals in the dataset is small. The homogeneity of slopes between the individuals determines the probability of finding a significant common regression line between two continuous variables. We used Systat 10, (Chicago, Ill., USA).

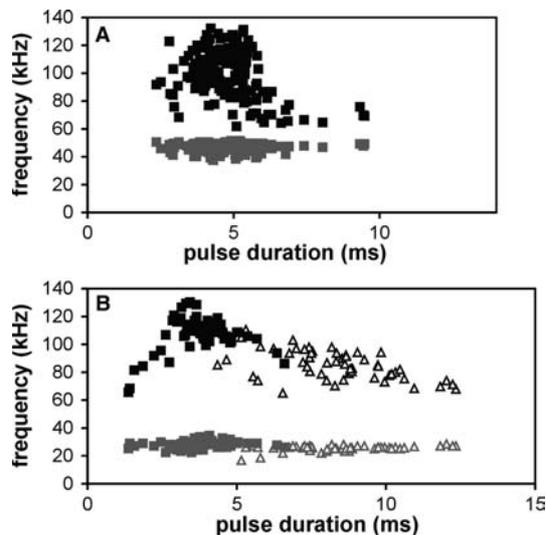
## Results

### Signal inventory

Both species varied signal duration and signal structure conjointly over a wide range, probably in relation to the distance of the bats to background targets such as vegetation, walls and/or the ground. The variation in start and end frequency at different pulse durations of all analyzed signals is displayed in Fig. 2.

In *P. pipistrellus* (Fig. 2a) durations ranged from 2.4 to 9.5 ms (23 individual bats). All signals had a rather similar terminal frequency with an average at 46.1 kHz (SD=3.1 kHz). For signal durations between 2.5 and 6 ms the start frequency varied strongly between 60 and 130 kHz. The highest start frequencies (between 120 and 130 kHz) were found at durations between 4 and 6 ms. Low start frequencies and therefore narrow bandwidths were typical of signals above 6 ms duration.

In *M. myotis* (Fig. 2b) durations ranged from 1.5 to 6.6 ms in signals recorded in the dense environment (nine individual bats) and from 4.4 to 12.3 ms in signals recorded in the open (eight individual bats), thus dem-



**Fig. 2a, b** Start and end frequencies of echolocation pulses. **a** *Pipistrellus pipistrellus*: black start frequency; gray end frequency. **b** *Myotis myotis*: black start frequency; gray end frequency; squares dense environment; triangles open environment

onstrating the dependence of signal structure from distance to background targets. All signals had a rather similar terminal frequency of on average 28.7 kHz (SD=2.8 kHz) in dense and 25.6 kHz (SD=2.0 kHz) in open environments. For signal durations between 3 and 12 ms, the start frequency decreased from about 120 to about 70 kHz. Pulse durations below 3 ms show a decreasing start frequency with decreasing duration.

The signals we recorded in the dense and the open environment show an overlap in their durations between 4.4 and 6.6 ms. The signals falling in the range of overlap did not differ in their duration-dependent start and end frequencies, thus demonstrating that basic signal structure is similar in both situations.

The investigated bat species produce emissions, which are strongly dominated by the fundamental frequency. Higher harmonics are attenuated by at least 20 dB. Therefore, in weak echoes the higher harmonics will hardly be above the hearing threshold of the bat.

### Quality of fitting

To demonstrate the quality of our exponential fit we plotted sonograms of signals with the fitted functions (Fig. 3). The quality of the fit can be quantified as the root mean square (rms) error. Independent of species and signal duration the error was mainly between 400 and 1,500 Hz.

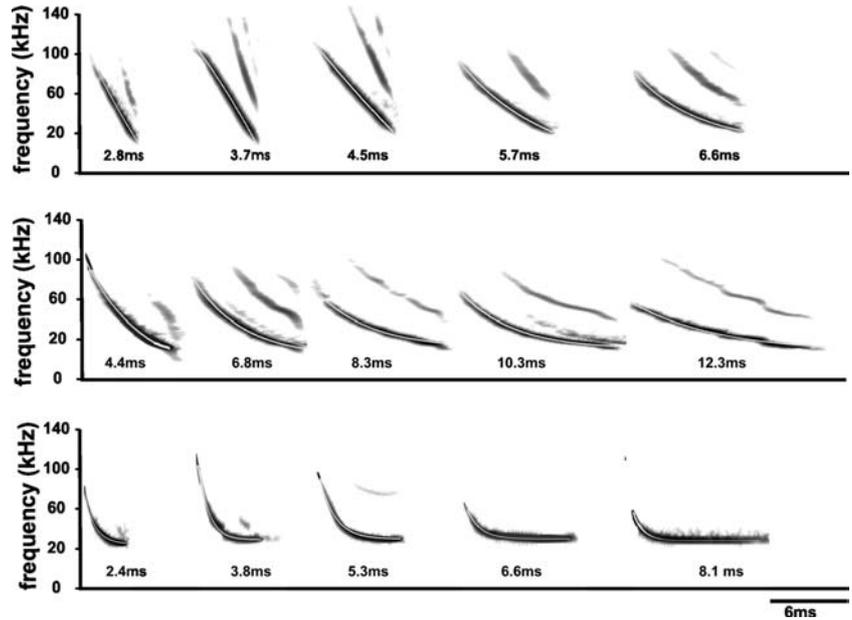
We also tested the quality of a hyperbolic model. The hyperbolic function (Eq. 4) has only two parameters and is therefore less flexible than the exponential function. In *P. pipistrellus* rms errors between 1,200 and 4,000 Hz were measured. In the shorter signals (below 5 ms) of *M. myotis*, rms errors between 5,000 and 9,000 Hz were determined. Only to the longer signals of *M. myotis*, the hyperbolic model fitted as well as, or sometimes even better than the exponential model.

Since the quality of any fit is both dependent on the frequency–time course of the data as well as the scatter of the data points, we used a scatter-independent measure to assess ‘hyperbolicness’ which we termed ‘hyperbolic similarity’ (see Materials and methods). With this approach we also found that *M. myotis* signals longer than 5 ms in duration have a hyperbolic similarity of 98%. In pulses shorter than 5 ms, hyperbolic similarity was only 77%, reflecting the less curved pulses. Hyperbolic similarity in the pulses of *P. pipistrellus* was found to be 137% reflecting pulses more curved than hyperbolic pulses.

### Modulation patterns

The exponentially fitted and therefore linear modulation functions (sweep-rate against frequency) describe the modulation patterns of the analyzed signals (Fig. 4). To characterize the dependence of the modulation functions on signal duration we displayed the two parameters

**Fig. 3** Exponential fits to pulses of different durations. *Top panel: Myotis myotis* in dense environment; *middle panel: Myotis myotis* in open environment; *bottom panel: Pipistrellus pipistrellus*

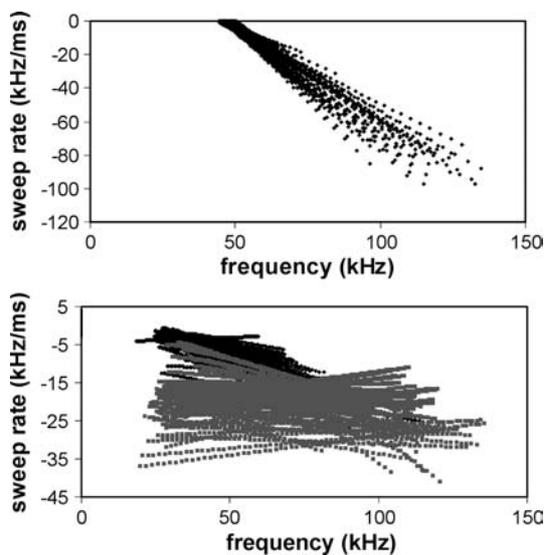


which characterize a modulation function for different signal durations. Figure 5a displays the change in sweep-rate ( $dS$ ) within a pulse. Negative values indicate a decrease, or deceleration, of sweep rate within a signal indicating that the frequency–time plot, or sonagram, of a downward FM signal changes from a steep to a shallow modulation rate. Positive values indicate increase of steepness within a signal. Zero values indicate a linear frequency modulation with no change in steepness. The more different from zero the values are, the larger is the change in steepness, and the more curved are the pulses. Fig. 5b displays the constant of the modulation func-

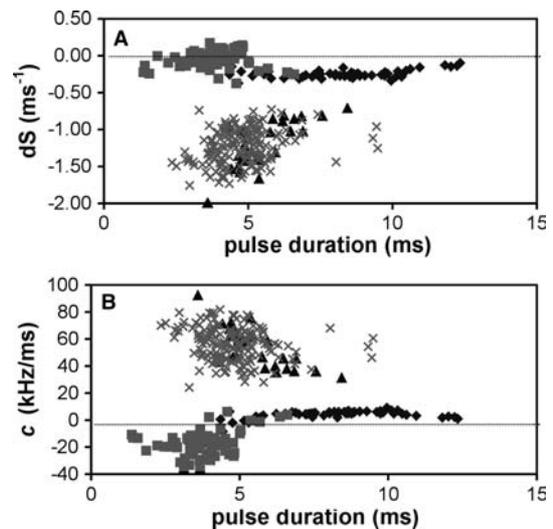
tions. Pulses with the same values of  $c$  and  $dS$  have the same modulation function.

The pulses of *P. pipistrellus* yield modulation functions with a  $dS$  varying in the range of  $-2.0$  to  $-0.7 \text{ ms}^{-1}$  (Fig. 5a). The modulation functions have a tendency to intersect near the end frequency (Fig. 4a). Sweep-rate values near zero at the end frequency indicate that the pulses leveled out into a terminal part of nearly constant frequency (Fig. 4a).

The pulses of *M. myotis* yield modulation functions with  $dS$  varying in the range of  $-0.37$  to  $0.17 \text{ ms}^{-1}$ . At signal durations above 6 ms (mainly recorded in the open) the modulation functions were rather similar,



**Fig. 4** Modulation plots of pulses emitted by *Pipistrellus pipistrellus* (a) and *Myotis myotis* (b). In b black characterizes pulses emitted in open and gray in dense environments



**Fig. 5** Parameters characterizing the modulation functions of pulses emitted by *Myotis myotis* in dense (*squares*) and in open environments (*diamonds*); and of pulses of 23 individuals (*crosses*) and a single individual (*triangles*) of *Pipistrellus pipistrellus*. 5a depicts the parameter  $dS$  and 5b the parameter  $c$

which is indicated by similar  $dS$  and  $c$  (Fig. 5, diamonds) with averages of  $dS$  at  $-0.24 \text{ ms}^{-1}$  and  $c$  at  $4.9 \text{ kHz ms}^{-1}$ . When using long pulse durations, e.g., in open space, the mouse-eared bat therefore appears to emit pulses that can be seen as cut-out of a broadband exponential sweep. Pulses below 5 ms were characterized by near-zero positive and negative values of  $dS$  and more negative values of  $c$ , thus indicating steep FM signals with a frequency modulation varying from convex, linear, to concave.

To test the hypothesis that  $dS$  and  $c$  remain constant and are unaffected by changes in pulse duration in pipistrelle bats, we tested the dependence of  $dS$  and  $c$  on pulse duration. Unless stated otherwise, bandwidth also influenced  $dS$  and  $c$  significantly in the two investigated species. As explained in the statistical methods' section, we removed the influence of bandwidth by using the residuals of  $dS$  and  $c$  in further statistical analyses. In all situations, the value of  $dS$  was also influenced by the individual bat. We also accounted for this influence in subsequent analyses by using a GLM procedure.

In the pipistrelle bat,  $dS$  and  $c$  appeared unaffected by pulse duration (GLM  $F_{1,21}=1.090$ ;  $P=0.308$ ) and (GLM  $F_{1,21}=1.210$ ;  $P=0.284$ ) respectively, in 23 individual bats, although both parameters did vary. The parameters  $dS$  and  $c$  proved to be strongly correlated  $R^2=0.956$ .  $dS$  became significantly less negative with increasing pulse duration (linear regression:  $F_{1,28}=19.485$ ;  $P<0.001$ ), whereas  $c$  decreased significantly with increasing pulse duration (linear regression:  $F_{1,28}=19.610$ ;  $P<0.001$ ) in a single individual pipistrelle bat, using a dataset of 30 pulses. In this individual,  $dS$  and  $c$  were also strongly correlated  $R^2=0.998$ . This strong correlation is due to the CF component varying little between pulses.

As in pipistrelle bats  $dS$  differed between individual mouse-eared bats (ANOVA,  $F_{7,47}=11.9$ ;  $P<0.001$ ) in the open environment. In further statistical analyses the factor individual was therefore taken into account. The statistical analysis was performed separately on the data originating from the open environment, and the data originating from the dense environment because  $dS$  differed between the two environments (hypothesis test of GLM nested design:  $F_{1,15}=30.1$ ;  $P<0.001$ ).

In the dense environment  $dS$  also differed between individuals (ANOVA,  $F_{8,59}=9.3$ ;  $P<0.001$ ). In further statistical analyses the factor individual was therefore taken into account.

To test the hypothesis that  $dS$  and  $c$  remain constant and are unaffected by changes in pulse duration in mouse-eared bats, we tested the dependence of  $dS$  and  $c$  on pulse duration. In the open environment,  $dS$  did not depend on pulse duration (GLM,  $F_{1,7}=0.007$ ;  $P=0.935$ ). The constant  $c$  was also independent of pulse duration (GLM,  $F_{1,7}=0.807$ ;  $P=0.399$ ). This non-significance was not due to individual variation since the scatter was low (Fig. 5, diamonds). The  $R^2=0.373$  value of the correlation between  $dS$  and  $c$  was low, which indicates that the modulation functions do not intersect.

The findings above indicate that, in an open environment where pulse durations above 6 ms prevail, mouse-eared bats use similar sweep-rates between pulses, i.e., use 'temporal cut-outs' of one function.

In mouse-eared bats flying in the dense environment,  $dS$  did not depend on pulse duration (GLM,  $F_{1,8}=0.003$ ;  $P=0.960$ ).  $c$  was just not significantly dependent on pulse duration (GLM,  $F_{1,8}=3.698$ ;  $P=0.091$ ). This non-significance could partly be due to the large scatter in the values of  $c$  against pulse duration (Fig. 5b, squares). Modulation functions of *P. pipistrellus* reach much higher maximal sweep rates (Fig. 4a) and higher  $dS$  values (Fig. 5a) than those of *M. myotis* (Figs. 4b, and 5a) indicating that the pulses of pipistrelle bats started with a steeper sweep and were more curved than those of mouse-eared bats.

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## Discussion

In this study, we describe the modulation patterns in search signals of two species of vespertilionid bats and test whether the modulation functions of the echolocation signals can be described by a common principle. This would support the two hypotheses published to date to explain the modulation patterns of hyperbolic-like FM signals.

Our results reveal striking differences in pulse design between the two species. This result rules out the notion that a single common principle, e.g., as described by our model, is valid for all bat species. Even within each of the two species the modulation patterns do not lend support to our model.

According to present hypotheses, it is assumed that (1) hyperbolic pulses minimize Doppler errors (Altes and Titlebaum 1970), and (2) hyperbolic pulses are the result of an adaptation to filter properties of the peripheral hearing system thus improving ranging accuracy (Menne 1988b). A common principle seems to be rather unlikely when looking at the large variety of signal structures of bats using hyperbolic-like FM signals. However, a rather wide spectrum of signal designs could be explained by a common principle if every signal of the large signal inventory of the studied bats would be the cut-out of a hyperbolic-like exponential sweep starting with high and ending with low modulation rate (Fig. 1). This possibility was tested in our approach.

Pulse structure used by the two species follows different design rules. In *P. pipistrellus* sweep-rates in the low-frequency portion of the pulse are similar between pulses. Our data of all individuals show a non-significant trend of the high frequency portion of the pulse becoming more linear and less steep with increasing pulse duration. In the single individual pipistrelle bat that was investigated separately, this trend was indeed significant with  $dS$  becoming less negative and  $c$  decreasing with increasing pulse duration.

In *M. myotis* pulse design differs between longer and shorter signals. Pulses with durations below about

6 ms—mainly emitted when flying in dense environments—tend to have a high bandwidth, a  $dS$  around zero, and a trend of  $c$  increasing with signal duration. This indicates that the steepness of the more or less linearly frequency modulated signals decreases with increasing duration.

Pulses emitted by the mouse-eared bat with durations above about 6 ms—mainly emitted in the open—decrease in bandwidth with increasing duration but have rather similar  $dS$  and  $c$  between pulses. Therefore, each pulse can be viewed as a temporal cut-out of one particular sweep, as stated by our proposed model where  $dS$  and  $c$  are constant. No simple rule can be used to describe the entire repertoire of echolocation signals of the mouse-eared bat.

We not only tested whether the signals of the two species are designed according to a common principle but also whether the exponential fit is also close to hyperbolic. Only the pulses of *M. myotis* that were longer than about 6 ms and were emitted when flying in the open fulfilled this condition. In these pulses, the hyperbolic model fitted as well as, or sometimes even better than the exponential model. However, closer to background targets *M. myotis* produced short and steep linearly modulated signals, which do not result in the advantage of an optimized ranging accuracy as formulated in the two hypotheses. None of the signals emitted by *P. pipistrellus* was hyperbolic. Nevertheless, it could be argued that at least the longer signals of *M. myotis* are organized according to the Doppler and/or cochlea hypothesis as they are characterized by a common design principle. However, we assume that the Doppler-tolerant signal design of the long duration pulses emitted by *M. myotis* is a mere coincidence since a small improvement in ranging accuracy would make no sense at long-range echolocation.

To describe and quantify the modulation patterns of the echolocation signals, we fitted an exponential model to the frequency-time functions of the signals. It may be argued that our method of fitting the frequency time-course of echolocation pulses by using an exponential model produces artificial results and our paper describes artifacts of the fitting procedure rather than describing signal design in bats. However, the errors in fitting proved to be low.

The modulation patterns we found in the two investigated bat species did not conform to the idea of a common design principle. Signal structure in bats may, therefore, be caused by other factors. It is generally accepted that signal structure has evolved to perform species-specific echolocation tasks. Therefore, the differences between the two species and the change of modulation pattern within each species reflect differences in species-specific echolocation tasks. Longer narrowband shallow FM sweeps are well suited to long-range detection of small targets whereas shorter broadband steep FM sweeps are well suited to localize targets at shorter ranges, and maybe also to characterize background targets such as vegetation (Siemers and

Schnitzler 2004). When both advantages are combined into one signal—a so called mixed signal—the modulation rate must be changed dramatically within the signal from steep to shallow or vice versa, which leads to the concave (e.g., pipistrelle bats) or convex (mormoopid bats besides *Pteronotus parnellii*) FM signals which are found in many bat species (Schnitzler et al. 2003).

*P. pipistrellus* belongs to the guild of “edge space aerial foragers”. When foraging in edge space pipistrelle bats have the dual task to find prey and also to orient in space relative to background targets. This dual task is reflected in their mixed search signals. The closer the bats fly to an edge, the shorter the signals are, and the more prominent is the steep initial component. The further bats are away from background targets, the longer the signals are, and the more prominent the shallow terminal part becomes (Kalko and Schnitzler 1993; Schnitzler et al. 2003). *M. myotis* belongs to the guild of “narrow space gleaning foragers”. When foraging in narrow space they use prey-generated cues to detect and classify prey and to localize it (Arlettaz et al. 2001). Echolocation signals are only used for spatial orientation and should therefore be called orientation signals rather than search signals (Schnitzler et al. 2003). A similar reaction in relation to the distance to background targets has been observed in *Eptesicus serotinus* in a study on the effect of flight altitude on signal design (Jensen and Miller 1999). Our data demonstrate that the broadband steep FM signals emitted in narrow situations have durations below about 6 ms, are linearly modulated ( $dS$  around zero), and vary in steepness (variable  $c$ ). The bats use these signals for typical spatial orientation tasks such as localization and characterization of nearby background targets. These tasks are similar to the orientation of *P. pipistrellus* when flying in edge-space. Both bat species use broadband steep FM signals or signal components to perform similar orientation tasks. Since in the dense environment the main task of the mouse-eared bats was short-range spatial orientation rather than the detection of insects in the air, the bats used steep FM pulses without a shallowly modulated component, and therefore showed a fairly linear frequency modulation pattern. The relevance of a purely linear, or slightly curved frequency modulation pattern to specific echolocation tasks or optimization of echo processing is still unknown.

In transfer flight in open situations *M. myotis* produces signals with durations above about 6 ms and a fixed modulation pattern. We assume that such long signals are adapted for long-range spatial orientation, i.e., the localization and characterization of far-away background targets. To perform this task, the bats produce shallowly modulated signals, which are produced by starting at a lower frequency and extending the low frequency part of the signal. The lower sweep rate at each frequency, resulting from this signal type, constitutes a trade-off between an improved long-range orientation, while still retaining a fair degree of accuracy. This situation is different from the strongly curved pul-

ses used by pipistrelle bats, which are adapted to both short range localization/classification and detection of prey at the same time.

In short, our data do not support a common principle for signal design. We assume that the variable structure of bat signals reflects adaptations to multiple and varying echolocation tasks with signal duration, frequency, and bandwidth being the most relevant parameters. Since the sweep rate in signals—and with it the modulation pattern—strongly depends on the signal parameters duration and bandwidth, it is necessary to understand the role of these parameters in specific echolocation situations such as prey finding with the tasks detection, localization and classification of prey, and spatial orientation with the tasks localization and classification of background targets such as vegetation. Our conclusions do not exclude the possibility that the modulation pattern is also relevant for the optimal information processing of each task-specific signal element with a receiver that has a proper processing algorithm to extract the relevant information. If this is the case, we do not see any hypotheses to date, which explain the relationship between curvature and its effect on echo processing. All approaches in which common design rules are derived only from the task of an very accurate estimation of range of a point target will not be successful as they do not reflect the multitude of continuously changing tasks encountered by bats in natural echolocation situations.

**Acknowledgements** We wish to thank the following people: Egbert Brieskorn, Annette Denzinger, Jörg Kindermann, Klemen Koselj, Dieter Menne, Jo Ostwald, Peter Pilz, Andrea Schaub, Björn Siemers, and Peter Stilz for critically discussing our findings. We thank Mitch Masters for correcting and commenting on an earlier draft of the manuscript. We thank the Deutsche Forschungsgemeinschaft (DFG) for financial support.

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