

Source levels of echolocation signals vary in correlation with wingbeat cycle in landing big brown bats (*Eptesicus fuscus*)

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SUMMARY

Recordings of the echolocation signals of landing big brown bats with a two-dimensional 16-microphone array revealed that the source level reduction of 7 dB per halving of distance is superimposed by a variation of up to 12 dB within single call groups emitted during the approach. This variation correlates with the wingbeat cycle. The timing of call emission correlates with call group size. First pulses of groups containing many calls are emitted earlier than first calls in groups with fewer calls or single calls. This suggests that the emission of pulse groups follows a fixed motor pattern where the information gained from the preceding pulse group determines how many calls will be emitted in the next group. Single calls and call groups are centred at the middle of the upstroke. Expiration is indicated by call emission. The pause between groups is centred at the middle of the downstroke and indicates inspiration. The hypothesis that the source level variation could be caused by changes in the subglottic pressure due to the contraction of the major flight muscles is discussed.

Key words: source level, respiration, timing of call emission, microphone array, bat, echolocation.

INTRODUCTION

Landing *Eptesicus fuscus* exhibit the same typical approach pattern as other bats, which is characterized by a switch from a single echolocation pulse to groups with two, three or more pulses when the bats close in on the landing site (Melcon et al., 2007). Studying the source level (SL, the sound pressure level a sound source would produce on the acoustic axis at a distance of one meter without atmospheric attenuation) of the approach signals with a 16-microphone array, we found that the SL is on average reduced by approximately 7 dB per halving of distance (J.C.K., unpublished observations). However, we also observed that the source level within and between groups varied considerably, resulting in an oscillating pattern. From this observed pattern, we derived the hypothesis that the variation pattern is correlated with the wing-beat cycle. Here, we investigate how the variations of signal SL during the approach to a landing site correlate with wingbeat.

Flying bats perform three motor processes simultaneously: flight, respiration and production of echolocation signals. During flight, sound emission is often correlated with the wingbeat and respiratory cycles. In this paper, we determine how the timing of call emission correlates with wing position and varies with group size. We use the correlation between sound emission pattern and wingbeat as an indirect indicator for the correlation between respiratory cycle and wingbeat. We then discuss the variations in signal SL in relation to the presumed respiratory cycle.

Past studies have shown that respiration and wingbeat are linked in a one-to-one relationship (von Saalfeld, 1938; Suthers et al., 1972). Inhalation in *Phyllostomus hastatus* occurs during the downstroke, expiration during the upstroke (Suthers et al., 1972). Bats approaching a target or obstacle emit groups of two, three or more calls, separated by a longer 'in between group pulse interval' (Galambos and Griffin, 1942; Kalko and Schnitzler, 1989). Grinnell and Griffin (Grinnell and Griffin, 1958) first proposed that this grouping of calls corresponds to the respiratory cycle. In experiments

where sound emission and respiratory cycle were monitored in parallel, it was found that call emission is linked to the respiratory cycle in resting bats (Möhres, 1953; Schnitzler, 1968) and also for bats in flight (Suthers et al., 1972). Flying bats emit calls mostly during the upstroke, coinciding with expiration (Schnitzler, 1971; Suthers et al., 1972). Consequently, pauses between call emissions indicate inhalation (Schnitzler and Henson, 1980; Wilson and Moss, 2003). This has been confirmed by Lancaster and colleagues (Lancaster et al., 1995) who recorded diaphragmatic myopotentials from flying bats and showed strong evidence for inspiration during the pauses between call emission.

The timing of call emission relative to wing position has been studied in various bat species in the field and in flight rooms. Some of these experiments validate that sound emission, and probably expiration, extends from the end of the downstroke through the upstroke to the beginning of the downstroke. This was confirmed for *Myotis lucifugus* emitting single calls, dyads (groups of two calls) and triplets (Schnitzler, 1971) and for single calls and dyads emitted by *P. hastatus* (Suthers et al., 1972). Single calls of *Myotis daubentonii* and *Pipistrellus kuhli* flying in the field were emitted when the wings were around the upper turning position (Schnitzler et al., 1987; Kalko and Schnitzler, 1989). *Pipistrellus pygmaeus* flying in a flight room emitted single calls either at the end of the upbeat or at the beginning of the downbeat. Dyads were emitted at the end of the upbeat and at the beginning of the downbeat (Wong and Waters, 2001). *Mystacina tuberculata* emitted calls either at the end of the downstroke or early in the upstroke (Parsons et al., 2010). However, other studies presented different results. For instance, Kalko (Kalko, 1994), studying free-flying pipistrelle bats, describes a wingbeat pattern where most of the signals during search flight were emitted during the downbeat. Some studies show that bats sometimes override the tight coupling of wingbeat and call emission and emit calls at any wing position (Suthers et al., 1972; Lancaster et al., 1995; Moss et al., 2006). These discrepancies might

indicate that the correlation between sound emission, wingbeat cycle and respiration is not as strict as assumed so far.

MATERIALS AND METHODS

Training and holding of bats

Four adult big brown bats (*Eptesicus fuscus*, Beauvois 1796, 3 males, 1 female) were trained to start from the experimenter's hand, fly across the flight room and land on a landing grid 5.4 m away. When no training or experiments were carried out, bats were held in holding facilities in a reversed day–night cycle (with lights on at 17:00 h, lights off at 09:30 h) at a constant temperature of 24°C and humidity of 70%. Water was provided *ad libitum*, supplementary vitamins were given in the form of Nutrival paste once per month. When bats were trained or when recordings were made, food (*Tenebrio* sp. larvae) was only given as a reward during sessions. During trials and training, the light in the room was turned off to exclude visual orientation.

Experimental setup and recordings

The walls and floor of the experimental room [6.0 m × 3.6 m × 2.9 m (length × width × height)] were covered with foam sheets to reduce echoes. The landing grid was positioned at a height of 1.3 m at the far end of the room. A planar microphone array, consisting of 16 Knowles FG-3329 electret microphones, arranged in a four-by-four grid was positioned vertically, forming one plane with the landing grid. The spacing between the microphones was 0.35 m, allowing the bat to land on the grid without touching the microphones closest to the landing grid. Absolute calibration of each microphone was achieved by comparison with a calibrated Brüel&Kjær 4138 microphone.

The flights of the bats were recorded with three Sanyo IRP infra-red-sensitive video cameras. Two cameras overlooked the entire flight of the bats, the third camera was used to determine the exact time of landing. Video recordings were made with 25 (interlaced) frames per second, and each half-frame was illuminated with a flash of duration 1 ms from an infra-red strobe system at a rate of 50 Hz, resulting in a pin-sharp picture of the bat in flight. Recordings were digitalized using Sony DCR-PC8E camcorders and stored on a computer.

Recordings from the two cameras overlooking the flight room were used to reconstruct the three-dimensional flight path of the bat and the positions of the microphones with the software Simi-Motion (Simi Reality Motion Systems GmbH, Version 6.5, Build 245). The software used a direct linear transformation algorithm to compute a 3-D position from the 2-D coordinates of the two video recordings.

A custom-built ultrasonic microphone (PC-Tape microphone, Animal Physiology, University of Tübingen, Germany) with a flat frequency response (± 3 dB between 18 and 200 kHz) was positioned directly behind the landing grid, and recordings made with a sampling frequency of 480 kHz were synchronized with the video recordings. Control and synchronization of infra-red strobe, video and audio recordings was managed by PC-Tape (Animal Physiology, University of Tübingen, Germany).

The signals from the 16 microphones were amplified and then digitized with a sampling rate of 360 kHz and stored on a computer. For each approach flight, 4 s of audio and video recordings before landing were saved.

Synchronization of the video with the sound recordings was accomplished by comparing the sound pattern of three distinctive acoustic events on one of the 16 microphone recordings with the pattern of the PC-Tape microphone recording, which itself was synchronized with the video system through the VITC-code of the video cameras. The resulting synchronization accuracy was ± 1 ms.

Data analysis

3-D movement analysis

Recorded videos were analyzed using the 3-D-Movement-Analysis software Simi-Motion (version 7.5.0.288). The beginning of the sequence was defined as the frame when bats were visible on the recordings of both cameras. The end of the sequence was the time of landing as determined with the third camera. For all recorded flights, the position of the head of the bat was determined on each half-frame (every 20 ms), and the resulting flight path was calculated. The reconstruction error was ± 5 cm.

Sound analysis

Sound recordings were analyzed with a custom-made colour spectrograph using a 256-point FFT, a Hann-window and zero padding. The beginning and end of each call were defined at 6 dB below the maximum amplitude. The position of the bat at each call emission was interpolated from the position information available in intervals of 20 ms.

Computation of emission SPL

A custom-written Matlab (Version 7.0, The Mathworks, Natick, MA, USA) program called Sonarbeam was used to reconstruct the emission intensity at a distance of one meter (the reference distance) from a sound source (e.g. the mouth of a bat), depending on the direction and frequency band. A power spectral density (PSD, Welch's) was estimated over the time-window containing the call for each of the 16 microphone recordings. Each PSD was corrected for atmospheric and geometric attenuation by using the distance between the bat and each microphone, the directional frequency response of each microphone, as well as atmospheric parameters in order to obtain the emitted PSD one meter in front of the mouth of the bat in the direction of the microphones. From these resulting 16 PSDs, the emitted PSDs permeating a sphere of radius one meter around the source were interpolated on a fine spherical grid using cubic spline interpolation. The sound pressure level corresponding to the root mean square (r.m.s.) intensity was computed by integrating the PSD intensities for frequency bands between 20 and 110 kHz. The main axis or direction of the call was defined as the direction from the bat towards the highest interpolated SPL on the sphere. The source level refers to the SPL at one meter from the source in this direction. For an accurate interpolation of the maximum SPL of a call, the extent of the array must sample at least a large part of the central lobe, but the spatial sampling density of the microphones must be considerably tighter than a fraction of the width of the lobe. The minimum width of the emitted central lobe can be estimated from wave acoustics for a given maximum source size and emission frequency. The array dimensions used here are suited to study the SPL of bats, given the size of the mouth opening of the bat and using a piston model for a rough estimation of emission characteristics at 40 kHz.

Determination of the wingbeat cycle

By scoring the wing position from top (+5) to bottom (−5) in intervals of one, the position of the wing of the bat relative to its horizontal axis was determined for each frame until the wing position was not clearly visible [0.1–0.4 s before landing (Fig. 1)]. Using a frame rate of 50 Hz when recording a wingbeat at 10–15 Hz, we can reconstruct the wing movement without any aliasing effects. Cubic spline interpolation between scored wing positions was used to derive the wingbeat sequence (wing position over time). This wingbeat sequence was low-pass filtered using a Hanning window with a duration of slightly more than the wingbeat period in order

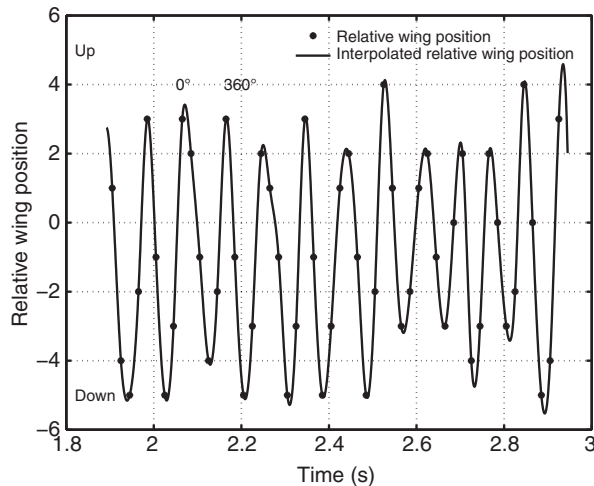


Fig. 1. Relative scored wing position and interpolated relative wing position for one flight. The maximal upward wing position is +5, maximal downward wing position is -5, horizontal wing position is 0. Wingbeat rate is relatively constant, with a cycle duration of 90 ms. Angular presentation in subsequent figures uses 0 deg and 360 deg as the topmost position of the interpolated wing position, and 180 deg as the undermost interpolated wing position.

to eliminate an offset due to unequal scoring (Fig. 4B). The residual between each wing position and the low-passed signal was used as the wing oscillation. This resulting oscillation was transformed through Hilbert transform into its corresponding analytic function. The angle of the analytic function was used as the phase of the wingbeat [0–360 deg (Fig. 1)].

Computation of the SL variation

Source levels for all calls emitted were high-pass filtered as a function of time to account for the individual-specific range-dependent SL reduction as the bat approached the landing site. In order to synchronize wing position with call emission, the distance between the bat and the landing site was used to compute and correct for the runtime of each call. Calls were categorized as single calls, groups of two (dyads) and groups of three (triplets). Calls emitted during the last part of the approach – that is, groups larger than three calls – were not analyzed. These calls were emitted when the bat was close to the array, where SL measurements were not very reliable. Here, the distance of a bat to the plane of the array is shorter than the distances between microphones, so the acuity of the interpolation process is insufficient. Additionally, the bats start to make the turn within this distance in order to land upside down. During this turn, some of the echolocation calls were directed away from the array. In addition the wingbeat was often not clearly visible 0.1 to 0.4 s before landing.

For each of the four bats, two flights were analyzed, resulting in 249 calls, of which 158 that were emitted as single calls (10), in dyads (73) or triplets (75) were considered for further analysis. Ninety-one calls were emitted in groups containing more than three calls and ignored in consequent analysis. Differences in the emission timing were tested using a Mann–Whitney *U* test with Holm–Bonferroni correction in SPSS 15 (Zar, 2009).

RESULTS

Timing of call emission relative to wing position

While approaching the landing site, the bats changed from single calls to groups with two, three or more signals. Call emission was

synchronized with wing position. The emission of single calls, dyads or triplets was not evenly distributed over the entire wingbeat but showed a trimodal distribution, with one peak at the end of the downstroke, one peak during the upstroke when the wings were horizontal, and one peak at the topmost wing position (Fig. 2). Very few signals were produced in a range of a 60 deg width just before the middle of the downstroke. The centre of all call groups was positioned in the middle of the upstroke. Single calls and the second calls of triplets were therefore emitted at this wing position. Calls of dyads were emitted at the lowest wing position and just before the uppermost wing position, thus before and after the centre of the dyad. The first and the third calls of triplets were emitted earlier and later in the wingbeat, respectively; the first call at the end of the downbeat and the third call around the topmost position of the wing (Fig. 3). The group size-dependent timing of emission relative to the wingbeat cycle is significant. The first calls of triplets are emitted earlier than the first calls of dyads ($P=0.003$), which are emitted earlier than single calls ($P<0.001$). The same pattern can be seen for the second calls in each group [second of dyads and second of triplets, $P<0.001$ (Fig. 3)].

SL variation

The SL decreased while the bat approached the landing grid. This decrease was not steady, however, but showed a regular modulation when plotted over time (Fig. 4A). The maximum modulation within one period was 12 dB peak-to-peak (pp). The SL varied with the same frequency and phase as the wingbeat (Fig. 4C). Comparing the wing position with the SL modulation revealed an increasing positive SL deviation (from the moving average of the SL) during the upstroke, reaching maximal positive SL modulation just before the upper turning point of the wings. The average modulation was approximately 4 dB pp (Fig. 5). SL deviation decreased during the first part of the downstroke, and, during the second half of the downstroke, the average SL modulation reached a maximal negative modulation at 1.5 to 2 dB below the moving average (Fig. 5).

DISCUSSION

The aim of this study was to understand how variations of signal SL during the approach to a landing site correlate with and depend

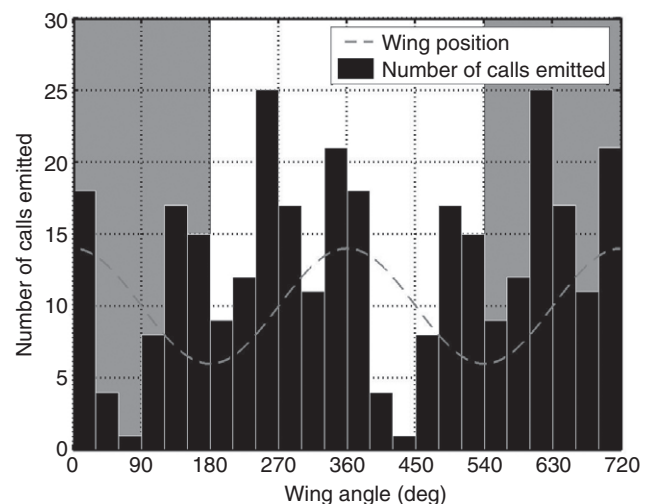


Fig. 2. Number of calls emitted during each 30 deg section of the wingbeat cycle (total number of calls considered: 158). Representation of two wingbeat cycles (grey dashed line) to illustrate circularity.

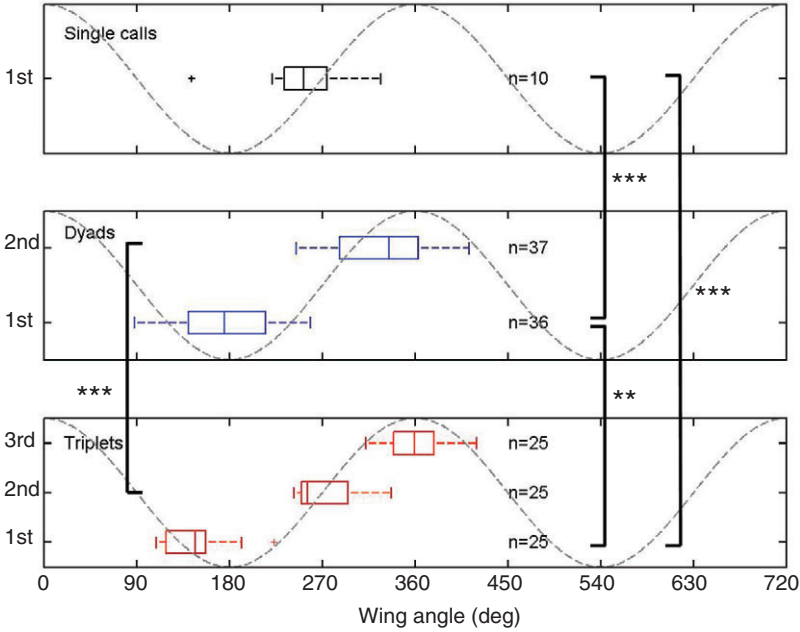


Fig. 3. Timing of call emission relative to wing-angle. The grey dashed line represents wing movement, incorporating two wingbeat cycles to illustrate circularity. Box plots show median, upper and lower quartile of the wing-angle at which calls were emitted for each call category. The number of calls included in each category is stated. The first calls of dyads are emitted significantly earlier in the wingbeat cycle than single calls. The first calls of triplets are emitted significantly earlier than first calls of dyads. Second calls of triplets are emitted significantly earlier than second calls of dyads.

on wingbeat and respiratory cycle. In flying bats, sound emission is often correlated with wingbeat and respiratory cycle. Therefore we will use the correlation between sound emission pattern and wingbeat as an indirect indicator for the correlation between respiratory cycle and wingbeat. We will then discuss the variations in signal SL in relation to the presumed respiratory cycle and hypothesize about the influence of muscle movements during each wingbeat cycle on the source level. Finally, we will discuss how group size correlates with the timing of call emission in relation to the wing position.

Respiratory cycle as indicated by the correlation between sound emission and wingbeat cycle

When approaching a target, *E. fuscus* group their echolocation calls into dyads, triplets and larger groups. All groups and also single calls emitted are centred at about the middle of the upstroke. The pauses between groups are centred just before the middle of the downstroke. Grinnell and Griffin (Grinnell and Griffin, 1958) first proposed that the grouping of calls, already apparent in the earliest recordings of bat echolocation signals (Galambos and Griffin, 1942), reflect the respiratory cycle. Recordings of diaphragmatic

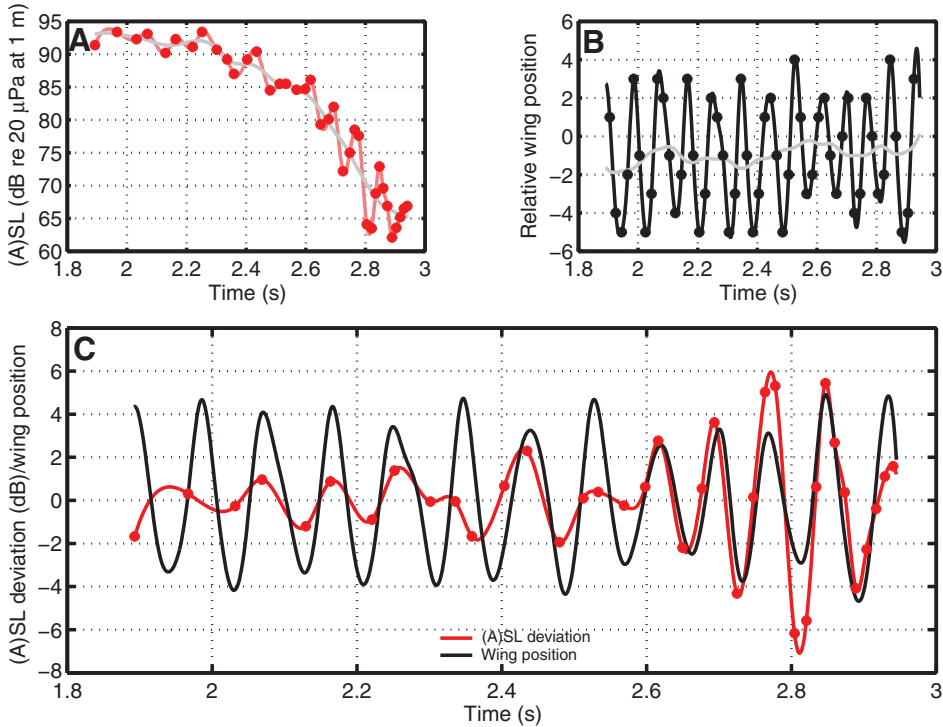


Fig. 4. (A) Source level (SL; ASL for the first calls) within 1.2 s while one bat approaches the landing grid. Red dots indicate (A)SL for each call, the red line interpolated (A)SL, and the grey line the low-pass-filtered (A)SL. (B) The relative scored wing position and interpolated relative wing position for same flight. The maximal upward wing position is +5, the maximal downward wing position is -5, and horizontal wings are 0. The grey line is the low-pass-filtered wing position. (C) Overlaid (A)SL variation and wingbeat.

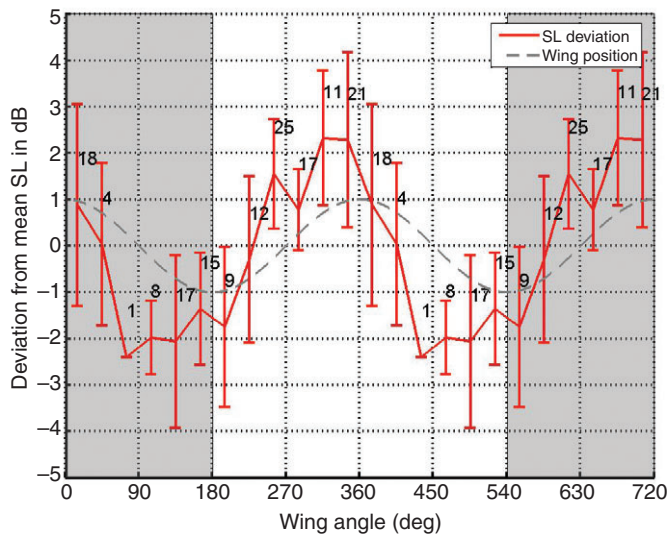


Fig. 5. Mean (A) SL modulation (\pm s.d.) relative to wing position for each 30 deg section of the wingbeat cycle. Representation of two wingbeat cycles (grey dashed line) to illustrate circularity. The sample sizes of each 30 deg section are given next to the error bars.

myopotentials showed that inhalation in flying *P. parnellii* occurred during the pauses between call emissions (Lancaster et al., 1995). Other experiments confirmed that calls are emitted during exhalation and that pauses between groups are due to inhalation in stationary horseshoe bats (Schnitzler, 1968) and for flying *Phyllostomus hastatus* (Suthers et al., 1972). We therefore conclude that *E. fuscus* approaching a landing platform inhaled in the pauses between groups just before the middle of the downstroke and exhaled with the potential to emit signals from the end of the downstroke throughout the upstroke until the first part of the downstroke. Correlation patterns between wingbeat and call emission found in most previous studies are similar to our pattern – that is, the pauses are positioned in the downbeat, thus indicating the inspiration phase (Schnitzler, 1971; Suthers et al., 1972; Schnitzler and Henson, 1980; Schnitzler et al., 1987; Kalko and Schnitzler, 1989; Wong and Waters, 2001; Wilson and Moss, 2003; Parsons et al., 2010). There are, however, some exceptions. Kalko (Kalko, 1994), studying free-flying pipistrelle bats, describes a wingbeat pattern where most of the signals were emitted during the downbeat. Schnitzler and Henson (Schnitzler and Henson, 1980) described that bats intercepting an insect make several wingbeats while emitting a long terminal group. An example of this can be seen in Fig. 4C, where the bat emits a series of 11 calls at a pulse interval of 11–16 ms during the last 1.5 wingbeats shown. Inspiration in the terminal group will most likely be omitted for one or more wingbeats. Moss and colleagues (Moss et al., 2006) found that *E. fuscus* sometimes overrode the tight coupling of wingbeat and call emission. In conjunction with landing, obstacle avoidance or take-off, call production was shown to occur during any point of the wingbeat cycle (Lancaster et al., 1995). This indicates that bats can voluntarily break the strict coupling of wingbeat, respiratory cycle and emission of either single signals or signal groups. The bats in this study, however, were trained to make stereotyped approach flights and did not break this tendency when emitting single calls, dyads or triplets.

Correlation between SL variation, wingbeat and subglottic pressure

The SL decrease during the approach to a landing platform was superimposed by regular wingbeat-cycle-coupled oscillations. During the upstroke, the SL was raised in relation to the moving average. The maximal positive SL modulation was reached just before the uppermost turning point of the wings. Calls emitted at the uppermost turning point were on average already more than 1 dB less intense. Calls emitted around the lowermost turning point of the wings were on average 4 dB lower in SL than calls emitted just before the uppermost turning point. Previous studies did not describe a comparable modulation, possibly owing to methodological limitations. There are some indications that other species also modulate the SL in the rhythm of the wingbeat. Parsons and colleagues (Parsons et al., 2010) found that calls emitted during the upstroke of *Mystacina tuberculata* were on average 1.5 dB more intense than during the downstroke. However, this difference was not significant and was not discussed further. Using only one microphone, modulations could also be caused by scanning movements of the bat. By using a 16-microphone array, we measured the SL and the modulation thereof accurately and showed that the variations are not caused by head movements. Recordings of *Myotis daubentonii* using one microphone also indicate a modulation of the SL in the rhythm of the wingbeat [fig. 3A in Boonman and Jones (Boonman and Jones, 2002)].

The SL variation is most likely caused by changes in the subglottic pressure during the wingbeat cycle. Subglottic pressure increases immediately before vocalization and is positively correlated with the SPL of the echolocation calls (Fattu and Suthers, 1981). Abdominal wall muscles generate the primary power for vocalization, and there is little difference in abdominal wall muscle activity between vocalizing bats at rest and during flight (Lancaster et al., 1995; Lancaster and Speakman, 2001). Lancaster and colleagues (Lancaster et al., 1995) proposed that the coincident contraction of the flight muscles *pectoralis* and *serratus ventralis* during flight could cooperate in the pressurization of the thoraco-abdominal cavity. This increase of pressure in the thoraco-abdominal cavity could lead to an increase of the subglottic pressure and thus provide the precondition for echolocation calls with a slightly higher SL. The SL increase relative to the average in the second half of the upstroke coincides with the onset of the flight muscle contraction (Hermanson and Altenbach, 1981; Hermanson and Altenbach, 1983). Flight muscle contraction terminates during the first half of the downstroke, which could cause the reduction of the SL relative to the average. Inhalation then takes place after the major wing muscles have ceased activity (Lancaster et al., 1995). To validate this hypothesis, accurate measurements of the SL of free-flying bats in combination with electromyographic recordings of the major flight muscles are necessary.

Theoretically, the described dependency of signal SL on wing position would give bats the possibility of changing the SL of single signals by emitting them at different phases of the upstroke. When signals with a high SL are needed – that is, when searching for prey – calls should be emitted at the end of the upstroke. This could explain why bats searching for prey in the field emit loud echolocation calls when the wings are near the topmost position (Schnitzler et al., 1987; Kalko and Schnitzler, 1989). Whether bats actually use this possibility must be investigated in further studies.

The strong variation of SL in correlation with wingbeat challenges the intensity compensation theory, according to which a reduction of the SL in bats closing in on a target compensates for the increase of the received echo level at the ear of the bat owing to a reduction of transmission loss and keeps the echo level constant (Kobler et

al., 1985; Hartley et al., 1989). During an approach, the SL is reduced by approximately 30 dB over a distance of about 2.0–1.5 m. However, if the SL fluctuates by a maximum of 12 dB (on average about 4 dB) within a single wingbeat, one can hardly speak about a constant received level available for the bat. This supports the hypothesis that the average reduction of the SL during an approach by approximately 6 dB per halving of distance is not made in a tightly coupled feedback control system (J.C.K., unpublished observations).

Correlation of group size and call emission timing

Single calls were emitted relatively late in the wingbeat cycle – during the upstroke. The first calls of dyads were emitted earlier, starting at the end of the downstroke, and second calls of dyads were made mainly during the second half of the upstroke. In triplets, this pattern continued: first calls were again emitted earlier, already during the downstroke, second calls during the upstroke and third calls during the upper turning point of the wings. The temporal patterning of the calls relative to the wing position was changed so that the centre of the group relative to the wingbeat remained constant during the upstroke when the wings were approximately horizontal. When group size was increased, first calls were emitted earlier, last calls slightly later, and the variability tended to decrease.

This indicates that the number of calls a bat is going to emit in the upcoming group is indicated by the timing of the first call relative to the wing position when the bat produces single pulses, dyads and triplets in a stereotyped pattern. This suggests that the emission of pulse groups follows a fixed motor pattern, where the information gained with the preceding pulse group determines how many calls will be emitted in the next group. This might be the reason why pulse groups are separated by rather long ‘in between group pulse intervals’, which should be in the range of the vocal reaction time to new auditory information.

LIST OF ABBREVIATIONS

ASL	apparent source level
PSD	power spectral density
r.m.s.	root mean square
SL	source level
SPL	sound pressure level

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animal facilities at the University of Tübingen (approved by the Regierungspräsidium Tübingen).

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