Intensity control during target approach in echolocating bats; stereotypical sensori-motor behaviour in Daubenton's bats, *Myotis daubentonii*

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Summary

When approaching a prey target, bats have been found to decrease the intensity of their emitted echolocation pulses, called intensity compensation. In this paper we examine whether intensity compensation in the echolocation of bats is flexible or stereotyped. We recorded the echolocation calls of Daubenton's bats (*Myotis daubentonii*) while the animals attacked targets of different dimensions. *Myotis daubentonii* reduced the peak sound pressure level emitted by about 4 dB for each halving of distance, irrespective of the target presented (mealworms and two different sizes of spheres). The absolute sound pressure level emitted by the bat is not or only a little affected by target strength. Furthermore, the decrease in emitted intensity over distance shows less scatter than the same intensity over time for the last 20 cm of target approach. The bats matched the emitted intensity to target distance equally well for the spheres (aspect-invariant target strength) as for the mealworms (aspect-dependent echo strength). We therefore conclude that intensity compensation does not rely on feedback information from received intensity, but instead follows a stereotyped pattern.

Key words: echolocation, sonar, compensation, feedback, target strength, Daubenton's bat, *Myotis daubentonii*.

Introduction

When sensory information is used by animals for guiding their movements, coupling between action and perception is probably essential to ensure high accuracy in maintaining a specific trajectory that is followed by the animal (Heisenberg and Wolf, 1988).

Bats are good model systems for studying the interaction between sensory and motor systems because they use echoes from calls generated by their motor systems as sensory information. Bats cannot perceive echo information about their environment without sending motor commands to emit a call. By recording the echolocation calls emitted by the bat, the investigator can monitor precisely when and how bats update their sensory information. Bat echolocation is highly adaptable and is strongly dependent on the surroundings of the bat as well as the task that it faces (Neuweiler, 1990; Fenton, 1995; Schnitzler and Kalko, 2001).

In this paper, the extent to which echolocation behaviour is stereotypical or flexible is assessed in a bat responding to sensory information from a target. Daubenton's bat (*Myotis daubentonii*) hunts in its natural habitat for small insects by trawling and aerial hawking (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Vaughan, 1997). Because of the agility of its natural prey, *Myotis daubentonii* must have a short response time, but to catch its prey also requires good accuracy. Here we have studied the adaptation of signal intensity in echolocation behaviour during prey capture.

Technical difficulties mean that the reduction of emitted signal intensity in bats during target approach (intensity compensation) has only been studied in three species: *Pteronotus parnellii*, *Noctilio leporinus* and *Eptesicus fuscus* (Kobler et al., 1985; Hartley et al., 1989; Hartley, 1992b). None of these studies tested the flexibility of the bat to adjust absolute emitted signal intensity, according to target size.

We assessed the flexibility of intensity compensation in *Myotis daubentonii* by offering the animals three target types (small sphere, big sphere or mealworm) that differed in dimensions and thus target strength. Our goal was to determine whether intensity compensation is independent of target type, or is tightly coupled to sensory input. Our hypothesis was that the intensity emitted by the bat becomes higher at small (weakly reflecting) targets, and lower at big (strongly reflecting) targets.

We also tried to determine whether emitted intensity of echolocation is under closed-loop or open-loop (with no, or little, sensory feedback) control. In greater horseshoe bats *Rhinolophus ferrumequinum*, accuracy in emitted frequency to

compensate for Doppler effect, matching a simulated target speed, depends on how well the bat can hear the echo-frequency while emitting the same pulse (Schuller, 1977). Greater overlap of the echo with the emission means a higher degree of feedback, and greater accuracy in compensating the emitted frequency for Doppler shift in the echo. This type of echolocation is therefore under closed-loop, sensorimotor control, because its motor production relies on sensory feedback.

In our experiments we assessed the degree of feedback control by measuring the flexibility in intensity compensation with changing sensory information. Our hypothesis was that if the intensity pattern is variable, the bats should show a reduced variability when plotted against distance as opposed to time. A corroboration of this hypothesis means that the pattern of intensity compensation is not a fixed motor programme, but relies on feedback of sensory information, and is therefore flexible.

We measured the differences in emitted intensity *between* attacks on targets with different reflective properties. Then we tried to find evidence that emitted intensity is controlled by feedback of sensory information (echoes) from the target, during (*within*) target approach. Answers to these questions will reveal more about the role of intensity perception in guiding the approach flight of echolocating bats.

Materials and methods

Experimental procedure

Four individual *Myotis daubentonii* Kuhl 1817, caught and kept under license from English Nature, were trained to approach a mealworm on a string and capture it directly, without first flying around the prey. After each bat had learned this task, it was released in a flight room (1.85 m×1.86 m×6.12 m), where it was trained to capture the mealworm prey and eat it while hanging on a wall on the far end of the room. After 3–4 test flights we started to collect data. We presented three

target types, a 9.5 mm diameter sphere, a 3 mm diameter sphere, or a mealworm, in random order to each bat on a 0.08 mm diameter string. Spheres were chosen because of their aspect-invariant target strength, whereas the mealworm has an aspect-dependent echo-strength. The two sizes of spheres reflected targets of differing target strengths (see below).

We recorded the attack sequences of each bat until it had learned to reject the non-mealworm targets. To eliminate the use of vision by the bats (Hope and Bhatnagar, 1979), we used a custom-made red filter (<10% transmission at <624 nm) to reduce the ambient light to a maximum level at the prey of 6.02×10^{17} photons m^{-2} s^{-1}.

Sphere target strengths

The frequency of echolocation pulses was between 20–100 kHz (Fig. 1). The 3 mm sphere is therefore in the Rayleigh scattering region, meaning that the reflection strength is strongly frequency-dependent. The 9.5 mm sphere is partly in the region of geometric scattering where reflection strength depends little on frequency (Stanton, 1990). To calculate the absolute pressure of the echoes received by the bat, we first calculated the target strength (*TS*) of the two spheres, assuming
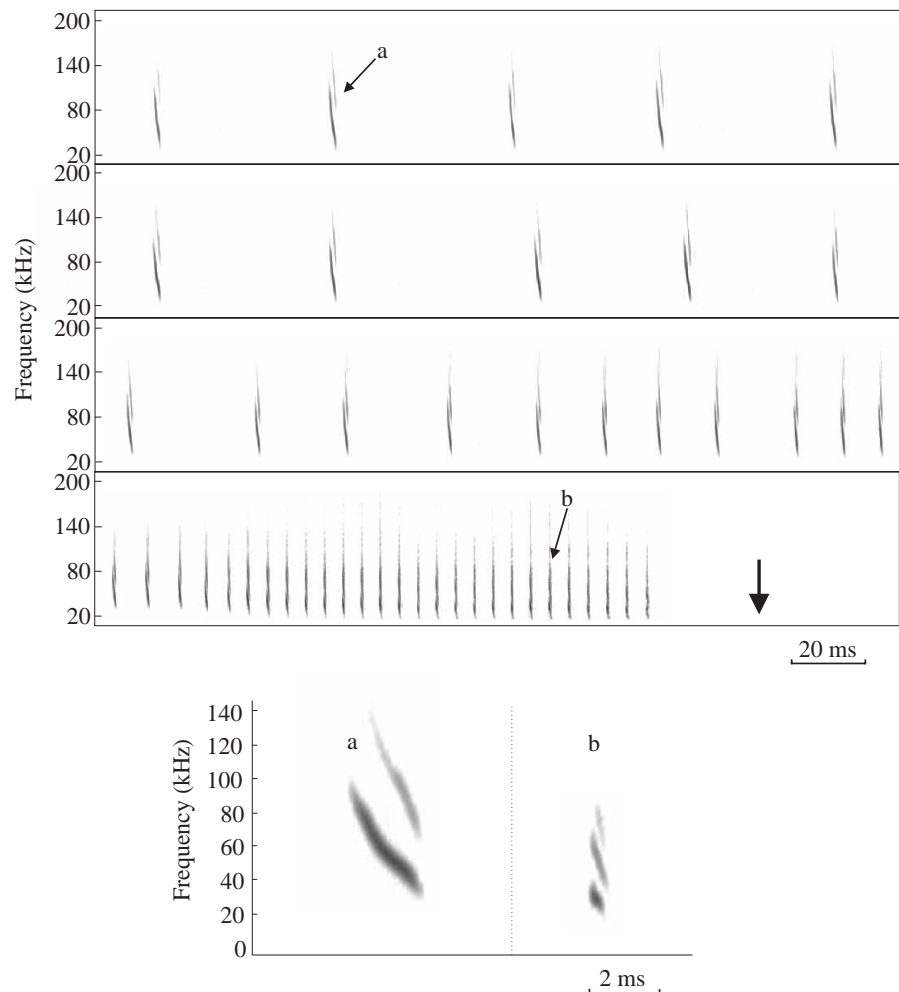

Fig. 1. A sonagram of calls emitted by a Daubenton's bat attacking a target. The vertical arrow indicates the time at which the bat first hits the target. The lower panel shows an enlargement of pulses 'a' and 'b', representing a pulse emitted far away (±1.5 m) and near (±0.1 m), respectively, from the target. The consecutive panels show that the pulse repetition rate is increased during the approach, whereas the bandwidth of the first harmonic is decreased during the final stage of target approach. At this stage, energy in higher (>3rd) harmonics can be visible when the bat is recorded at a close distance (upper panel).

both to lie in the region of geometric scattering, from Urick (1983):

$$TS = 20\log_{10}\left(\frac{1.0936a}{2}\right), \qquad (1)$$

where *a* is the radius of the sphere in metres, and 1.0936 is the conversion factor from yards to meters. The target strength (*TS*) is defined as the ratio of the incident energy to reflected energy at a distance of 1 m from the target (Au, 1993). Target strength should be –45.7 dB at 1 m from the target for the 9.5 mm sphere and –55.7 dB at 1 m from the target for the 3 mm sphere, if both are ensonified with a frequency such that $ka \geq 1$ (where k=frequency/c, and c is speed of sound in air, 343 m s^{-1}). Both target strengths are the maximum respective values attainable with the spheres. In reality, however, because the frequencies in the first harmonic of the echolocation calls of Daubenton's bats are <114 kHz (Fig. 1) (ka=1 for the small sphere), the assumption of $ka \geq 1$ does not hold for the 3 mm sphere. Additional frequency-dependent filtering for the small sphere was modelled to approximate loss 10 dB per halving of frequency, based on data provided by Stanton (1990), and used subsequently as coefficients in a 70th order FIR (Finite-duration Impulse Response) filter, implemented as a Matlab (The Mathworks Inc., Natick, MA, USA) script. Mealworm reflection characteristics were modelled as for the big sphere, on the basis that the predicted target strength of the 9.5 mm sphere (–45.7 dB) is similar to the measured target strength of a mealworm (–46.3 dB) (Siemers et al., 2001).

Experimental setup

During each attack by the bat on a target, we recorded the emitted echolocation calls while using multiple-flash stereo photogrammetry (Rayner and Aldridge, 1985; Norman et al., 1998) to register the bat's positions over the duration of the attack. This technique allowed a detailed reconstruction of the bat's flight path by inferring depth from the disparity between two photographs, taken from two parallel camera positions 0.249 m apart, enabling a reconstruction of the *x, y* and *z* coordinates of a bat in real space (Rayner and Aldridge, 1985). During the bat's approach to the target, eight flashes, each of 250 μs, were fired at a rate of 15 Hz. Two Nikon FM2 cameras with opened shutters, f-stop 16, 55 mm lenses, and loaded with ISO 400 film, recorded the bat's position at each flash, while at the occurrence of each flash a spike was recorded on a second channel of a Racal 4DS instrumentation recorder, along with the received echolocation calls.

Using a magnifier, the film was later projected onto a sheet of A4 paper on which was marked the bat's head. Images were subsequently digitised on a SummaSketch III (Summagraphics) digitising tablet. The *x, y* and *z* coordinates of the bat's head at each position and the target were calculated using a custom-made programme written by J. M. V. Rayner. The bats' trajectory was between 1.20 and 2 m in front of each camera. At 1.55 m from the plane of the cameras,

a cube with a mean side length of 14.92±0.18 cm could be reconstructed from stereo-pairs to have a side length of 14.67±0.13 cm (*N*=12 sides). The accuracy and rationale of the photogrammetry, resection and differentiation algorithms are discussed in detail by Spedding et al. (1984) and Rayner and Aldridge (1985).

From the coordinates of the bat's consecutive positions we calculated the bat's speed relative to the microphone, using a Matlab routine. We used the flight speed data to align the sequence of pulses correctly with the flash spikes (see below).

When to open the shutters of the two cameras and trigger the flashguns was determined visually, helped by using a bat detector (Batbox III, Stag Electronics) set to a quiet level, to determine when the bat had taken off.

During the bat's approach to the target, we recorded the emitted echolocation calls by using a Larson Davis 2520, 1/4 inch microphone, with the grid (7 mm diameter) on, positioned 0.60 m behind the target, suspended on a thin string. Without the grid, the frequency response of the microphone was ±2 dB at 1–100 kHz. The difference in frequency response over the relevant frequency range with the grid on was measured and compensated for using an FIR filter in Matlab. The placement of the grid protected the delicate membrane as the bats frequently collided with the microphone. The microphone type was chosen and positioned to introduce as little clutter as possible behind the target while keeping directional sensitivity low.

The directionality of a comparable microphone (1/4 inch; Brüel & Kjær) with grid is still very broad at 80 kHz (–6 dB beamwidth of 110°). Flying Daubenton's bats also show a low directionality (–6dB beamwidth of 72–80°, ±40 kHz) in the emission pattern of echolocation calls (Holderied, 2001), so neither position, flight direction nor head-aim of the bat should strongly influence the intensity measurements in our experiment.

The microphone signal was amplified using a Larson Davis 2200C amplifier and fed to a Racal 4DS Instrumentation recorder, operating at a tape speed of 0.762 m s^{-1}. Before each session the system was calibrated using a constant test tone of 1 kHz at 114 dB sound pressure level (SPL), produced by a Dawe Instruments D-1411E calibrator. All bat calls recorded subsequently were related to the measured voltage, resulting from the test tone. For analysis, the tape was replayed at a speed 16 times slower than the recording speed, while the sequence of interest was digitised at a rate of 50 kHz and a bit-depth of 12 bits, using a National Instruments BNC 2110 soundcard. The effective sampling frequency was therefore 800 kHz. Two separate sequences belonging to a single attack, one consisting of the pulses emitted by the bat, and the other consisting of spikes denoting the occurrence of each flash, were stored as data files. All further analysis was performed by using Matlab v5.3, with Signal Processing, Data Acquisition and Statistics Toolboxes.

Reconstruction of pulse parameters

Each pulse arriving at the microphone was reduced in

intensity because of spherical spreading and atmospheric attenuation, and Doppler-compressed at emission due to the bat's flight speed. Moreover, each pulse registered at the tape was recorded later than it was produced, because of the travelling time from bat to microphone, which in turn depended on the distance from the microphone when the pulse was emitted.

The SPL at emission, at the target and at reception was reconstructed for a point 10 cm in front of the bat's mouth by applying the laws of spherical spreading, using frequency-dependent filtering to mimic the effects of atmospheric attenuation (Bazley, 1976).

The SPL peak (in dB) was defined as the maximum voltage (not peak to peak) of the reconstructed pulse relative to the reference voltage, as in:

$$SPL_{peak} = 114 + 20\log(V_{peak}/V_{ref}) . \qquad (2)$$

The reference voltage (V_{ref}) is the voltage measured when the calibration tone of 114 dB SPL was recorded with the microphone. To calculate the SPL_{rms}, the root mean square (rms) voltage at each position was calculated as:

$$V_{rms} = \sqrt{\frac{1}{T} \int_0^T V^2(t)\mathrm{d}t} , \qquad (3)$$

in which T denotes pulse duration, measured as the −42 dB duration of each pulse as emitted by the bat. SPL_{rms} was calculated as SPL_{peak}, where V_{peak} was replaced by V_{rms} in Equation 3.

The Doppler compression of the pulses received by the microphone was corrected by Doppler expanding the sequence of received echoes by a factor: $c/(c–v)$, where v is the speed of the bat (m s^{-1}). In the Doppler expansion, v was varied over the sequence, depending on the linearly interpolated bat's flight speed, which was obtained by means of multiple-flash stereo photogrammetry (see above). The technique used in Doppler-expanding the echo sequence can be compared with resampling the data at a sampling rate dependent on the bat's flight speed, but below the original sampling rate. The Doppler expansion of the sound sequence corrects the compression of the intervals between, and of the pulses themselves.

Because the x-axis of the sound sequence is scaled in time and not in delay units, the Doppler expansion does not correct the distance flown by the bat between pulse emission and reception by the microphone. The positional coordinates obtained with the photogrammetry programme are the coordinates of the bat, after having flown over a distance corresponding to the time it took for the pulse to arrive at the microphone. The further the bat is from the microphone, the longer it takes for the emitted pulse to reach the microphone and the longer the distance flown by the bat. The resulting error depends on distance and flight speed. The coordinates of the bat at pulse emission were recovered by Doppler-expanding the bat's distance to the microphone according to: $D_{emission}=D_{reception}c/(c–v)$, where $D_{emission}$ is distance to microphone at emission and $D_{reception}$ is distance to

microphone at reception. This Doppler expansion was applied as a time shift: $[D_{reception}/(c–v)]–(D_{reception}/c)$, to each pulse in the sequence.

The latter Doppler expansion is independent of the expansion of the intervals between the pulses and of the pulses themselves, which is unrelated to microphone distance. With both corrective measures taken to align the sequence of pulses and the sequence of spikes, each representing a 'flash' and its resulting spatial coordinates of the bat, the distance from bat to target is known from the moment at which the bat starts to emit a pulse.

We used a linear interpolation to estimate the distance between bat and target at each sample point. A more formal mathematical description of the methods used in reconstructing the emitted pulse at the distance of emission can be found in Hartley et al. (1989).

Statistical analysis was performed with Systat 10 (Systat, Chicago, Illinois, USA).

Results

Intensity compensation behaviour

All four bats attacked all of the presented targets, apparently mistaking the spheres, which they frequently tried to bite, for prey items. On the first day of the experiment, some bats seemed to be scared by the flashes. We therefore offered mealworms only and triggered the flashes after the bat had committed itself to an attack. As soon as the bats had learned that most attacks led to capturing a mealworm, their behaviour appeared to be like capturing prey in the wild. After 3–4 days, each with 15–30 attacks, the bats gradually started to reject the small sphere, but by then we had usually obtained an adequate dataset.

Echolocation calls emitted by the bats 2–0.5 m from the target consisted of a first harmonic sweeping from 100 kHz to 32 kHz in 1.5–2 ms (Fig. 1). Because of the indoor conditions, the lowest frequency may have been slightly higher, and the pulse duration shorter far away from the target, than in outdoor conditions (Kalko and Schnitzler, 1989). But echolocation behaviour 0–1 m from the target showed no differences from echolocation behaviour in the wild (Kalko and Schnitzler, 1989).

The four bats reduced the emitted intensity of their calls by 2.7–5.8 dB per halving of bat-to-target distance (Table 1). On average, the peak SPL was reduced by 3.9 dB and the rms SPL by 5.2 dB, per halving of target distance. For comparison with previous studies the intensity compensation behaviour was quantified from 0 to 70 cm from the target, using a logarithmic model. In all individuals, the main portion of the intensity reduction (±15 dB) took place between 0 and 30 cm from the target, showing a fairly linear decrease with distance (e.g. Fig. 3).

Intensity compensation occurred with all three target types. Disregarding atmospheric attenuation, the increase in peak and rms SPL received by the bat while halving its distance to the target could be calculated by subtracting the peak or rms SPL

Table 1. *The intensity compensation in four individual Daubenton's bats, expressed as peak and rms SPL (dB decrease per halving of distance from bat to target), for three different target types*

Individual	Target	Peak SPL	rms SPL	Number of flights	Number of calls
1	Small sphere	3.9	5.4	6	203
1	Big sphere	4.0	5.5	2	67
1	Mealworm	4.4	5.8	5	185
2	Small sphere	4.6	5.4	3	113
2	Big sphere	3.9	4.8	6	222
2	Mealworm	4.0	5.0	7	253
3	Small sphere	3.7	5.7	5	172
3	Big sphere	2.7	4.6	3	99
3	Mealworm	3.5	5.3	7	232
4	Small sphere	4.1	4.6	2	58
4	Big sphere	4.6	5.5	2	63
4	Mealworm	3.8	5.2	2	73
Total		3.9	5.2	50	1740
S.D.		0.5	0.4		

SPL, sound pressure level; rms, root mean square.

Each of the figures under 'peak' and 'rms' is the regression coefficient of the function describing the best fit to the intensities emitted during a specific number of flights, totalling a specific number of calls.

values listed in Table 1 from 12 dB. This means that, on average, the peak SPL in the bat's ears when approaching the target increased by 8.1 dB per halving of distance and rms SPL by 6.8 dB per halving of distance. Calculated received SPLs, which include the effects of atmospheric attenuation, showed an average increase per halving of distance of 8.4 dB for peak and 7 dB for rms SPL.

Compensation of absolute intensity

When the 9.5 mm sphere was replaced by the 3 mm sphere (Table 2), three bats increased the intensity (over all distances) of their emissions by only 4 dB.

The values displayed in Tables 2 and 3 are the constant terms of the $\log_2$ function describing the intensity

compensation between 0 and 70 cm from bat to target, which serve well for mutual comparisons.

Fig. 2 shows the actual emitted and received peak SPLs by bat 1 at different distances from the target, with a slope of –6.9 dB per doubling of distance and an intercept for peak SPL of 41.7 dB. Table 3 shows that despite the small compensation in overall intensity, the echoes returning from the small sphere are still 17–18 dB weaker than the echoes returning from the big sphere at any distance. The bats therefore lower their emitted intensity over time to reduce the increase in received intensity from 12 dB to 7–8 dB per halving of distance, but they fail to alter the emitted intensity to compensate for a lowered target strength, even when the target strength is lowered by at least 17 dB.

Control of emitted intensity during target approach

On average, bats first reduced the intensity of their echolocation calls at 0.54±0.22 m (mean ± S.D.). This distance was measured as the breakpoint between a logarithmic slope and a constant ceiling, obtained with a piecewise nonlinear regression analysis, calculated per individual. The compensation distance did not differ between peak and rms SPL (ANOVA, $F_{1,22}=0.973$, $P=0.335$), but differed significantly between individuals, thus: 0.79 m, 0.63 m, 0.43 m and 0.30 m (ANOVA, $F_{3,20}=27.157$, $P<0.001$). Target type had no influence on the distance at which the bat started to decrease emitted intensity (ANOVA, $F_{2,21}=0.321$, $P=0.729$). The distance at which intensity was first reduced is therefore independent of the intensity received by the bat. Thus, the distance at which intensity was first reduced (0.54 m; minimum echo intensity, 30 dB at peak SPL) appears to be a reaction- rather than a detection-distance.

The hypothesis that emitted intensity is under closed-loop control from sensory information acquired during target approach predicts that changes in the execution of motor commands (intensity over time) should match the bat's consecutive positions relative to the target (intensity over distance). In other words, if feedback is used, emitted intensity over time should show more variability than the same intensity values plotted against distance. This is logical because a bat having access to information about its present distance to a

Table 2. *The constant term (rms and peak SPL) of the logarithmic function describing the intensity compensation between 0 and 0.70 m from the target as three target types are approached by the bat*

		rms SPL			Peak SPL		
	Individual	Small sphere	Big sphere	Mealworm	Small sphere	Big sphere	Mealworm
	1	104.5	100.4	102.9	108.1	104.0	106.6
	2	106.8	102.5	104.1	111.8	107.3	108.6
	3	103.1	99.8	102.5	106.3	102.9	105.6
	4	103.9	103.7	102.2	109.6	108.9	105.8
	Mean	104.6	101.6	102.9	109.0	105.8	106.7

SPL, sound pressure level; rms, root mean square.

Note that the absolute pressure emitted by the bat depends very little (maximum difference 4 dB), if at all, on the target that was intercepted.

Table 3. *The same function constants as in Table 2, but now representing rms and peak SPL received by the bat, corrected for geometric spreading, atmospheric attenuation and target reflection characteristics*

	rms SPL			Peak SPL		
Individual	Small sphere	Big sphere	Mealworm	Small sphere	Big sphere	Mealworm
1	18.0	34.7	36.4	21.6	41.7	40.1
2	20.2	36.0	37.5	25.2	40.7	42.0
3	16.5	33.2	36.0	19.7	36.3	39.1
4	17.2	37.1	35.5	23.0	42.3	39.2
Mean	18.0	35.2	36.3	22.4	40.3	40.1

SPL, sound pressure level; rms, root mean square.
The differences in emitted intensity between the different targets displayed in Table 2 were taken into account.
Throughout prey capture, the echoes from the small sphere are 17–18 dB weaker than the echoes from the big sphere and mealworm.
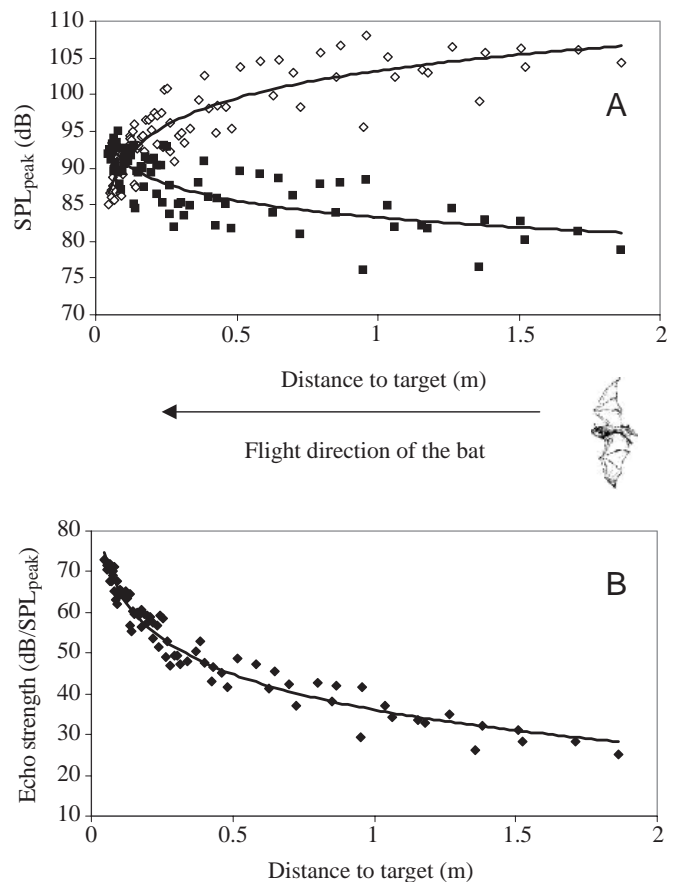
target can adjust the emitted intensity better relative to the target than a bat lacking any updates on its position. For each target type and individual bat (N=12) we found that the fit of the regression line describing the decrease of intensity over the last 0.20 m to the target had mean squares residuals of 9.3 when plotted against distance and 12.6 when plotted over time. This difference is significant when tested in an ANOVA, as repeated measures within individual bats (ANOVA, $F_{1,8}$=8.448, P<0.05) and within target type (ANOVA, $F_{1,9}$=6.306, P<0.05). The mean-squares residuals were not different between individuals (ANOVA, $F_{3,8}$=1.201, P=0.370) or target type (ANOVA, $F_{2,9}$=1.429, P=0.289).

From the difference in the mean squares residuals between the data plotted against distance and against time, we conclude that the emitted intensity by bats shows less variability over distance than over time (see bat 4 in Fig. 3). The two attack sequences on a small sphere are not typical of all attacks, but illustrate the hypothesis that bats use received sensory information to 'scale' emitted intensity to target distance.

Since the reduction in variability of intensity over distance, relative to the same intensity over time, was not apparent in all attacks, the problem was assessed in a different way. Flights with extreme rates of intensity reduction over time should result in less extreme rates of intensity reduction over distance. 13 of 50 flights showed extreme intensity reduction rates over time, so we plotted them against the reduction rates over distance of the same flights as y-values. If the bat adjusted its emitted intensity over time to its distance to the target, a slope in intensity reduction that deviates strongly from the average slope (5.2 dB rms SPL per halving of distance) over time, should be closer to the average slope when plotted against distance.

Plotting the two rates of the 13 flights against each other resulted in a best fit of 'distance' rate (dB m^{-1}) = 0.914 × 'time' rate (dB s^{-1}) + 10.9. Both rates are expressed as the percentage deviation from the average rate of reduction over distance and time, respectively. The fitted regression line shows that deviation from the average fit along distance is 91.4% as high as the deviation from the average fit along time. This means a reduction of 8.6% in the variability of the slope around the average intensity reduction of the same data when plotted against distance, instead of time.

Fig. 2. The intensity compensation behaviour of bat 1 while approaching the big sphere. (A) Emitted sound pressure level (SPL) per halving of distance is reduced by 4 dB (open diamonds); SPL incident on the target increases by 2.0 dB per halving of distance (filled squares). (B) Received SPL per halving of distance increases by 7 dB. The function of received SPL between 0 and 70 cm from target is given by: SPL$_{peak}$=–6.9×log$_2$(d)+41.73, where d = distance (in m).
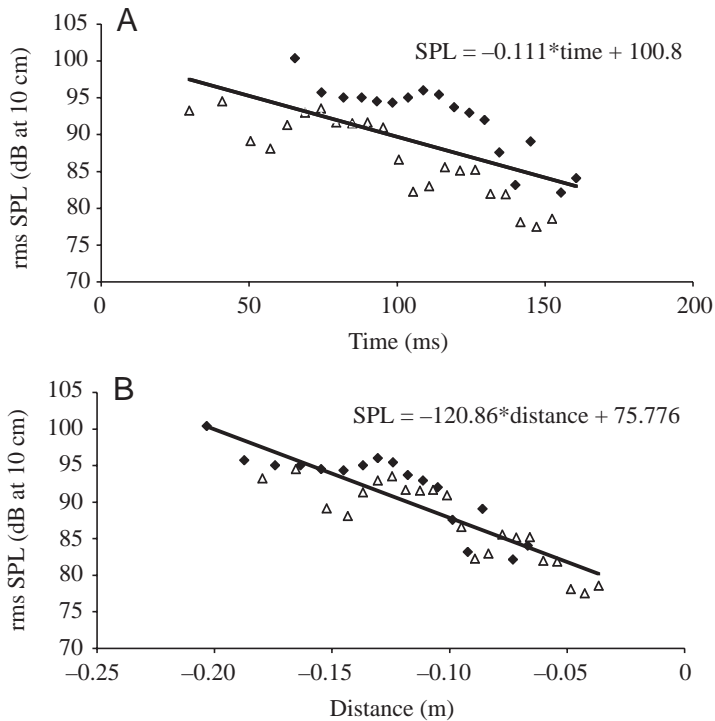
Fig. 3. The emitted intensity (rms SPL at 10 cm) by bat individual 4 while attacking the small sphere, measured over two flights, indicated by diamonds and triangles. During the approach the bat reduces intensity over time in a seemingly disorganised fashion (A). However, when plotted against distance between bat and target (B), the same emitted intensities appear to fit the distance to the target with much less variation around the best-fitting regression line. Not all individuals showed a clear decrease in variability in intensity reduction over distance compared with the intensity reduction over time. (A) r^2=0.4129, $F_{1,37}$=25.023, P<0.001. (B) r^2=0.7738, $F_{1,37}$=117.22, P<0.001.

Discussion

Flexibility in emitted intensity

We found that target strength did not influence emitted intensity in *Myotis daubentonii*. Furthermore, if sensory information is used to 'scale' emitted intensity, this scaling leads to an improvement of only 8.6% from random (distance-independent) variation in emitted intensity.

The absolute intensity emitted by *Myotis daubentonii* when flying 1 m from the target in this study is equal to the intensity emitted by other *Myotis* bats while flying indoors, but measured by using a different method (Waters and Jones, 1995). However, the measured absolute intensity of 103–105 dB rms SPL (at 10 cm from the mouth), referred to above, is somewhat lower than the intensity used by *Myotis daubentonii* while flying outdoors (103–113 dB rms SPL; Rydell et al., 1999). Measured from a distance of 70 cm to the target (to allow direct comparison with previous studies), the emitted peak SPL is reduced by about 4 dB per halving of distance, and the rms SPL by about 5 dB per halving of distance. It is not surprising that the intensity compensation expressed as rms SPL is higher than when expressed as peak

SPL, since the peak of the emitted waveforms is expected to increase with decreasing pulse duration, close to the target.

A surprising result of this study, however, is that the target strength does not influence the emitted intensity by the bat. Table 2 shows that the emitted absolute intensity by the bat remained the same, even when the target strength was reduced by 17–18 dB. Weak echoes, do not apparently trigger the bat to call louder when approaching a target. The distance at which the bats started to reduce emitted intensity was also independent of echo strength, since it was independent of target type. One explanation is that the bats either waited for a preferred distance after the detection of the target to start intensity compensation, or they started to compensate intensity according to an expectation of the target's position. In either case, the received absolute intensity would have no influence on the initiation of intensity reduction by the bat.

The intensity compensation during target approach also stayed the same (4–5 dB per halving of distance) for each target type, as would be expected, as spreading losses will be similar between targets. Intensity compensation in *Myotis daubentonii* therefore appears to be a stereotyped behaviour, since the emitted absolute intensity is not related to the size of objects in the bat's environment.

The values of intensity compensation found in this study are somewhat lower than those found in previous studies, which reported a decrease in emitted peak SPL of 6 dB per halving of distance in both *Noctilio leporinus* and *Eptesicus fuscus* (Hartley et al., 1989; Hartley, 1992b). In our experiments, we took care to introduce as little background clutter as possible, using a small microphone positioned 0.60 m behind the target, whereas in the study by Hartley et al. (1989), a radar apparatus was positioned 0.28 m behind the target. However, if the bats in the study by Hartley et al. also compensated their emitted intensity for the echoes reflecting off the radar apparatus, whereas the bats in this study only compensated for the target, we would expect our bats to compensate more strongly than the bats in the study by Hartley et al. (1989). In fact, the opposite trend was found. We therefore assume that the difference in magnitude of the intensity compensation between the bats in this study and those in Hartley's study truly reflects a behavioural difference between the different species used in the two studies.

Feedback

One of the main questions we sought to answer is whether intensity compensation in bats is a fixed, pre-programmed behaviour, or whether emitted intensity is precisely adjusted to the sensory conditions at any instant. The results in this paper show that any possible information that a bat receives about the reflection strength of a target is not relayed to adjust the intensity of its emissions, indicating a lack of feedback. Our first hypothesis, stating that the intensity emitted by the bat

becomes higher at weakly reflecting targets, and lower at strongly reflecting targets, is therefore rejected. Changing echo intensity information of a target *between* attacks is not used by the bat to adjust its emitted call intensity.

This study also tests the hypothesis that a bat uses feedback information from target intensity or distance to adjust emitted intensity over time *within* target approach. If a bat adjusted the emitted intensity over time to its changing distance from a target, a plot of intensity reduction over time may look chaotic, but the same pattern should precisely fit a specific decrease of emitted intensity along distance. However, if the emitted intensity pattern is a fixed behaviour, independent of sensory feedback, the fit of the decreasing intensity should be equally tight whether plotted against time or distance. Our results do show a better fit in the regression line between intensity against distance than against time, over the last 20 cm of target approach. However, the differences in variability between time and distance were often small and could have been caused by a more non-linear relationship with intensity over time than over distance. Fig. 4 shows that, also in terms of slope, a deviant rate (from the average rate) of intensity compensation against time is only slightly less deviant (9 %) when expressed as intensity compensation against distance.

The data therefore provide some evidence that the emitted intensity could be fine-tuned to fit the target distance by using sensory feedback during target approach. However, the improvements achieved by controlling emitted intensity to match target distance are marginal, and the variation in emitted intensity during each flight appears considerable. A reason for this could be the bat's wing movements, which may influence the intensity produced during the last 20 cm of target approach caused by the physiological coupling of wing beats with pulse emission (for a review, see Wong and Waters, 2001). Because of the inaccuracy of intensity compensation, it seems unlikely that the bat uses feedback information from each target echo to control each subsequent emission. Furthermore, the fact that the bat achieves similar accuracy in intensity compensation for mealworm targets as for the spheres shows that feedback information, at least on reflected intensity, is unlikely to be used. This is because mealworms, as opposed to spheres, have a strong aspect-dependent target strength that will introduce extra variability in returned intensity on top of the received intensity, depending on distance.

In conclusion, most of the variation found in intensity compensation seems to be present without any apparent reason. It could be caused partly by the changing head aim of the bat, or by its wing beats influencing emitted intensity. We found no conclusive evidence in this study that emitted intensity during target approach by echolocating bats is not a fixed, pre-programmed behaviour.

Reasons for intensity compensation

During pulse emission, some bats contract the middle ear muscle in the ear to attenuate the sensitivity of the ear (Henson, 1965; Suga and Jen, 1975). The sensitivity of the
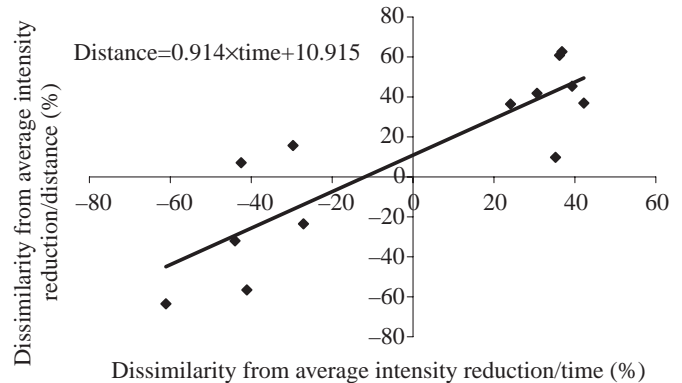

Fig. 4. Intensity reduction is more dissimilar from the average intensity reduction when plotted against time, than against distance. Equal dissimilarity would result in a slope of 1. Dissimilarity from average intensity reduction over time (*x*-axis) is plotted against dissimilarity from average intensity reduction over distance (*y*-axis), and the units of both are % dissimilarity from slope of the average linear regression line of reduction against time and distance, respectively.

hearing system is quickly regained after emission at a certain rate. This system is called automatic gain control (AGC). The attenuation applied by AGC is necessary to protect the hearing system from over-stimulation due to loud sound SPL levels during the emission. Suga and Jen (1975) found that this contraction leads to a maximum attenuation of 20–30 dB, with the middle ear muscle starting to relax after pulse emission. The relaxation period during which sensitivity of the hearing system returns to normal lasts for approximately 5 ms. This means that when the echo returns within 5 ms after the emission (distance to target <0.86 m), the echo will be attenuated, depending on its delay. Kick and Simmons (1984) and Simmons et al. (1992) measured the increase in hearing sensitivity per doubling of distance (or delay) in *Eptesicus fuscus* to be 11–12 dB. However, Hartley (1992a) found AGC to result in an increase in hearing sensitivity of 6–7 dB per doubling of target distance in both *Eptesicus fuscus* and *Noctilio leporinus*.

Hartley (1992b) suggested that the phenomenon of intensity reduction may serve to make a bat perceive each echo during target approach as equally loud. If the 11–12 dB recovery rate of the AGC system in *Eptesicus fuscus* reported by Simmons et al. (1992) is correct, the bat should reduce emitted intensity during target approach by 0–1 dB per halving of distance. Hartley's (1992a) data suggest a reduction of 5–6 dB per halving of distance, which he reported behaviourally (Hartley 1992b). Patheiger (1998) found a recovery slope of the AGC system of 3.6–5.7 dB per doubling of distance around 0.90 m from the target and 7–7.3 dB per doubling of distance around 0.60 m from the target in *Eptesicus fuscus*, indicating that the increase in sensitivity depends on the distance to the target, with the quickest recovery at a close distance to the target. If Patheiger's data are also valid for Daubenton's bat, the combined effects of AGC and the measured intensity

compensation of 4 dB per halving of distance would lead to a constant sensation level of all received echoes during target approach.

An important question is why bats would need to have a constant sensation level to all returning echoes. At present, we are unable to answer this question. This paper only provides evidence to disregard the importance of a constant cochlear stimulation level as a possible reason for bats to exhibit intensity compensation. In our study, differences in the reflected absolute intensity received from different target types only had a marginal (maximum 4 dB) influence on the emitted absolute intensity (Table 2). At the same time, the bats would steer themselves to any of the targets in the same way and capture them equally well. These results show that Daubenton's bats can process echoes over a dynamic range of at least 35 dB. This figure is derived from a conservative estimate of the weakest echoes the bat can detect from the small sphere, 30 dB at peak SPL at 54 cm (the average reaction distance; see Results) from the target, and the average intensity it will receive from the big sphere at 10 cm (65 dB at peak SPL). A cochlear dynamic range of at least 35 dB would certainly be typical of mammals, whose hearing systems are mostly sensitive from 0–10 dB SPL to more than 60 dB SPL (>50 dB dynamic range) (Fay, 1994). Most of the investigated bats respond to acoustic stimuli between 0 and at least 70 dB SPL (Moss and Schnitzler, 1995). Therefore, we conclude that the hearing system of bats should be able to process all returning echoes, even without the bat performing any intensity compensation. Our conclusion is therefore that Daubenton's bats hardly adjust emitted intensity to target strength, but do reduce intensity when approaching a target for reasons other than optimising the stimulation level of the cochlea.

Conclusions

We found no strong indications that echolocating *Myotis daubentonii* adjust emitted intensity continuously to the changing sensory information during target approach. Presentation of targets with different target strengths between trials did not significantly affect the emitted intensity. Our data suggest that intensity compensation may be a fixed, open-loop behaviour under little or no control once initiated. Thus, during target approach, *Myotis daubentonii* will be unlikely to use received intensity as an important guiding parameter to control its flight because it is quite variable, and based on a fixed programme, rather than a physical parameter changing instantaneously with the bat's movements. Our results have important consequences for treating intensity as a possible 'acoustic flow' parameter in studies of acoustic scene analysis in bats (Lee et al., 1992; Müller and Schnitzler, 1999; Moss and Surlykke, 2001).

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