

Flight and echolocation behaviour of whiskered bats commuting along a hedgerow: range-dependent sonar signal design, Doppler tolerance and evidence for ‘acoustic focussing’

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Summary

Echolocating bats obtain three-dimensional images of their surroundings in complete darkness by emitting sonar signals and evaluating returning echoes. When flying close to objects, bats risk collision and therefore depend on the accuracy of images – particularly in the perceived distance of obstacles, which is coded by the time delay between call and echo. Yet, during flight, such accuracy is perturbed first because bats call and receive echoes at different positions and second because echoes are modified by Doppler shifts. Certain call designs avoid both sources of ranging error, but only for a limited range of distances [the ‘distance of focus’ (DOF)]. Here, we show that whiskered bats (*Myotis mystacinus*) using broadband echolocation calls adjust call design in a range-dependent manner so that nearby obstacles are localised accurately. Such behaviour is adaptive because it reduces collision

risk. The bats also reduced call duration to some extent as they approached obstacles so that most returning echoes arrived after they finished calling. This reduction in call duration during the approach to obstacles was neither the only nor the main factor that influenced DOF. Indeed, both duration and bandwidth of calls influenced DOF independently, with lower bandwidths and longer durations giving greater DOF. Our findings give a new perspective on the adaptive significance of echolocation call design in nature and have implications for sonar engineering.

Key words: bat echolocation, acoustic flight path tracking, sonar signal design, Doppler-errors, ranging, distance of focus, *Myotis mystacinus*.

Introduction

Bat echolocation calls are shaped by natural selection to meet perceptual demands. Some call designs are better than others for specific echolocation tasks, and thus bats adjust traits such as duration and spectral composition of their calls selectively to gather information needed in each particular instance (Griffin, 1958; Kalko and Schnitzler, 1998; Neuweiler, 1989; Schnitzler and Kalko, 1998). Because radar and acoustical theory can be used to predict sonar performance achievable with a certain call design, understanding echolocation provides remarkable opportunities for studying ‘good design’ by natural selection (Dawkins, 1988). Yet, quantitative tests of whether naïve free-ranging bats in their natural habitat in fact choose call designs that are in agreement with such predictions only became possible through recent methodological advances. The present study combines 3D laser scans of habitat structures with a method to acoustically track flying bats in order to investigate how free-ranging whiskered bats change their call traits while mastering the

challenges associated with swift commuting flight along a hedgerow.

We know general rules of good signal design for different echolocation tasks, e.g. long narrowband calls for long-range detection in contrast to short broadband calls for accurate localisation and extraction of object features (Schnitzler et al., 2003). Yet, even in a stereotyped situation such as close-range orientation in fast flight along a hedgerow, bats show a remarkable range of call designs that change in a gradual manner. Three examples of calls used by whiskered bats in this context (Fig. 1A–C) show how the basic motif of a curved downward frequency modulated sweep is altered with respect to duration, bandwidth and frequency modulation. Such changes can be interpreted as adjustments to the rapidly changing acoustic scene encountered by the flying bat and are supposedly linked to some sort of instantaneous perceptual advantage. Recent theoretical advances permit quantitative predictions on the perceptual advantages of such gradual changes in call traits. Specifically, we will

address the relevance of call duration and bandwidth for flying bats.

Signal duration

The perceptual relevance of call duration is that it influences the minimum distance that a target can be detected at. Bats that echolocate at low duty cycles (signal 'on' for short proportion of time) reduce call duration as they approach prey in order to

avoid temporal overlap of their powerful vocalizations with the returning faint prey echoes, which would cause masking and make tracking of prey difficult if not impossible (Schnitzler and Kalko, 1998). The spherical zone around the bat in which targets' echoes are overlapping with and thus masked by the emitted call is named the signal overlap zone (SOZ). Reducing call duration when approaching targets is clearly adaptive because each 1 ms of signal duration adds 17 cm to the SOZ.

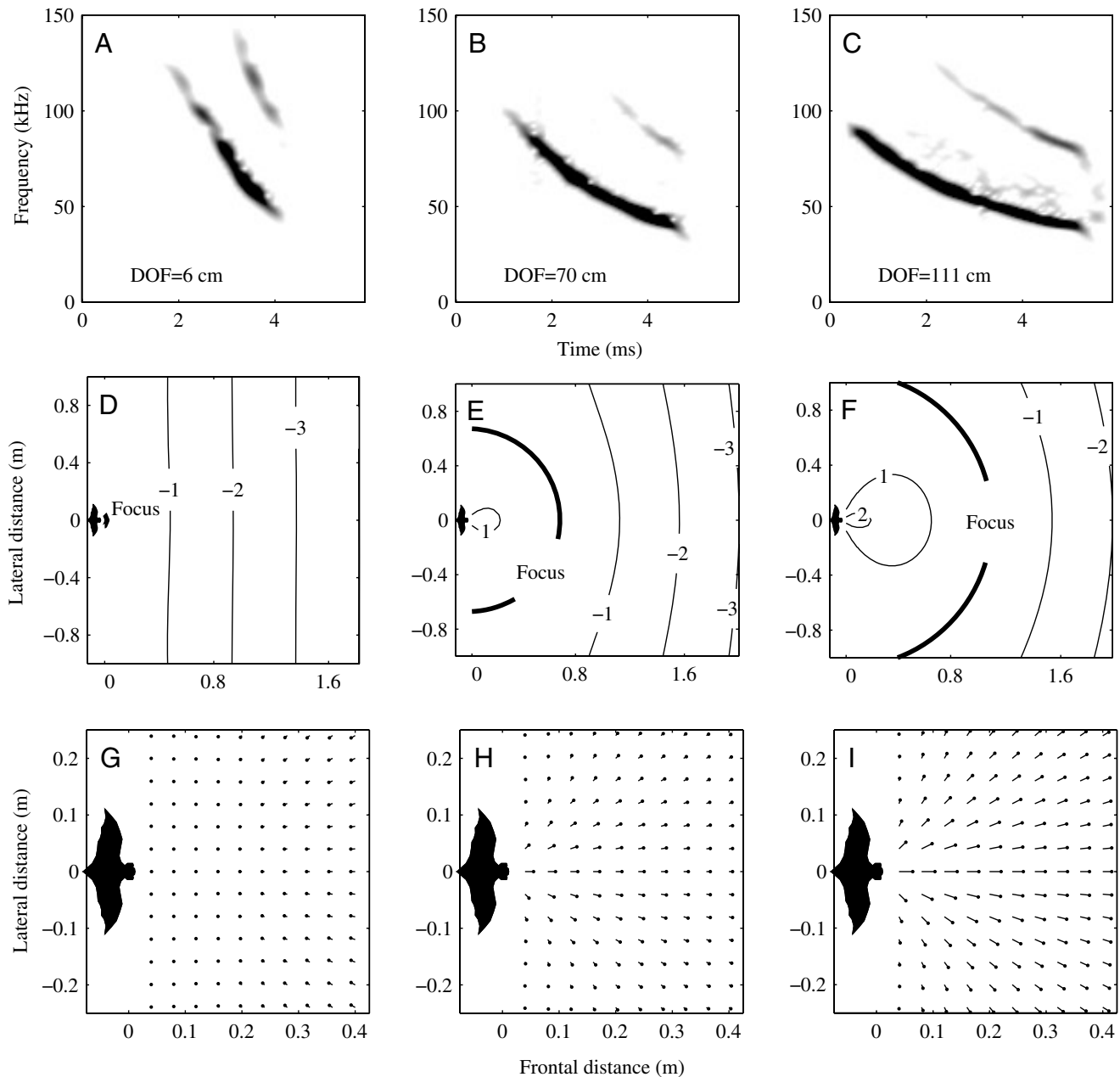


Fig. 1. Three examples of the effect of call design on ranging errors. (A–C) Spectrograms (FFT size 512, 256 points Hanning window, 240 points overlap). Two calls (A,C) were emitted at the locations indicated in Fig. 7B by stars. DOF indicates the distance at which overall ranging errors were zero. (D–F) Ranging errors calculated for these calls and indicated as lines of identical error. Labels on lines indicate size of ranging error in centimetres (>0 represents overestimation and <0 represents underestimation of distance). The thick line labelled 'focus' indicates locations where the overall ranging error is zero. (G–I) Ranging errors as in D–F but for a smaller distance range. 'Pinheads' indicate perceived positions and 'pin tips' the actual positions of targets.

This should be particularly relevant for the bats in the present study, which were flying at short distances from the hedge and thus risked collisions. We therefore hypothesize that call duration is reduced according to the instantaneous distance of the bat to the hedge.

Bandwidth, frequency modulation and Doppler tolerance

Understanding the significance of signal traits such as bandwidth and frequency modulation requires a brief introduction into the cross correlation function (CCF). The CCF is a mathematical representation of how bats might time the delay between call and returning echo, and it works by gradually shifting echo and call towards each other, while quantifying how well both signals match up. The time-shift of optimal alignment, indicated by the position of the peak in the CCF, is an optimal measure of the delay between call and echo and hence the distance of the target. The CCF has a more or less bell-shaped envelope, and the width of this envelope indicates how accurately the position of the peak, and thus the echo delay, could possibly be determined (e.g. see Fig. 2, second row). In complex habitats, where echoes from several targets temporally overlap, a narrow CCF envelope helps bats to segregate the complex compound echo into individual

targets, e.g. resolving single leaves that constitute a vegetation surface.

Bats mainly echolocate in flight, which means that, compared with the signals they produce, the echoes they receive are compressed and their pitch is increased due to Doppler effects that are related to flight speed. For bat species using downward FM (frequency-modulated) calls, like the species in the present study, such an increase in pitch negatively affects the CCF and thus the ranging performance in two different ways. First, the position of the CCF peak will shift such that the measured call–echo delay increases, which means an equivalent overestimation of the actual target distance. The peak's position shifts because each particular frequency occurs a little later in the Doppler-shifted echo than in the unaltered echo and therefore its time delay is perceived as correspondingly longer. This first Doppler-related error will be called *Doppler ranging error*. Secondly, the width of the CCF envelope is likely to widen with increasing Doppler shift. This second Doppler-related effect results in a reduced ranging *acuity* (Altes and Titlebaum, 1970; Boonman et al., 2003; Cahlander, 1967; Glaser, 1974; Masters and Raver, 2000; Pye, 1986; Strother, 1961).

The bandwidth of the echolocation signal greatly influences

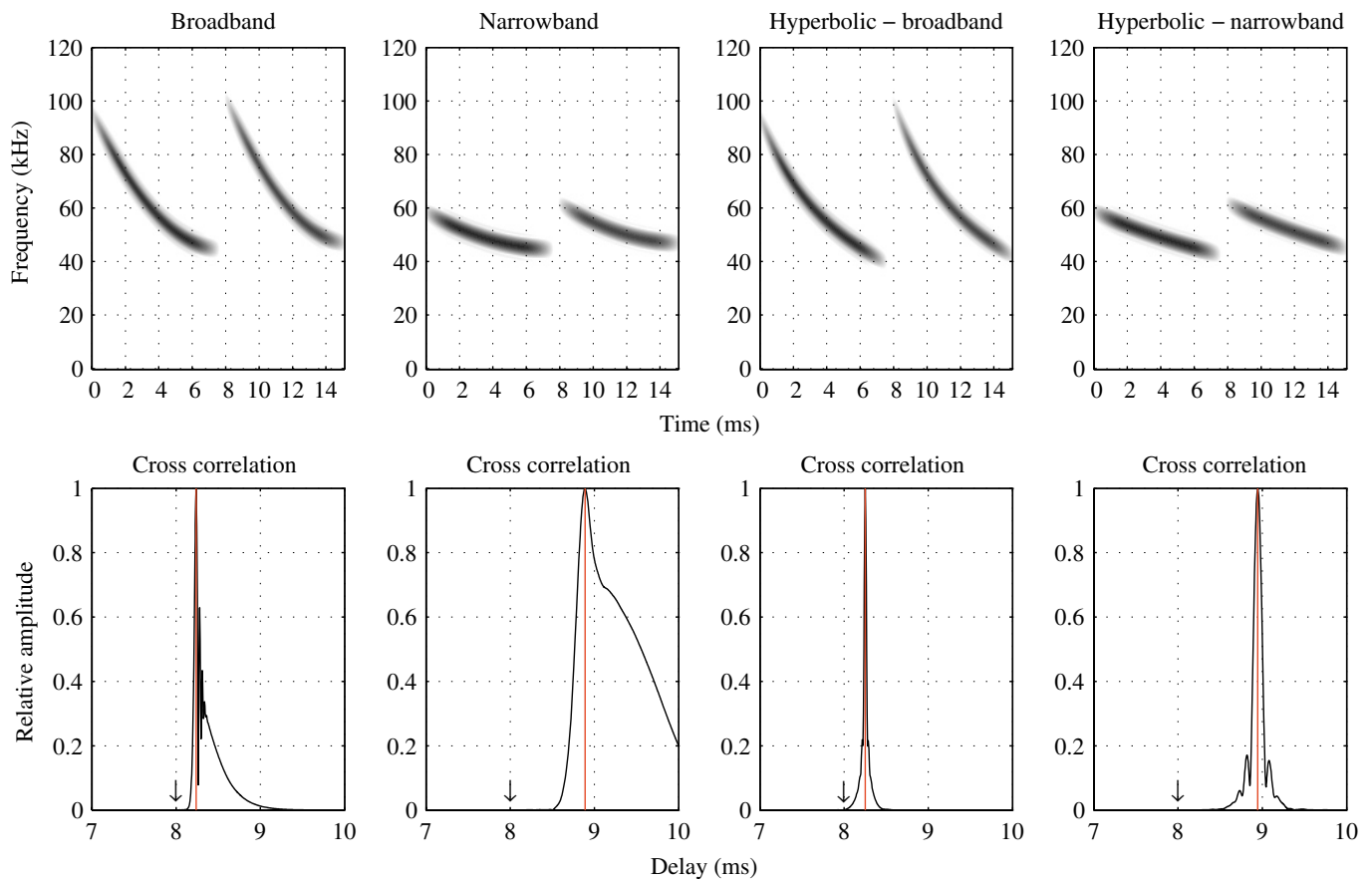


Fig. 2. Four examples of the influence of call bandwidth and frequency modulation curvature on Doppler-related ranging errors at a flight speed of 8 m s^{-1} . Upper row: spectrograms of four call echo pairs. Lower row: envelope of the cross correlation function (CCF). Arrows indicate the actual time delay of 8 ms between call and echo. Red lines show the position of the peak in the CCF.

the magnitude of both the ranging error and the ranging acuity. For a given signal duration, the Doppler-related ranging error decreases and the ranging acuity increases with increasing bandwidth (Fig. 2, columns 1 and 2). At a given bandwidth, a reduction in call duration has an analogous effect (Boonman et al., 2003). Therefore, both bandwidth and duration affect Doppler-related ranging errors independently of one another. For this reason, short broadband FM pulses, with a steep frequency modulation, are well adapted for in-flight localisation (Simmons, 1973).

The curvature of the frequency modulation offers an additional way to influence ranging acuity: FM call designs with hyperbolic frequency modulation have been called Doppler-tolerant because their ranging acuity is not at all impeded by Doppler shifts (Altes and Titlebaum, 1970; Kroszcynski, 1969). But note that even hyperbolically modulated calls suffer from Doppler-related ranging errors.

Indeed, bats have been shown to sometimes produce such broadband calls with hyperbolic frequency modulation (Cahlander, 1967). Yet, many FM calls produced by flying bats are far from being Doppler-tolerant (Boonman et al., 2003; Escudíé, 1988; Parsons et al., 1997). This suggests that bats may actively control call design and hence Doppler tolerance to somehow make use of ranging acuity and ranging error caused by Doppler shifts (Boonman et al., 2003; Glaser, 1974).

The 'distance of focus'

It is difficult to imagine a direct payoff for a low-ranging acuity or a large-ranging error; however, other benefits might counterbalance this. In echolocation, a general conflict occurs between localisation and detection, with signals that are well adapted for long-range detection being typically long and narrowband. Such signals, on the other hand, give reduced localisation performance compared with short broadband signals. Thus, altering signal bandwidth is a means to shift from long-range low-quality ranging to short-range high-quality ranging. During flight in the proximity of structures (in particular under an increased risk of collision,) large bandwidth is obviously adaptive as it reduces ranging error and increases ranging acuity in general. Yet, long-range detection is of little if any adaptive value in close-range orientation. Thus, one must assume further, hitherto unknown, competing perceptual needs that explain why bats facing close-range orientation tasks use calls other than the shortest ones of maximum bandwidth. Recently, however, a directly quantifiable payoff for choosing call designs with certain Doppler ranging errors has been suggested: the Doppler ranging error might be used to compensate for another ranging error incurred during flight. This second ranging error arises because the flying bat approaches the target between calling and receiving the echo produced by that target (Boonman et al., 2003). The distance the bat flies reduces the distance that the sound travels, and accordingly the time delay of the echo is shortened. As a result, at the instant of echo reception, the target's range is measured closer by half the distance flown than it was at the time of

calling. This underestimation of target distance is more pronounced the faster the bat flies. It also increases with target distance, because the echoes of more-distant targets take longer to return, giving the bat more time to cover a longer distance between call and echo.

The fact that the first Doppler-related ranging error creates an overestimation, and the second flight-induced error creates an underestimation of the actual target distance, means that both errors can cancel mutually. Bats would make optimal use of this if they actively adjusted their signal design such that the Doppler-related range overestimation (dependent on signal design) exactly compensates for the range underestimation due to the bats' own movement. There are limits though to the working range of this elegant and computationally straightforward mechanism: because the range underestimation depends on the initial target distance while the range overestimation does not, the two ranging errors can fully cancel each other only for one particular target distance. Signal design determines at which distance this is the case (Boonman et al., 2003). Only targets at this distance are ranged without any flight-speed-related error; targets at other distances systematically appear to be further away or closer than they actually are. By adopting a suitable call design, bats could adaptively influence at what distance ranging errors are cancelled. The selection of this moveable distance of zero ranging error is similar to focusing, or more specifically accommodation, in vision, and the distance was therefore named 'distance of focus' (DOF) (Boonman et al., 2003). We calculated the three-dimensional distribution of the overall ranging errors bats must expect with a given call design at a given flight speed. The resulting three-dimensional 'surface of focus' is nearly spherical, with the DOF as its radius (Fig. 1D–F).

Fig. 1 exemplifies call designs and the corresponding ranging errors for three calls emitted by the bats flying along a hedge. Fig. 1D–I gives the two-dimensional distribution of the corresponding ranging error for two different distance ranges. Note that the line of focus is a circle with the calling bat in its centre and also that the radius of this circle, i.e. the DOF, differs between the calls as a result of the different call design.

The adaptive relevance of this concept of 'acoustic focusing' is that a flying bat can actively shift the spherical surface of focus back and forth from call to call by choosing call designs with the appropriate Doppler ranging errors (e.g. Fig. 1). That way, bats can modify the spatial distribution of location errors such that the most relevant objects are localised most accurately. The further away an object is from the DOF (closer or more distant to the bat), the larger will be the error in its perceived distance. Bats manoeuvring close to vegetation risk collision, especially because they have to correctly plan their whole flight trajectory up to at least the place of their next call, which is where they update their acoustic image of the environment. Therefore, they particularly depend on accurately perceiving obstacle distances. In this situation, they might prefer calls with a surface of focus exactly reaching the

obstacle, because then they perceive the obstacle distance accurately and minimize the risk of collision. If they focus closer than the obstacle, they underestimate its distance and therefore fly with a certain security margin, but if they focus beyond the obstacle, they overestimate the obstacle's distance and might fly too close, thereby risking collision (see Fig. 1G–I). We therefore hypothesize that bats reduce the risk of collision by adapting their calls to their distance to nearby obstacles such that the surface of focus either exactly reaches the obstacle or is somewhat shorter but does not reach beyond the obstacle. Here, we assessed actual flight and echolocation behaviour in the field to test whether signal design is distance dependent in the way predicted by the theory of acoustic focussing.

To investigate how bats' positions relative to obstacles are reflected in their call design, we studied free-ranging whiskered bats that were commuting undisturbed along a hedge to their feeding grounds. In particular, we tested (1) whether they adjusted their call duration and thus the SOZ to their instantaneous distance to the hedge, (2) whether they chose call designs that change systematically with respect to their Doppler tolerance (i.e. ranging error and/or acuity) and, especially, (3) whether such changes are in agreement with the theory of acoustic focusing, i.e. call designs that control ranging errors for nearby obstacles in a distance-dependent manner.

Materials and methods

Recording site and bats

Flight paths of whiskered bats (*Myotis mystacinus*, Kuhl 1817) flying along a hedge away from their nearby nursery colony located in southern Germany were reconstructed in three dimensions by the method of acoustic flight path tracking. To avoid possible impact of the presence of conspecifics on call design, we mainly used bats flying solitarily along the hedge. The surface of the hedge was rastered using a theodolite (Jenoptik 080A; Jena, Germany) in combination with a laser distance meter (Leica Disto Memo; Leica Geosystems, Heerbrugg, Switzerland).

Acoustic flight path tracking

The bat's position at the time of call emission was determined acoustically by evaluating the differences in arrival time of the echolocation call at eight microphones (Knowles BT1759; Itasca, IL, USA) (Aubauer, 1994; Aubauer and Ruppert, 1994). As flying bats were calling repeatedly, individual call-by-call localisations were strung together to reconstruct the bat's flight path (Holderied and von Helversen, 2003; Schul et al., 2000).

Acoustic recordings and analysis

Calls were recorded with Knowles BT1759 microphones filtered for flat frontal frequency response (± 2 dB) between 20 and 100 kHz. As the sensitivity of the recording microphone decreases over 100 kHz, bandwidth of calls containing such

high frequencies might be underestimated. The microphone was located at $X=0$ m, $Y=0$ m and $Z=0.98$ m in Fig. 3A, aiming 45° upwards in the Y -direction. Because call intervals and flight speed at the position of recording were similar to those measured over the preceding 6 m of the flight path and because the bats were much closer to the hedge than to the microphone we do not believe that the microphone array influenced call design significantly in our dataset. Calls were sampled at 500 kHz with 11-bit resolution on a custom-made digital recorder. Only calls with a sufficiently high signal-to-noise ratio and a propagation pathway unobstructed by the hedge were evaluated. Each call was resampled initially to correct for the Doppler compression of the recorded signal (Boonman and Jones, 2002; Schuller et al., 1974). The minimum target distance without call/echo overlap (SOZ) was calculated as half the call duration multiplied by the speed of sound in air. The measure of ranging acuity was the width of the envelope at half the peak amplitude of the CCF between call and a copy of the call Doppler-shifted corresponding to a flight speed of 6 m s^{-1} . The narrower its envelope, the higher is the ranging acuity and the better is the temporal resolution of a particular call. Effects of flight speed on ranging were calculated by successively Doppler-shifting the call for flight speeds up to 8 m s^{-1} in steps of 0.25 m s^{-1} and cross-correlating the results with the initial call. The ranging error, i.e. time offset of the maximum of the CCF, increases almost linearly with flight speed. Doppler tolerance was taken as the slope of the linear interpolation of time offset against flight speed. It is measured in $\mu\text{s} (\text{m s}^{-1})^{-1}$ flight speed (i.e. range-Doppler coupling in Boonman et al., 2003) and was converted to $\text{mm} (\text{m s}^{-1})^{-1}$ flight speed by multiplication with $0.17 \text{ mm } \mu\text{s}^{-1}$. The actual Doppler-related range overestimation in mm for a certain target is derived from this by multiplication with the relative flight velocity between the bat and the target. We used cross correlation because it is computationally straightforward to calculate, yet estimates Doppler-related range overestimation with an outcome very similar to that of an alternative filterbank model (Boonman et al., 2003).

The second ranging error, the flight-speed-related range underestimation, was calculated as half the distance the bat itself flew between the time of call emission and echo perception. The overall ranging error at a given location was calculated as the difference between (1) the Doppler-related range overestimation and (2) this flight-speed-related range underestimation due to the bat's own movement towards a grid of positions where a target might be located. This assumes that bats use the concept of a single image of their surroundings correct for the time of sound emission rather than for the time of hearing the echoes. We calculated the three-dimensional distribution of overall ranging errors accordingly, taking into account the bat's relative velocity towards each location, which depends on the relative angle to the bat's flight speed vector and the fact that the bat is not approaching off-axis targets in a straight line. The overall ranging error is zero on a near-spherical 3-D surface called 'surface of focus'. All calculations

were performed in Matlab v. 6.5. (The MathWorks, Natick, MA, USA) using the signal processing toolbox.

Results

Flight behaviour

We studied bats (22 different individual bats of a larger colony) while they were commuting from their day roost to their feeding area at dusk. Every evening, these bats flew in a stereotypical manner in a narrow flight corridor guided along one side of a hedgerow (see Fig. 3A–F; flight direction right to left). This flight corridor closely follows the surface of the hedge and is approximately 1 m wide and 2 m high. The bats

used distances between 0.3 and 1.7 m from the hedge (Fig. 3G). The largest distance to the hedge occurred at a Y -position of 5–7 m, when the bats were not fully following a recess in the hedge's surface.

The flight along the hedge can be divided into two distinct phases with a transition: in the initial phase, bats were flying above and alongside a low bulging part of the hedge ($Y=5.5$ – 8.5 m; Fig. 3E,F). At a position 5 m along the hedge, most of them descended (between Fig. 3D and Fig. 3E). In the final phase, they then continued their flight beneath a protruding portion of the hedge ($Y=1.5$ – 4.5 m; Fig. 3C,D). The important difference between these two phases lies in their potential danger for bats. In the initial phase, bats had the freedom to ascend and thereby reduce flight speed, whereas in the final phase the overhanging hedge confines the degrees of freedom for avoidance movements of the bats. We hypothesize that the confined spatial situation during the final phase increases the need for accurate flight path planning and thus requires a higher ranging accuracy. Individual bats also differed with respect to their relative position to the hedge, and we used this as a measure to test our hypotheses. Bats flew at a velocity of 5.2 – 8.3 m s⁻¹ (Fig. 3H).

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Echolocation behaviour

Bats called, on average, every 77.6 ± 28.2 ms. There was no significant increase in pulse interval (Int.) along the course of the hedge (Int. = $2.87Y + 63.05$; $r^2 = 0.50$, $F = 4.92$, $P = 0.08$, $N = 7$; Fig. 4A). The lowered values at ~ 5 m originate from the tendency of some individuals to emit one double pulse just before entering into the final phase (Fig. 4A). Mean call duration (Dur.) was 2.82 ± 0.78 ms and there was a very slight yet significant decrease in duration over the course of the hedge (Dur. = $-0.079Y + 3.04$; $r^2 = 0.72$, $F = 12.56$, $P = 0.0165$, $N = 7$). We found a slight reduction in mean call duration at a position of ~ 5 m concurrent with the increased tendency to produce double pulses (Fig. 4B). Call bandwidth (BW) increased significantly as bats proceeded along the hedge from a mean of 63 kHz at 8 m to 86 kHz at 2 m (BW = $-4.28Y + 95.65$; $r^2 = 0.99$, $F = 365$, $P = 0$, $N = 7$; Fig. 4C). As call

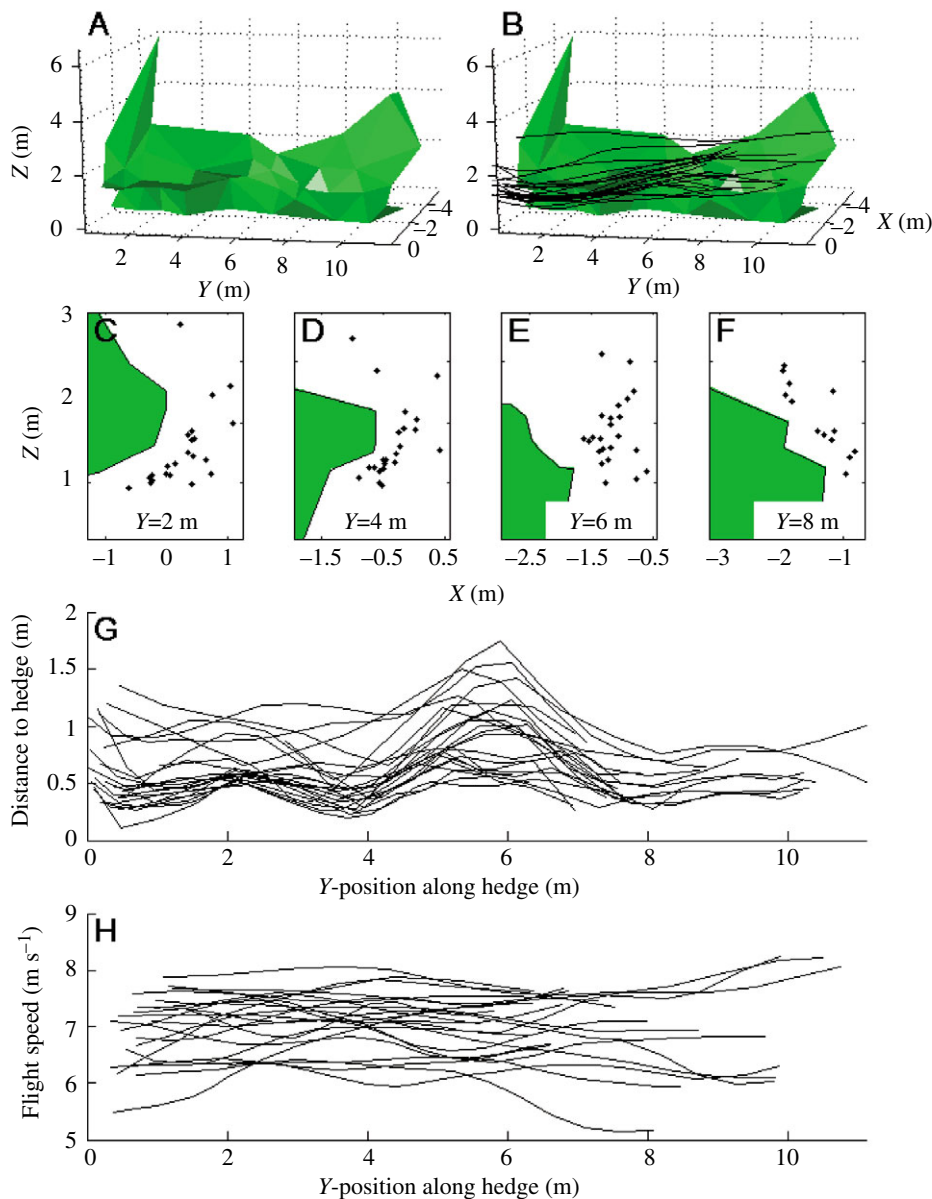


Fig. 3. Flight behaviour along the hedge. (A) 3-D surface of the hedge; (B) as in A, but with all flight paths; (C–F) flight corridor in four cross sections through the hedge and flight paths at the Y -positions indicated; (G) individual instantaneous distance to the hedge; (H) individual flight speed during the flight along the hedge. Flight direction from right to left, i.e. with decreasing Y .

duration did not increase at the equivalent rate, this increase in bandwidth resulted in an overall increase in sweep rate.

The first Doppler-related error, i.e. the error in target ranging, decreased from mean values around $1.2 \text{ mm (m s}^{-1})^{-1}$ in the initial phase to values of $\sim 0.6 \text{ mm (m s}^{-1})^{-1}$ in the final phase when bats flew below the hedge (Fig. 4D). Along the course of the hedge, these ranging errors (RE) reduced significantly ($\text{RE}=0.12Y+0.23$; $r^2=0.94$, $F=84.42$, $P=0$, $N=7$). The second Doppler error, i.e. ranging acuity measured as the width of the CCF-envelope (EW), did not change accordingly along the hedge ($\text{EW}=0.80Y+56.1$; $r^2=0.39$, $F=3.20$, $P=0.13$, $N=7$; Fig. 4E). Figs 5 and 6 exemplify aspects of signal design

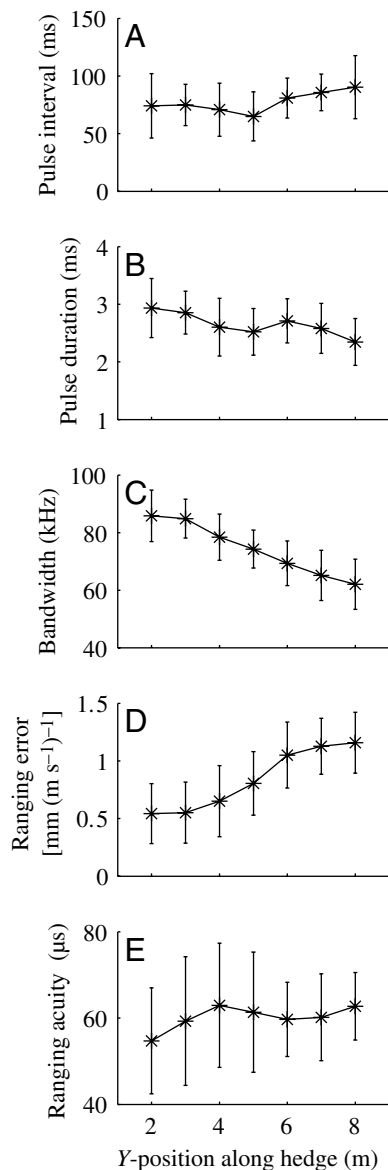


Fig. 4. Echolocation behaviour along the hedge (means \pm s.d.) in segments of 1 m. (A) pulse interval; (B) pulse duration; (C) bandwidth of the first harmonic; (D) Doppler ranging error; (E) width of the cross correlation function (CCF) envelope, i.e. inverse measure of Doppler ranging acuity, for a flight speed of 6 m s^{-1} .

(SOZ and DOF, respectively) of nine individual bats along the hedge.

Signal overlap with hedge echoes

Bats only very slightly increased pulse duration, and thus SOZ, during their flight along the hedge (Fig. 4B). This can also be seen in Fig. 5, showing the behaviour of nine individual bats. The hemispheres in Fig. 5 indicate the SOZ of each individual call, with the call uttered in the centre of the hemisphere. Again, there is no evidence for a systematic change in SOZ along the course of the hedge and, in particular, not with respect to the initial and the final phase. Bats did increase SOZ with the instantaneous shortest distance (SD) to the hedge ($\text{SOZ}=0.137\text{SD}+0.369$; $r^2=0.22$, $F=66.72$, $P=0$, $N=244$), but changes in SOZ were generally small with bats usually (but not always) avoiding pulse echo overlap. 19% of all calls had a SOZ reaching beyond the closest point of the hedge.

Fig. 7C depicts a cross-sectional plot at a Y-position of 2 m and shows that the SOZ varied very little, yet bats were flying at such distances that the SOZ was exactly reaching the hedge surface at least at this part of the final phase. There was a significant correlation between instantaneous shortest distance to the hedge and SOZ ($\text{SOZ}=0.23\text{SD}+0.38$; $r^2=0.66$, $F=38.9$, $P=0$, $N=22$).

Distance of focus at hedge

Bats used calls that were significantly less affected by Doppler ranging errors in the final phase than in the initial phase [$1.16\pm 0.26 \text{ mm (m s}^{-1})^{-1}$ at $Y=8 \text{ m}$ and $0.54\pm 0.26 \text{ mm (m s}^{-1})^{-1}$ at $Y=2 \text{ m}$; Fig. 4D]. This corroborates our second hypothesis. But are these changes in agreement with the predictions based on the DOF theory? Fig. 6 shows the DOF for the same nine individual flight paths as in Fig. 5. The hemispheres here indicate the surface of focus, i.e. the surface at which the overall flight-induced ranging error is zero. All bats reduced their DOF at the transition from the initial phase to the final phase. Moreover, the DOF almost always remained below the bats' instantaneous distance to the hedge. Only 3% of all calls, i.e. seven out of 233, had a DOF reaching inside the hedge, and only one of those by more than 9 cm. The bats' behaviour complies with the prediction by the acoustic focussing theory that DOF should stay below obstacle distance.

Fig. 4 shows that there is some variability in call design at each particular position along the hedge. A cross-sectional plot at a Y-position of 2 m (Fig. 7B) reveals that this inter-individual variation can be related to the different positions of the individual flight paths with respect to the hedge. The trend is that around a Y-position of 2 m calls uttered closer to the hedge have significantly shorter DOF ($\text{DOF}=0.55\text{SD}-0.08$; $r^2=0.76$, $F=65.0$, $P=0$, $N=22$) and also that those under the hedge have shorter DOF than those emitted by bats following the hedge more laterally. At this part of the final phase bats always focused to a distance close to but shorter than their actual distance to the hedge. Thus, obviously, the changes in

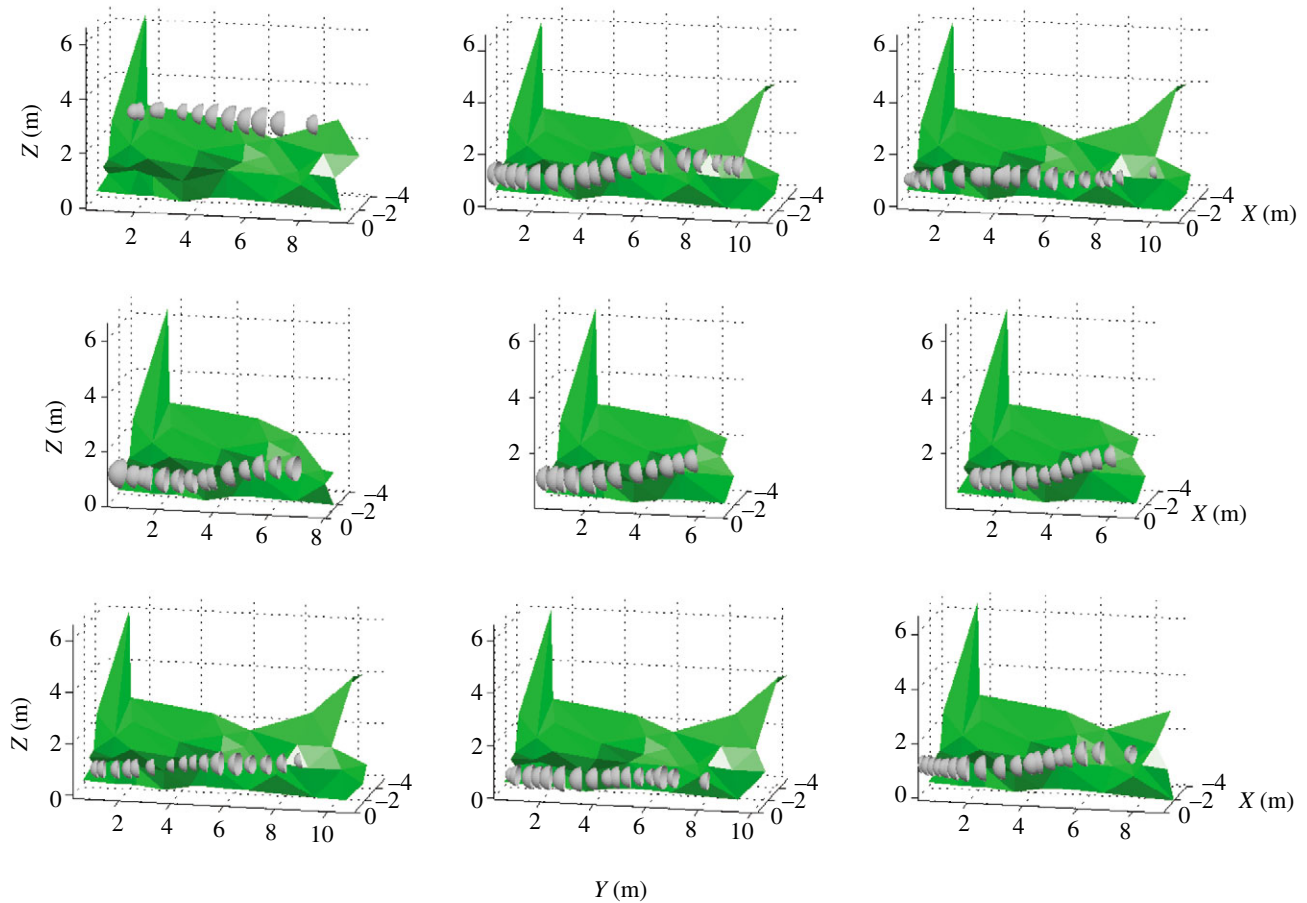


Fig. 5. Signal overlap zone (SOZ) of nine individual bats flying along the hedge. Flight direction from right to left. The first individual in the upper row was the only one not using the corridor below the hedge. Hemispheres indicate the sizes of the SOZ plotted around the position of the bat at the time of each call.

signal design in this situation are in agreement with the predictions of the acoustic focussing theory even in a distance-dependent manner.

To investigate the factors influencing DOF, we related DOF measurements to call duration and bandwidth of the first harmonic, factors which were easy to quantify and which are both predicted to affect Doppler tolerance (Boonman et al., 2003). Together, duration and bandwidth explained 83% of variation in DOF. Duration and bandwidth affected DOF independently, with bandwidth having a greater influence. Longer call durations increased DOF, while increasing bandwidth decreased it (Table 1).

Discussion

In this study, we recorded the flight and echolocation behaviour of free-ranging bats to test two quantitative hypotheses on the perceptual value of echolocation signal design for in-flight close-range orientation. The acoustic task for the bats in this situation is extremely difficult. The hedge will produce many overlapping single leaf echoes from different directions and distances, which first need to be

correctly segregated into single targets. In a second step, these single targets have to be combined into a 3-D representation of the hedges surface, which needs to be reliable enough to plan a safe flight trajectory without risking collisions. The problem is aggravated because bats flew fast and very close to the hedge and covered, on average, about 60 cm between two consecutive calls.

In the natural habitat, higher frequencies in the call attenuate more strongly than lower frequencies, and the echoes heard by the bat will have reduced high-frequency content. In particular, over long transmission distances this might affect ranging performance. However, relevant sound propagation distances in this study were so low (<4 m) that the resulting relative high-frequency loss to the relatively intense echoes returning over such short distances is highly unlikely to affect ranging significantly.

Against the expectations according to our first hypothesis, the pulse duration, i.e. SOZ, was not strictly kept below the instantaneous distance to the hedge, yet there is statistical support for some distance-dependent adjustments. Although pulse-echo overlap was normally avoided, in some cases close to the hedge (19% of all calls) a small amount of overlap did

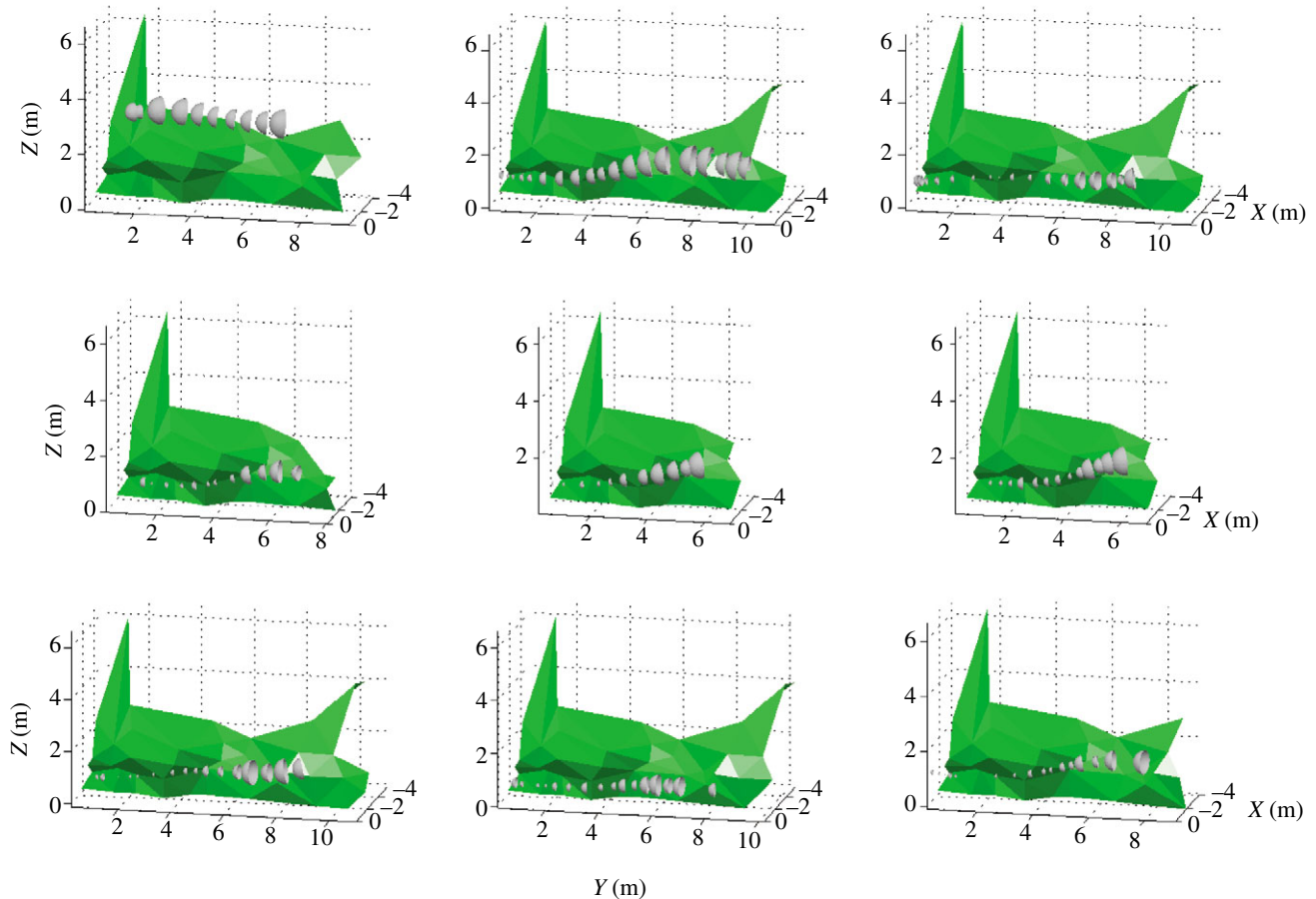


Fig. 6. Distance of focus (DOF) of the same nine individual bats flying along the hedge as in Fig. 5. Flight direction from right to left. The first individual in the upper row was the only one not using the corridor below the hedge. Hemispheres indicate the surface of zero ranging error, i.e. a hemisphere with the DOF as its radius, plotted around the position of the bat at the time of each call.

occur. This might indicate that bats paid less attention to the closest parts of the hedge to their side than to the more distant portions of the hedge in front of them.

However, we found a strong reaction in bandwidth during the final phase of the flight along the hedge. This increase in bandwidth results in a decrease in Doppler ranging errors (Fig. 4D), which is in agreement with our second hypothesis. Thus, call design is such that Doppler ranging errors change in an adaptive manner.

But is the control of Doppler ranging errors the actual perceptual aim of the observed changes in signal design (supporting our third hypothesis), or is it rather a side-effect of

other constraints on echolocation signal design? Evolution has shaped sonar signals such that they are optimally adapted to their specific echolocation task. Signals will thus combine as many informational advantages as possible, which means that benefits other than low Doppler ranging errors are not mutually exclusive alternatives but rather potential additional benefits.

A first additional benefit would be that the observed increase in bandwidth allows for a better temporal, i.e. depth, resolution (ranging acuity). Calls with a larger bandwidth in general have a narrower autocorrelation function and are thus better suited to segregate a rapid sequence of overlapping echoes (e.g. originating from separate leaves of a vegetation

Table 1. *Effects of call duration and bandwidth on distance of focus (DOF)*

Duration (ms)			Bandwidth (kHz)			Overall regression equation
<i>t</i>	<i>P</i>	<i>r</i> ²	<i>t</i>	<i>P</i>	<i>r</i> ²	
10.63	<0.001	30.8	-14.16	<0.001	44.1	DOF=0.689+0.191Dur-0.012BW; $F_{2,253}=600$, $P<0.001$, $r^2=82.6$

Results reported are from multiple regression analyses based on individual calls. Duration (Dur.; ms) was not related to bandwidth (BW; kHz) ($F_{1,254}=2.3$; $P=0.13$), so the actual, rather than residual, bandwidth values were used in the multiple regression analysis.

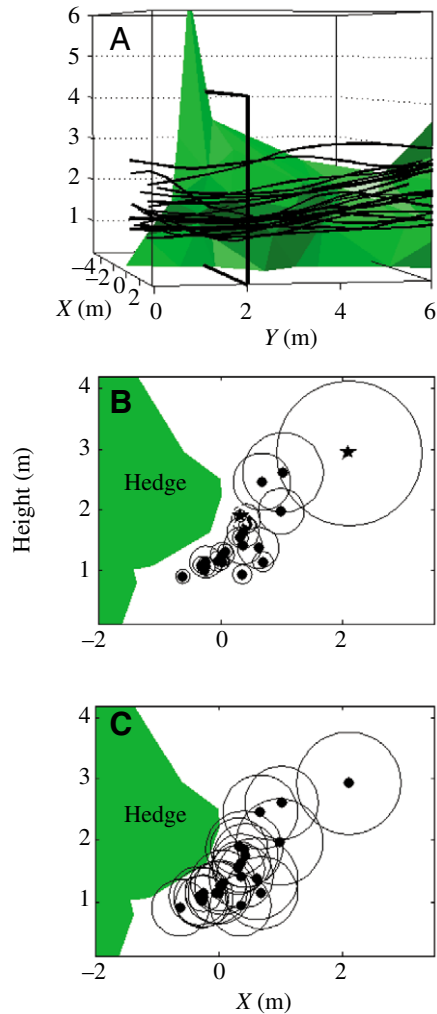


Fig. 7. Distance of focus (DOF) and signal overlap zone (SOZ) in relation to position to the hedge (shaded area). (A) Three-dimensional representation of the flight paths of 22 bats and of the hedge they were flying along. The open rectangle at $Y=2$ m indicates the size and position of the cross section shown in B and C. (B) Cross section through the hedge and flight paths as indicated by the rectangle in A. Symbols show where each individual bat has passed the cross-sectional plane. Circles around symbols have a radius that equals the DOF of the call emitted by the particular bat closest to the cross sectional plane. (C) Same cross-section as in B, with circles indicating the limit of SOZ.

surface) into distinct objects. Such an increased depth resolution would be clearly adaptive in the behavioural context of this study. Yet, with flying bats, one has to take Doppler-shifts of echoes into account. The respective Doppler ranging acuity, measured as the width of the envelope (EW) of the cross correlation function between call and Doppler-shifted echo, reveals that the observed increase in bandwidth does not result in the expected increase in ranging acuity ($EW = -0.077BW + 66.2$; $r^2 = 0.004$, $F = 0.96$, $P = 0.32$, $N = 233$; Fig. 4C,E). This happens because the curvature of the signal is crucially important. Only hyperbolically frequency-

modulated calls have optimal Doppler ranging acuity (see Fig. 2); yet, most calls were far from being hyperbolically frequency modulated, which resulted in a decreased Doppler ranging acuity. We conclude that the aim of the observed increase in bandwidth was not to increase Doppler ranging acuity, i.e. depth resolution.

A second alternative benefit of the observed increase in bandwidth would be a generally improved ability for object localisation and recognition. The basic assumption behind this is that broadband echoes can carry more spectral information conveying spatial and structural details of the target. It is unlikely that altering object recognition ability along the course of the hedge is adaptive; yet increased localisation ability would clearly be. We have shown above that depth resolution, i.e. ranging acuity, does not increase concurrently with the distance-dependent increase in bandwidth. As regards angular resolution, to date we have no means to quantify the potential effect of the observed changes in bandwidth.

One fundamental shortcoming of all these approaches to judge the adaptive value of signal bandwidth is that they only address how bats could benefit from a bandwidth increase. They do not explain why the bats in this study did not use such favourable broadband calls all the time. Inherently, they assume a gradual compromise towards other unknown constraints that would favour narrowband calls in this situation. Another shortcoming is that they only give qualitative trends but do not allow for quantitative predictions. Why do bats use exactly those bandwidths and call durations and not larger or smaller values?

The recently proposed theory of acoustic focussing is superior to the abovementioned approaches in both respects: it can explain the full range of observed bandwidths of itself and it also makes quantitative, falsifiable predictions as to which type of signal is best in which situation. DOF theory predicts that, at the hedge, bats could reduce ranging errors and thus collision risk by using call designs with DOFs adjusted to their instantaneous distance to the hedge.

How big is the advantage achievable by acoustic focusing? Fig. 1 shows in detail the effect of acoustic focusing on the spatial distribution of location errors for three calls uttered at the hedge. Two of these calls are indicated by stars in Fig. 7B. One call was emitted approximately 2.2 m distant from the hedge (Fig. 1C,F,I). The other was produced very close to the hedgerow (approximately 25 cm; Fig. 1A,D,G). The one call used in the vicinity of the hedge (Fig. 1A) has a very short DOF and is hence well suited to provide the bat with highly accurate localisations of the nearby hedge. The call used further away from the hedge (Fig. 1C) also gives adequate location accuracy at the large distance at which it was used. However, close to the hedge, at the place of the first call, this signal design would have resulted in a dangerous range underestimation of several centimetres, particularly in those lateral and frontal directions and distances most relevant for flight path planning. Range overestimations in the centimetre range increase collision risk because bats flew at lateral distances to the hedge not much larger than their wing length.

Indeed, we found that the changes in signal design are quantitatively in agreement with DOF-based predictions: first, absolute values for DOF were in a reasonable range, i.e. between 1 cm and 110 cm. Secondly, almost never did the DOF reach beyond the closest instantaneous distance to the hedge. Lastly, in the final phase, i.e. during flight below the hedge, DOF was adjusted to the distance to the hedge in a distance-dependent manner.

We also found remarkable agreement in absolute values of DOF and SOZ in the initial phase (compare Figs 5 and 6). This means that signal design was such that the first objects outside the SOZ, i.e. without signal echo overlap, were also localised most accurately. The distances of all more distant objects are systematically overestimated, thus the chosen signal design provides the bat with a security margin for flight path planning. This security margin increases with the distance of the objects.

These findings support the idea of acoustic focussing, i.e. that bats use their call design to mutually cancel the two flight-speed-related ranging errors. This strategy frees the bat from the high computational effort to accurately calculate and consider ranging errors caused by its flight speed – by simply knowing which call ‘focuses’ to what distance and (roughly) matching this to the obstacle distances as determined with the previous call, bats can achieve reliable and very accurate ranging results in spite of the inevitable flight-speed-related ranging errors.

These findings are highly relevant for understanding airborne in-flight sonar. Decades after the first hypotheses (Altes and Titlebaum, 1970; Cahlander, 1967; Kroszcynski, 1969; Strother, 1961) about the adaptive value of the details in FM call design, we have a new and powerful quantitative means to interpret why bats use a certain FM call design. The acoustic focusing theory sheds new light on our understanding of FM echolocation and may be used in the design of small autonomously moving vehicles using airborne sonar for orientation (Kuc and Viard, 1991). Our results strongly suggest that FM echolocation has made its own use of Doppler effects, not with extensive morphological adaptations as in constant frequency (CF) echolocation (Metzner et al., 2002; Schnitzler, 1968; Schuller and Pollak, 1979) but in a way that is equally elaborate and creative in terms of information gathering. Further studies will show whether bat species with differing signal designs or bats in other contexts employ acoustic focussing as well.

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