

THE SYNCHRONISATION OF SIGNAL EMISSION WITH WINGBEAT DURING THE APPROACH PHASE IN SOPRANO PIPISTRELLES (*PIPISTRELLUS PYGMAEUS*)

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Summary

Previous studies have shown that, during search flight in bats, wingbeat, respiration and echolocation are synchronised in a 1:1 relationship. An efficiently integrated locomotor–respiratory system enables bats to produce intense echolocation signals at little or no cost above that required for flight. In this study, we investigated the coupling of wingbeat with echolocation in the laboratory during approach flight in soprano pipistrelles (*Pipistrellus pygmaeus*) using high-speed digital video at 250 and 500 frames⁻¹. We found that soprano pipistrelles most commonly produce single or double pulses per wingbeat. Single pulses per wingbeat occurred in two alternative positions: immediately before the end of the upstroke or after the start of the downstroke. Double pulses per wingbeat were emitted in the same wingbeat positions on the upstroke and the downstroke, as in single pulses per

wingbeat. We suggest that, during approach flight, the coupling of more than one echolocation signal with a single wingbeat and expiratory cycle allows echolocation to remain energetically economic. When soprano pipistrelles approached a Perspex disc target, an increase in mean repetition rate was achieved by producing an extra pulse per wingbeat. Finally, we hypothesise that the bat's approach to potentially interesting targets in the same horizontal plane as its flight path, i.e. during flapping flight, may be characterised by the production of double pulses per wingbeat, resulting in a unique pattern of echolocation pulse intervals.

Key words: approach flight, echolocation, interpulse interval, bat, *Pipistrellus pygmaeus*, search phase, soprano pipistrelle, synchronisation, wingbeat coupling.

Introduction

Previous studies have shown that locomotor–respiratory coupling in running quadrupedal mammals is a widespread phenomenon, with stride and breathing phase-locked in a 1:1 relationship (e.g. Bramble and Carrier, 1983; Bramble, 1989; Bramble and Jenkins, 1993). The ability to synchronise wingbeat and respiration is also present in birds (Berger et al., 1970; Butler and Woakes, 1990) and in bats during flight (Suthers et al., 1972; Thomas, 1981; Carpenter, 1985; Carpenter, 1986).

Given the fact that intensity levels of echolocation calls in *Pipistrellus pipistrellus* (Schreber) are in the region of 80–90 dB peSPL (peak equivalent sound pressure level) at 1 m during flight (Waters and Jones, 1995), the energetic demands of producing such intense sounds could be high. For instance, Speakman et al. found that the cost of echolocation in resting *P. pipistrellus* was 9.5 times the basal metabolic rate and comparable with the high cost of flight itself (Speakman et al., 1989). Surprisingly, however, the cost of echolocation during flight is little more than the cost of flight alone (Rayner, 1991; Speakman and Racey, 1991). Echolocation during flight is energetically economic because the efficiently integrated locomotor–respiratory system facilitates echolocation as a by-product of flight.

Some 600–700 microchiropteran species are insectivorous. The echolocation of species that hunt for airborne prey may be divided into three distinct phases: the search phase, as the bat searches for insects; the approach phase, during which the bat detects and tracks potential prey; and the terminal phase, during which interception of the prey occurs (Griffin, 1958). A stereotypical increase in pulse repetition rate and shortening of pulse duration take place from the search through to the terminal phase (Griffin et al., 1960; Kalko and Schnitzler, 1989). Usually, during straight search flight, one echolocation pulse is produced on each wingbeat (Schnitzler, 1971; Suthers et al., 1972; Thomas, 1987; Kalko, 1994; Britton et al., 1997). With the onset of the approach phase, the pulse repetition rate increases, typically from 5–8 Hz during the search phase to around 12–20 Hz during the approach phase (Kalko, 1994). During approach flight, echolocation may be energetically more demanding than that during search flight (Britton, 1996).

Previous studies investigating the production of echolocation signals during the wingbeat cycle remain qualitative because of the low resolution resulting from stereo multi-flash photography and high-speed filming techniques. In this paper, we investigated the coupling of sound emission with wingbeat

cycle during the approach phase in *Pipistrellus pygmaeus* (Leach) in the laboratory. In view of the above, we used a high-speed analyser at a rate of 250 or 500 frames s^{-1} , allowing much finer resolution of the changeover from the upstroke to the downstroke. Our objectives were to quantify the precise wingbeat position during the emission of single and double pulses per wingbeat and to determine the relationship between the number and position of pulses produced during the wingbeat cycle and interpulse interval. We also compare mean repetition rates and the mean percentage of single and double pulses per wingbeat per run when bats were approaching a target disc as opposed to no disc.

Materials and methods

Study subjects

Six hand-reared soprano pipistrelles (*Pipistrellus pygmaeus*) (PP1–PP6) were kept in the laboratory on a staple diet of mealworms (*Tenebrio molitor*) supplemented with buffalo worms (*Alphitobius diaperinus*), waxmoths (*Galleria mellonella*), black crickets (*Gryllus bimaculatus*) and multivitamins. Until recently, it had been assumed that *Pipistrellus pipistrellus* was a single species. However, in the light of new evidence (for a review, see Jones, 1997), it is proposed that the pipistrelle is in fact two cryptic species: *P. pipistrellus* and *P. pygmaeus* (Jones and Barratt, 1999). Bats were maintained at a body mass of 5–6 g, and the light:dark cycle (12h:12h) was set so that experiments started in the morning, 1 h after the beginning of the night cycle.

Experimental set up

Experiments were carried out in a 4.6 m × 2.1 m × 1.5 m flight tunnel constructed from a Dexion frame covered in thin netting and lined with echo-attenuating foam. Bats were filmed face on using a high-speed SR-500 Kodak Motion Corder Analyzer at a rate of 250 or 500 frames s^{-1} , resulting in a time resolution of 4 and 2 ms, respectively, between images. The camera was placed outside the end of the flight tunnel, with the lens (Pentax Cosmicar f1.8 20 mm zoom fitted with a Jessops ×0.42 macro semi-fish-eye lens attachment) embedded in the foam lining. The optical axis of the camera was normal to the short axis of the flight tunnel at a fixed level, which would capture the bat's flight path. Captured images were transferred at a playback rate of 5 frames s^{-1} to Hi-8 tapes using a Sony GV-A5000E Video Walkman. Lighting consisted of dim red light and an infrared source, resulting in an overall illumination of 0.14 mW m^{-2} (Tektronix J16 digital photometer). Echolocation emissions were recorded with a microphone from an Ultrasound Advice U30 bat detector (frequency response ± 3 dB, 20–120 kHz) suspended above the bat's flight path. The time interval between the bat's emissions and the arrival time at the U30 microphone was ≤ 5.29 ms. The calls emitted by the bat were digitised at 391 kHz and 12-bit resolution (Das-1801AO, Keithley MetraByte). Recording from both the high-speed digital video and the U30 microphone was triggered by the bat flying across and breaking the beams of the first pair of vertical

infrared beam sensors (Fig. 1). Echolocation emissions were synchronised with individual frames by converting the analogue output from a suspended Stag Batbox III bat detector to a TTL pulse and coupling the digital output to the high-speed video *via* the Kodak Ektapro multi-channel data link (Fig. 1).

Bat's task

Bats were trained to fly on a straight flight path towards the camera lens so that both pairs of infrared beams were triggered (Fig. 1). Recordings were accepted only if both infrared beams were broken. Correct flights in which the bat did not land or swerve off a straight course were rewarded with a waxmoth or a buffalo worm. Blowing gently into the bat's face and withholding the food reward punished incorrect flights. Bats were then presented with a 3 mm thick, 60 mm diameter black Perspex disc suspended by a 0.15 mm diameter nylon monofilament fishing line from the ceiling of the flight tunnel and positioned between the infrared beams (Fig. 1). The disc was positioned in the same horizontal plane as the typical flight path of the bat. Each trial consisted of the random presentation of a disc and no disc (control). Each bat completed 10 trials per day until a total of 40 trials had been collected from each of the six bats.

Data analysis

Recordings were replayed on a Sony Hi-8 video recorder and digitised *via* NIH Image (US National Institutes of Health) on a Power Macintosh 8100AV. The angle between the perpendicular axis extrapolated from the nose and the elbow joint was measured for the wingbeat cycle prior to the bat reaching the disc. Angular measurements were made at the following points of the wingbeat cycle: (i) at the start of the downstroke, (ii) at the start of the upstroke and (iii) during echolocation. The mean angle at the start of the downstroke and the upstroke, and the mean angular deviation during echolocation on the downstroke from the start of the downstroke (MD), and the mean angular deviation during echolocation on the upstroke from the start of the downstroke (MU) were calculated for each individual during wingbeats with a single pulse and a double pulse. The MD was paired with the MU for each individual during single pulses per wingbeat, and the same type of pairing was made for all six bats. Results were analysed using the Wilcoxon signed-rank tests for two related samples (Siegel and Castellan, 1988). A similar analysis was performed for the MD and MU during double pulses per wingbeat, and between the MD during single pulses per wingbeat and double pulses per wingbeat, and the MU during single pulses per wingbeat and double pulses per wingbeat.

The mean percentage of single pulses per wingbeat and double pulses per wingbeat per run and the mean repetition rate (pulses s^{-1}) per run were calculated for each individual. A comparison was made between the percentage of single pulses per wingbeat emitted per run from each bat when presented with and without a disc. The mean percentage of single pulses per wingbeat per run from an individual when presented with

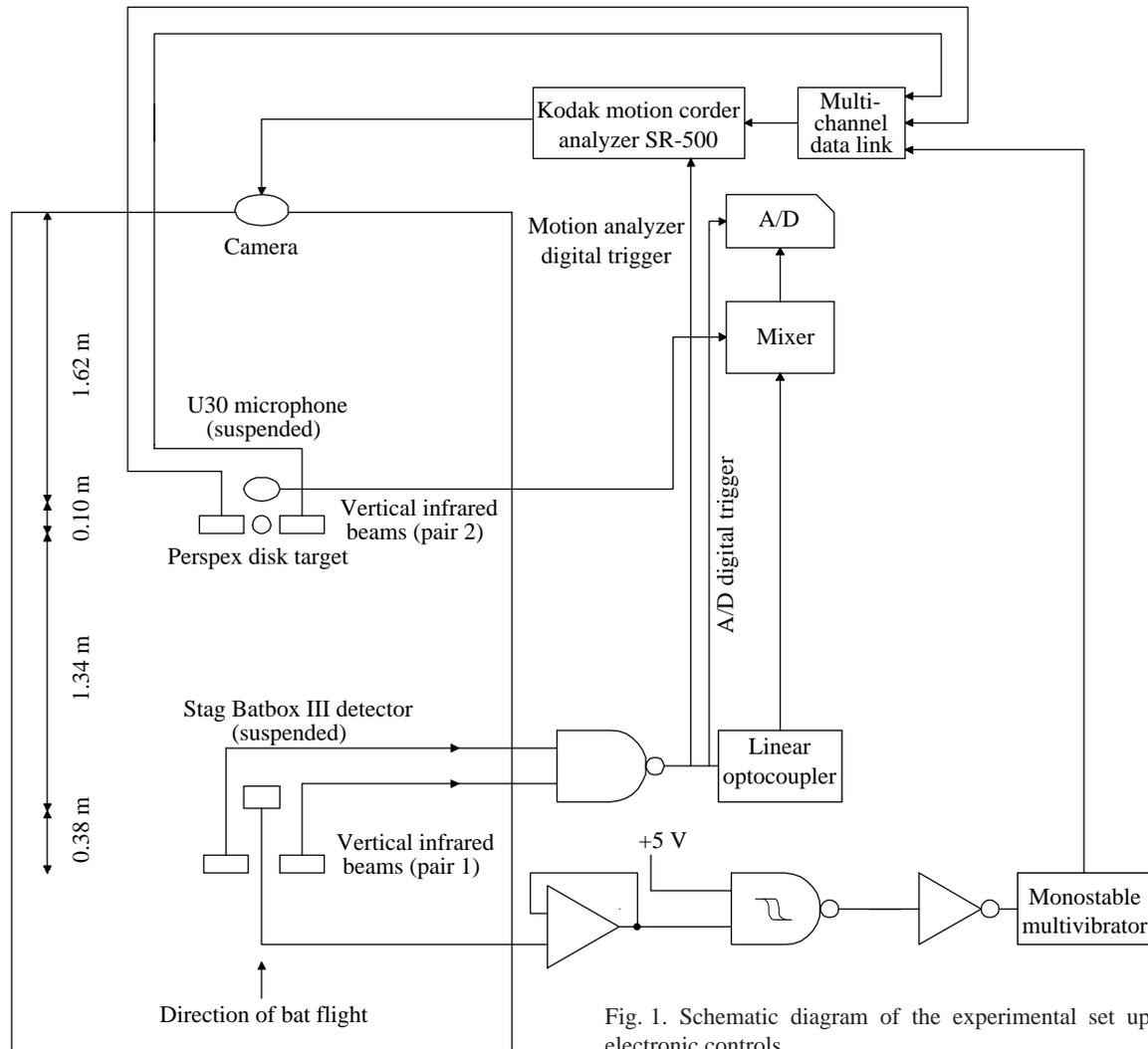


Fig. 1. Schematic diagram of the experimental set up and electronic controls.

a disc was paired with the mean percentage of single pulses per wingbeat per run from the same individual when presented with no disc. The same type of pairing was made for all six bats, and the results were analysed using the Wilcoxon signed-rank tests for two related samples. A similar type of statistical analysis was used for the mean percentage of double pulses per wingbeat and the mean repetition rate per run. Wilcoxon signed-rank tests were run on SPSS, v. 9.0. The distribution of interpulse intervals was determined for each individual from echolocation recordings of bats flying towards a disc using a custom-designed program in TestPoint (Keithley Metrabyte). By combining audio and video recordings, the distribution of pulse intervals within individuals could be described with respect to the frequency and position of echolocation emissions during the wingbeat cycle.

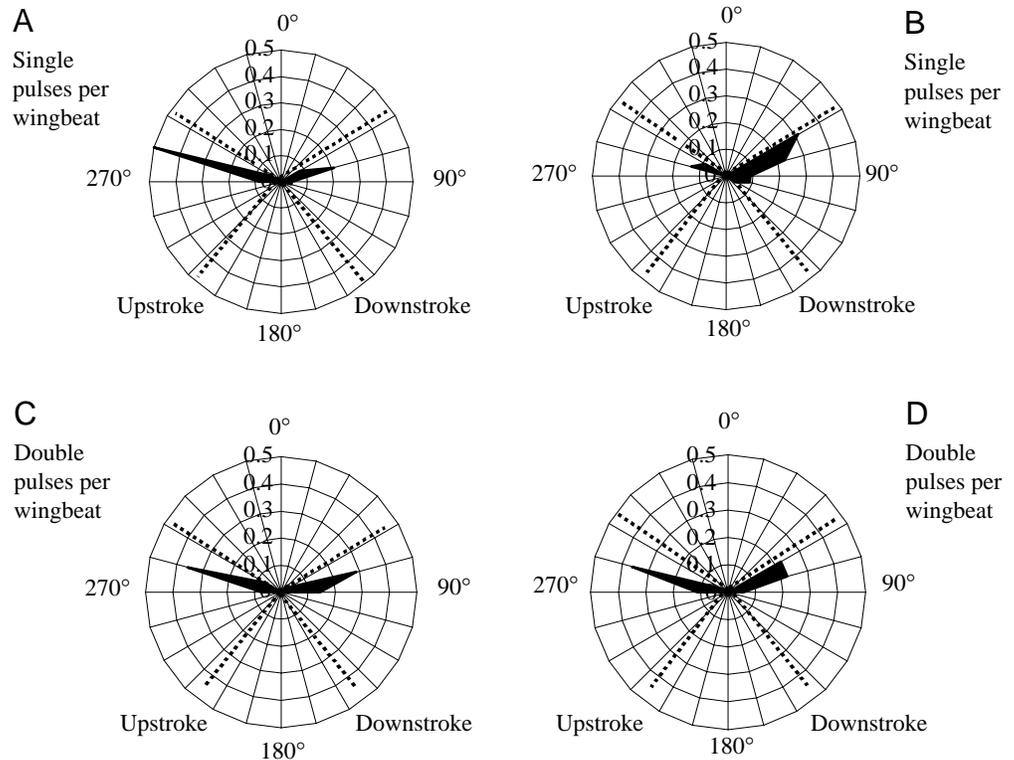
Results

Angular positions of echolocation

Bats emitted 1–4 echolocation pulses per wingbeat. A single pulse per wingbeat and a double pulse per wingbeat were the

most common. Three and four pulses per wingbeat were produced infrequently and only when bats were echolocating towards a disc. Single pulses per wingbeat were emitted in two alternative positions: either at the end of the upstroke or after the start of the downstroke (Table 1; Fig. 2A,B; see also Fig. 5A). Of the six bats, one individual (PP6) produced an equal number of pulses on the upstroke and the downstroke. PP2, PP4 and PP5 showed a bias towards pulse production on the downstroke, emitting pulses 77–97% of the time on the downstroke. PP1 and PP3 produced pulses 62% and 95% of the time, respectively, on the upstroke. Double pulses per wingbeat were produced in the same wingbeat positions on the upstroke and the downstroke as single pulses per wingbeat (Table 1; Fig. 2; see also Fig. 5B). The MD did not differ significantly between single and double pulses per wingbeat (Wilcoxon test, $Z=-0.52$, $P>0.05$). Similarly, the MU did not differ significantly between single and double pulses per wingbeat (Wilcoxon test, $Z=-0.73$, $P>0.05$). The mean angular deviation from the start of the downstroke was greater in pulses produced on the downstroke than in those produced on the upstroke in single pulses per wingbeat (Wilcoxon test,

Fig. 2. Concentric histograms showing the angular distribution of single and double pulses per wingbeat for two individuals (PP1 and PP4) when presented with a 60 mm diameter Perspex disc. (A) Single pulses per wingbeat in PP1, (B) single pulses per wingbeat in PP4, (C) double pulses per wingbeat in PP1 and (D) double pulses per wingbeat in PP4. 0–180° represents the downstroke and 180–360° represents the upstroke. Dotted lines represent the mean angles of the start of the downstroke and upstroke. Concentric circles represent relative frequency increments of 0.1. For single pulses per wingbeat, $N=24$ for PP1 and $N=22$ for PP4. For double pulses per wingbeat, $N=14$ for PP1 and $N=18$ for PP4.



$Z=-2.20$, $P<0.05$) and in double pulses per wingbeat (Wilcoxon test, $Z=-2.20$, $P<0.05$).

Relationship between mean repetition rates, single pulses per wingbeat and double pulses per wingbeat

Mean repetition rate (pulses s^{-1}) was significantly higher when the bats were presented with a disc than when presented with no disc (Wilcoxon test, $Z=-2.20$, $P<0.05$) (Fig. 3A). Bats emitted significantly more double pulses per wingbeat per run when echolocating towards a disc compared with no disc (Wilcoxon test, $Z=-2.02$, $P<0.05$) (Fig. 3B). Consequently, the emission of single pulses per wingbeat per run declined significantly when bats were presented with a disc compared with when they were presented with no disc (Wilcoxon test, $Z=-2.20$, $P<0.05$) (Fig. 3C).

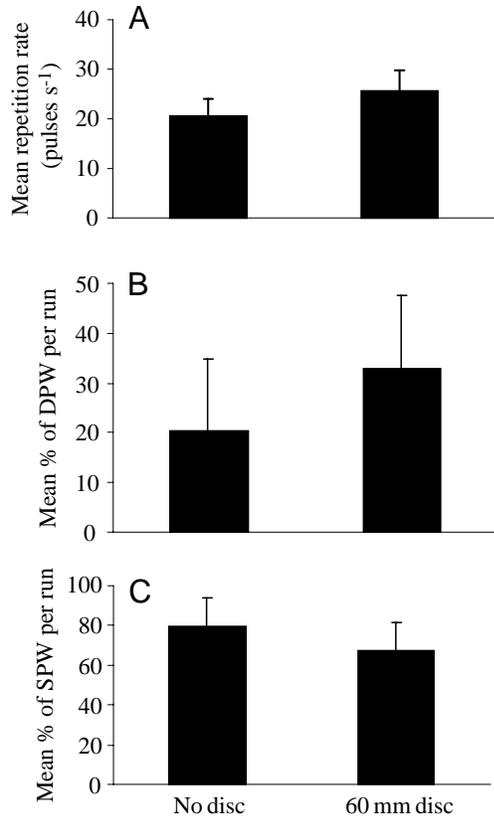
Relationship between pulse interval and signal emission during the wingbeat

The distribution of pulse intervals during approach flight was bimodal, typically with a first peak of short pulse intervals of approximately 20 ms and a second peak of longer pulse intervals of approximately 50–60 ms (with the exception of individual PP2) (Fig. 4). Closer inspection of video sequences showed that the longer pulse intervals of around 50–60 ms corresponded to single pulses per wingbeat, with pulse production occurring either on the upstroke or the downstroke of consecutive wingbeats. Pulse intervals above approximately 60 ms were uncommon and usually resulted from the emission of single pulses per wingbeat, with pulses emitted on the downstroke of the first wingbeat and on the upstroke of the next wingbeat (Fig. 5A). Shorter pulse intervals <30 ms were

Table 1. The mean angular distribution of single pulses per wingbeat and double pulses per wingbeat for six individuals when presented with a 60 mm Perspex disc

Individual	Single pulse per wingbeat			Double pulse per wingbeat		
	Mean angle on the upstroke (degrees)	Mean angle on the downstroke (degrees)	N	Mean angle on the upstroke (degrees)	Mean angle on the downstroke (degrees)	N
PP1	293.8±5.5	85.0±11.9	24	294.4±8.6	85.3±12.8	14
PP2	300.1±4.3	83.9±15.3	35	290.0±4.2	89.6±12.3	5
PP3	276.9±19.5	87.7±10.6	19	288.5±16.3	85.2±13.2	21
PP4	296.4±5.9	83.8±16.9	22	288.8±8.6	76.4±8.6	18
PP5	286.6±9.5	90.7±11.9	12	285.0±9.6	95.6±9.8	25
PP6	291.3±2.0	84.7±6.1	8	288.4±5.6	89.7±13.0	32

Values are means ± s.d.



the result of double pulses per wingbeat and corresponded to the time taken from a pulse produced before the end of the upstroke to one produced after the start of the downstroke (Fig.

Fig. 3. The relationship between target condition and (A) the mean repetition rate, (B) the mean percentage of double pulses per wingbeat (DPW) per run and (C) the mean percentage of single pulses per wingbeat (SPW) per run. The histograms represent the mean + s.d. from six individuals.

5B). Intermediate pulse intervals of approximately 40–50 ms were the result of the time taken for the production of a pulse at the beginning of the downstroke to the end of the upstroke in the same wingbeat (Fig. 5B). The absence of a peak in pulse interval at approximately 20 ms in PP2 was due to the fact that this individual produced mainly single pulses per wingbeat (Fig. 4). Pulse interval lengths corresponded well with the length of pulse intervals observed during the approach phase of *P. p. mediterraneus* in the field (Kalko, 1995). Recordings of *P. p. mediterraneus* in Spain by Kalko (1995) are assumed to be *P. pygmaeus*.

Discussion

The coupling of wingbeat with echolocation has a significant impact upon the energy budget of a foraging bat. Previous studies describing the occurrence of echolocation emissions during the wingbeat cycle are qualitative in nature. This investigation effectively quantifies the precise position of echolocation pulses during the wingbeat cycle. Our results clearly demonstrate that, during single pulses per wingbeat, sound production occurs in two alternative positions: either immediately prior to the end of the upstroke or after the onset of the downstroke. During flight, the major muscles that power

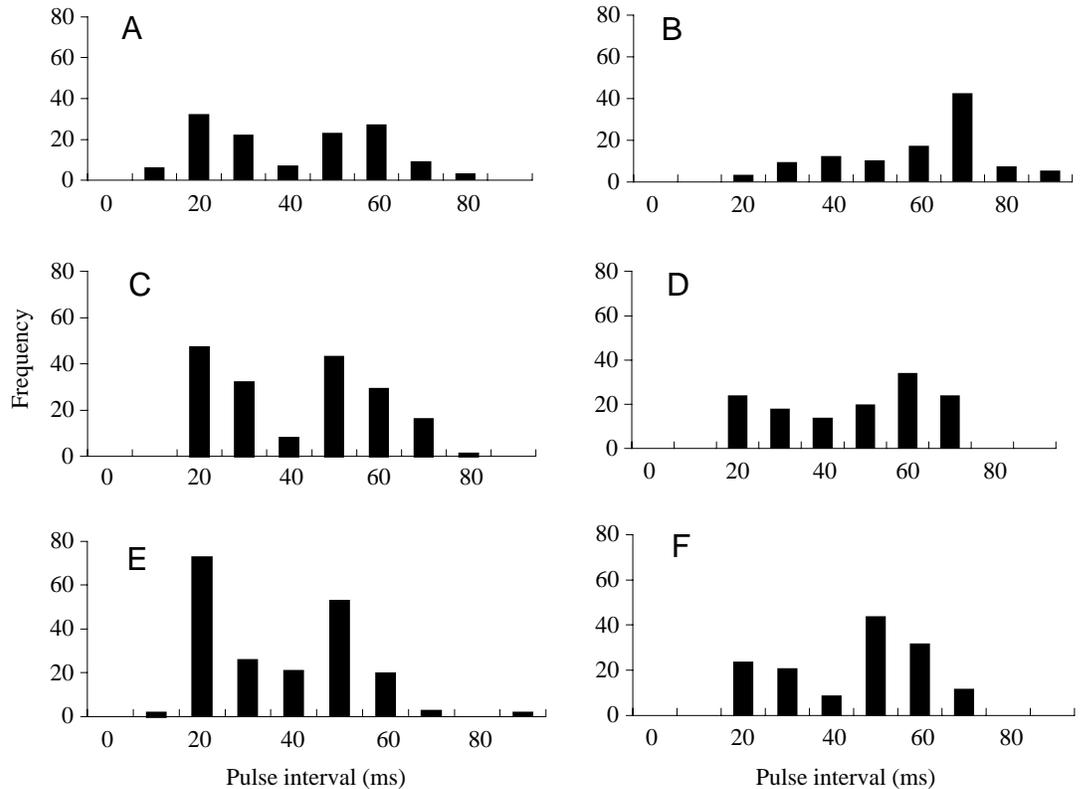


Fig. 4. The distribution of pulse interval (ms) during approach flight when the bats were approaching a 60 mm diameter Perspex disc. (A) PP1, (B) PP2, (C) PP3, (D) PP4, (E) PP5 and (F) PP6.

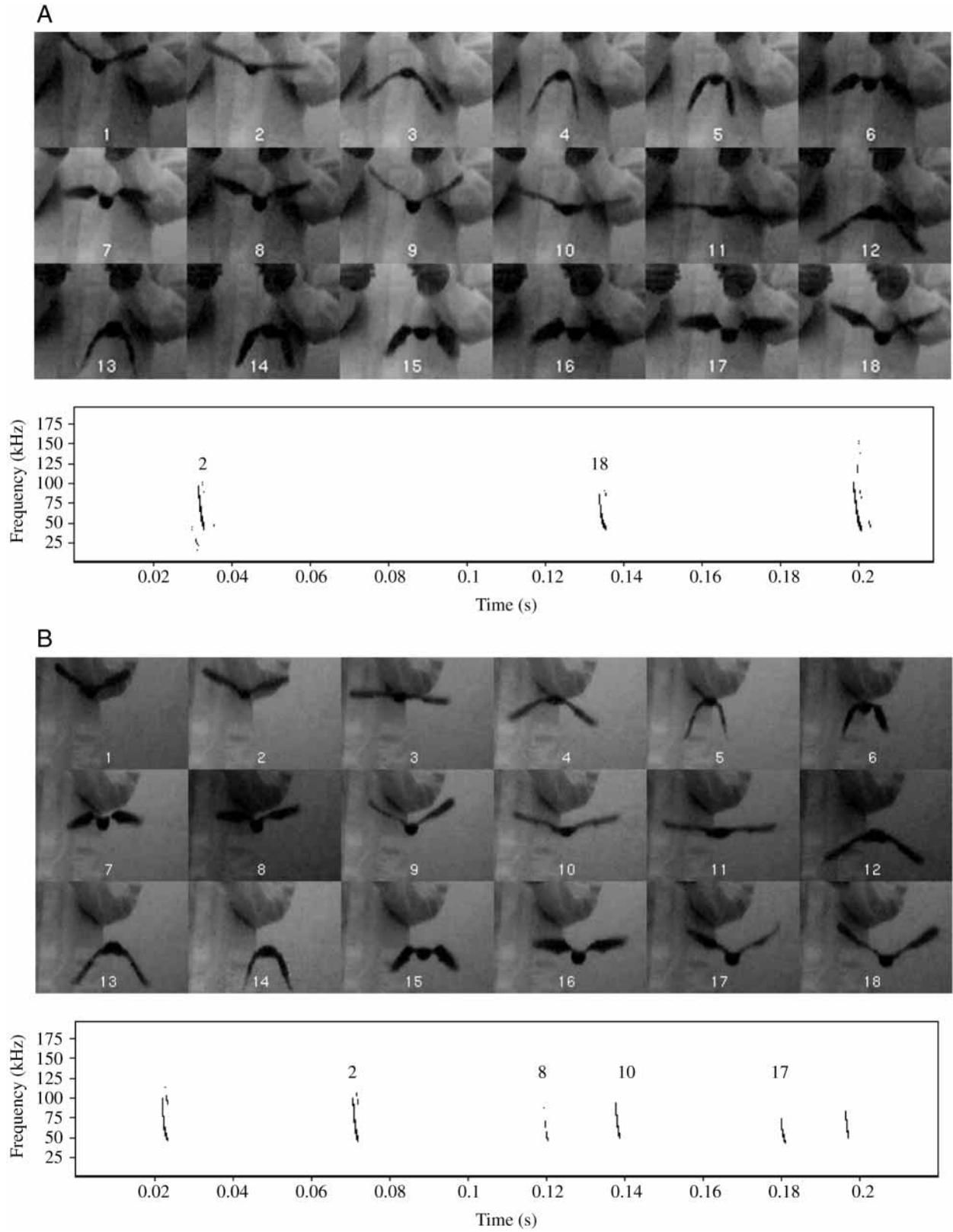


Fig. 5

the downstroke – the pectoralis and serratus ventralis – begin to contract during the latter stages of the upstroke (Hermanson

and Altenbach, 1983; Altenbach and Hermanson, 1987) and contraction continues during the transition between the

Fig. 5. The relationship between wing position and echolocation behaviour in individual PP1 when presented with (A) no disc and (B) a 60 mm diameter Perspex disc. Both sequences were filmed at 500 frames s^{-1} , resulting in approximately 30 frames per wingbeat cycle. Eighteen non-consecutive frames were selected from a total of 60 frames to illustrate two complete wingbeat cycles. Spectrograms were created using Avisoft-SasLab software [sampling rate 391 kHz, fast Fourier transform (FFT) length 256, time resolution 0.33 ms, overlap between FFTs 50%]. (A) Pulse emission occurs at the start of the downstroke in frame 2. In both wingbeat cycles, only one pulse is emitted per wingbeat cycle. In the next wingbeat cycle, a pulse is produced on the upstroke (frame 18). This results in a longer pulse interval (101 ms) than if the pulse had been produced on the downstroke of the second wingbeat. For example, the echolocation signal at 0.2 s occurred at the end of the upstroke and results in a pulse interval length of 65 ms. (B) Two pulses occur in both wingbeat cycles. First, a pulse occurs in frame 2 at the start of the downstroke. The second pulse in the same wingbeat cycle is produced at the end of the upstroke in frame 8. In the next wingbeat cycle, a pulse is produced at the beginning of the downstroke (frame 10) and at the end of the upstroke (frame 17). This results in a characteristic lengthening (frames 2–8) and shortening of the pulse interval (frames 8–10).

upstroke and the downstroke and into the first half of the downstroke. In flying bats, pectoralis and serratus ventralis muscle contractions coincided with lateral abdominal wall muscle activity (Lancaster et al., 1995). Both sets of muscle activity have been proposed to generate strong thoraco-abdominal pressure during flight, which ultimately compresses thoracic air volume (Lancaster et al., 1995) and increases subglottal pressure, enabling the production of vocalisations (Suthers and Fattu, 1973; Fattu and Suthers, 1981). This pattern of muscle activity corresponds well with observations that exhalation occurs mainly during the latter half of the upstroke and the first half of the downstroke (Heblich, 1986).

Our findings suggest that pulses are distributed in two narrow bands of the wingbeat cycle, immediately before the end of the upstroke and after the start of the downstroke. Thus, pulse production coincides with the muscular contractions that generate mechanical power on the downstroke. Consequently, sound production also coincides with muscular activity in the abdominal wall and with expiration. Pulses may be distributed in this narrow range of the wingbeat phase just before and after the top of the wing stroke because these points in the wingbeat cycle may coincide with the most intense activity of both the pectoralis and serratus ventralis muscles.

On the upstroke, the onset of pectoralis muscle contraction occurs earlier than the onset of serratus muscle contraction. Activity from both muscles occurs only immediately prior to the end of the upstroke. On the downstroke, both pectoralis and serratus muscle activity continues, with activity ceasing in both muscles just before the mid-downstroke (Hermanson and Altenbach, 1983). It is possible that muscular activity from both the serratus and pectoralis muscles is necessary to generate the thoracic pressure to facilitate sound production. This might explain the significantly smaller mean angular deviation of

pulse production on the upstroke from the top of the wingbeat than on the downstroke from the top of the wingbeat.

Previous observations on European pipistrelle species in the field reveal that single pulses per wingbeat were emitted mostly during the first half of the downstroke and only rarely at the end of the upstroke (Kalko, 1994). In addition, Britton et al. found pulse production to occur at or just after the end of the upstroke in *Myotis dasycneme* during commuting flight (Britton et al., 1997). Although our results generally concur with the above descriptions, they also demonstrate that intraspecific variability is possible. Soprano pipistrelles often exhibit a bias towards pulse production on either the upstroke or the downstroke during the production of single pulses per wingbeat. In contrast, our findings seem inconsistent with some earlier descriptions. For instance, single echolocation pulses produced during the wingbeat in flying *Phyllostomus hastatus* occurred most frequently just before or just after the transition from the downstroke to the upstroke (Suthers et al., 1972). In addition, four species (*Myotis lucifugus*, *Chilonycteris rubiginosa*, *Carollia perspicillata* and *Rhinolophus ferrumequinum*) emitted echolocation pulses consistently at the start of the upstroke (Schnitzler, 1971). The significance of these inconsistencies is unclear, but differences in echolocation and foraging modes could be responsible for these discrepancies among species.

The bats we studied emitted double pulses per wingbeat in the same wingbeat phase as single pulses per wingbeat. As in search flight, it is probable that each wingbeat cycle is synchronised with one respiratory cycle during the approach sequence (Kalko, 1994). Furthermore, bats can produce several echolocation signals per expiratory cycle (Suthers et al., 1972). The production of double pulses per wingbeat occurs in the wingbeat phase that is synchronised with muscular activity that powers the downstroke. This suggests that the production of two pulses can occur during a single exhalation and that the muscular contractions responsible for powering the downstroke during flight could also facilitate the production of several echolocation pulses. Therefore, the energetic efficiency of producing a double pulse per wingbeat could be as great as producing a single pulse per wingbeat. Observations on three and four pulses per wingbeat show that all pulses are produced between the end of the upstroke and during the first half of the downstroke (J. G. Wong, unpublished results). This suggests that the coupling between sound production and muscular activity is still maintained when more than two pulses are emitted per wingbeat. We also found evidence of double pulse per wingbeat emission during approach flight of foraging soprano pipistrelles in the field (J. G. Wong, unpublished results). Therefore, echolocation during approach flight could be as energetically efficient as search flight echolocation.

During approach flight, bats often reduce their flight speed (Schnitzler et al., 1987; Jones, 1988; Kalko, 1995). For European pipistrelle bats, flight speed decreases from 4–7 $m s^{-1}$ during search flight to 2–4 $m s^{-1}$ during approach flight (Kalko, 1995). A mean wingbeat frequency of 11 Hz was found for *P. pipistrellus* flying in a flight cage (Thomas

et al., 1990). Since flight speed and wingbeat frequency are negatively related (Schnitzler, 1971; Norberg, 1976; Aldridge, 1986; Britton et al., 1997), a reduction in speed (associated with a higher wingbeat frequency) requires an increase in mechanical power (Rayner, 1986). Presumably, the disadvantages of an increased energetic expenditure are offset by the overall net energetic gain from a greater prey-capture rate. A reduction in flight speed allows the bat finer control over capture manoeuvres and the ability to adjust for any unexpected changes in the insect's flight pattern (Kalko, 1995). In addition, higher flight speeds could create greater air turbulence and push the insect off the inter-femoral membrane (Kalko and Schnitzler, 1998).

During approach flight, the distribution of pulse interval is bimodal, with shorter pulse intervals corresponding to double pulses per wingbeat. Bimodality of pulse intervals has also been demonstrated during search flight, with shorter pulse intervals corresponding to one wingbeat cycle and longer pulse intervals associated with two wingbeat cycles or with short gliding flights in which no sound is emitted (Thomas et al., 1990; Kalko, 1994).

It is well established that bats increase their repetition rate when they detect and track a potential prey item. As the bat reacts to a potential prey item, a continuous reduction in pulse interval takes place, increasing the stream of information returning to the bat. This information flow allows the bat to monitor the precise position of the prey and to compensate for any last-minute deviations in prey position. Kalko suggested that 50% of insect pursuits observed in the field in European pipistrelles were associated with steep dives and narrow turns (Kalko, 1995). Usually, steep dives were associated with gliding flight during which the bats continuously emitted echolocation signals (Kalko, 1994). It is unclear whether bats still maintain the coupling between respiration and echolocation during gliding flight. In contrast, European pipistrelles pursuing insects detected above or near the same horizontal plane as the bat's search flight path used flapping flight (Kalko, 1994). In the present study, soprano pipistrelles detecting and reacting to a disc, in the same horizontal plane as the bat's flight path, increase their pulse repetition rate by producing a greater number of wingbeat cycles with double pulses. The emission of double pulses per wingbeat results in a characteristic pulse pattern: the shortening (end of the upstroke to start of the downstroke) and lengthening (start of the downstroke to end of the upstroke) of pulse intervals. It is suggested that flapping approach flight (i.e. during those pursuits in which the prey item occurs in or above the bat's flight path) is associated with this characteristic double pulse per wingbeat echolocation emission pattern, rather than with a continuous reduction in pulse interval. The emission of an extra pulse per wingbeat signifies the reaction of a bat to an item of potential interest and may therefore characterise the onset of flapping approach flight. Echolocation recordings currently being undertaken in the field of approach and terminal sequences in foraging soprano pipistrelles will test this hypothesis.

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