

## RESEARCH ARTICLE

# Tight coordination of aerial flight maneuvers and sonar call production in insectivorous bats

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## ABSTRACT

Echolocating bats face the challenge of coordinating flight kinematics with the production of echolocation signals used to guide navigation. Previous studies of bat flight have focused on kinematics of fruit and nectar-feeding bats, often in wind tunnels with limited maneuvering, and without analysis of echolocation behavior. In this study, we engaged insectivorous big brown bats in a task requiring simultaneous turning and climbing flight, and used synchronized high-speed motion-tracking cameras and audio recordings to quantify the animals' coordination of wing kinematics and echolocation. Bats varied flight speed, turn rate, climb rate and wingbeat rate as they navigated around obstacles, and they adapted their sonar signals in patterning, duration and frequency in relation to the timing of flight maneuvers. We found that bats timed the emission of sonar calls with the upstroke phase of the wingbeat cycle in straight flight, and that this relationship changed when bats turned to navigate obstacles. We also characterized the unsteadiness of climbing and turning flight, as well as the relationship between speed and kinematic parameters. Adaptations in the bats' echolocation call frequency suggest changes in beam width and sonar field of view in relation to obstacles and flight behavior. By characterizing flight and sonar behaviors in an insectivorous bat species, we find evidence of exquisitely tight coordination of sensory and motor systems for obstacle navigation and insect capture.

**KEY WORDS:** Sensorimotor integration, Adaptive sonar, Turning, Echolocation, Climbing

## INTRODUCTION

Insectivorous bats make agile flight maneuvers in the dark to navigate around obstacles and intercept prey. Bats adapt wing kinematics, including adjustments in wing camber, wing area, angle of attack and the rotation of the wing, in order to achieve maneuverable flight across different speeds and generate appropriate lift, thrust and vortex flow (Aldridge, 1986; Hubel et al., 2012; Norberg, 1976; Norberg and Winter, 2006; Riskin et al., 2008; Tian et al., 2006). Flapping flight allows rapid changes to aerodynamic forces, which is important for maneuverability. The generation of a leading edge vortex, a time-varying unsteady mechanism, increases lift during slow, hovering flight (Hedenström et al., 2007; Muijres et al., 2008, 2014). While many studies on bat flight have focused on straight or hovering flight, maneuvering, climbing and turning flight have not been as systematically investigated, where unsteady effects may be more pronounced. In the present study, we examined how the dynamics of flapping

flight interact with the timing and performance of the bat's sonar guidance system.

Echolocating bats emit sonar signals and process information carried by returning echoes to localize objects in their environment (Griffin, 1958). Insectivorous bats emit high-intensity calls, which can exceed 135 dB sound pressure level (SPL) at 10 cm (Holderied et al., 2005; Surlykke and Kalko, 2008). To maximize energy efficiency, bats often time the sonar call production with exhalation, which coincides with the upstroke of the wingbeat cycle (Schnitzler, 1971; Suthers et al., 1972). In addition, periods of silence primarily occur during inspiration along the downstroke of the wingbeat (Wilson and Moss, 2004). However, the relationship between sound production and respiration is not fixed; sounds can be produced throughout the wingbeat cycle (Moss et al., 2006), with sound intensity varying across the wingbeat (Koblitz et al., 2010). Variation in bat call intensity and timing with respect to wingbeat cycle indicates that task demands impart tradeoffs between energy efficiency in vocal production and sonar information acquisition.

Bats adjust the timing of sonar sounds as they operate in different environments or perform different tasks. When searching for food in open space, big brown bats emit sounds at a slow rate of 5–10 Hz (Griffin, 1958; Surlykke and Moss, 2000). When they near an insect or fly amidst clutter, they increase the rate of sound production, augmenting the rate of echo information updates per unit time (Moss and Surlykke, 2001). As bats capture an insect or prepare to land, they emit calls at a rate as high as 200 Hz, which is about 15–20 times the rate of the big brown bat's wingbeat cycle. Bats also emit groupings of sounds, which occur closely spaced in time (Moss and Surlykke, 2001; Moss et al., 2006). These sound groups are produced by bats at high incidence during obstacle navigation (Petrates et al., 2009), and sounds within groups become more tightly clustered with decreasing distance to the obstacles (Sändig et al., 2014). Sonar sound groups show the following relationship to the wingbeat cycle: the first calls in a group occur earlier in the upstroke phase of the wingbeat cycle, the last calls in a group occur later, in the beginning of the downstroke of the wingbeat cycle, and the group as a whole is centered on the peak of the upstroke, when single calls also occur (Koblitz et al., 2010). The temporal patterning of the group appears to be set by the emission time of the first call in the group, relative to the wingbeat, and indicates that the emission pattern of a sound group is pre-planned. The variable timing of sonar call production with respect to the wingbeat allows the bat to adapt to different environments and task requirements.

Insectivorous bats emitting frequency-modulated (FM) calls also adapt the duration, frequency, intensity and directionality of their signals. Bats reduce call duration to avoid pulse–echo overlap with nearby objects (Cahlander et al., 1964; Kalko and Schnitzler, 1989; Schnitzler et al., 1987), widen call bandwidth to better localize objects (Faure and Barclay, 1994; Hartley, 1992; Kalko and Schnitzler, 1993; Surlykke et al., 1993), reduce call intensity as they approach objects as a method for keeping target echo strength

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constant (Hartley, 1992; Hiryu et al., 2007), and decrease directionality to widen the field of view as they attack prey (Jakobsen and Surlykke, 2010). These adaptations occur as the bat adjusts the timing of sonar sounds, and may also be influenced by the temporal dynamics of respiration and flight kinematics.

In this study, we examined flight motor output with the relative timing of sonar vocalizations to better understand the coordination of flight kinematics and sonar behavior. We tested big brown bats, *Eptesicus fuscus*, in a challenging flight task that required animals to make two sharp turns and a steep climb in order to capture a tethered insect. We investigated flight and echolocation systems as drivers for coordinated behaviors and examined fine-scale changes to call production as bats navigated a complex environment.

## MATERIALS AND METHODS

Five adult, wild-caught big brown bats, *Eptesicus fuscus* (Palisot de Beauvois 1796), were trained to participate in these studies, and complete data sets were collected from three of these animals. Experiments took place in a large flight room (7.5×6×2.5 m) lined with sound-absorbing foam (Sonex One, Acoustical Solutions, Inc.), in low light conditions, at the University of Maryland, College Park, USA. All experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Maryland, College Park.

### Experimental setup

Over 2 months, bats were trained to fly through a corridor created with two parallel nets, spaced 0.9 m apart. The nets had two small openings, which served as an entrance and exit to the corridor (deer block netting, PVC mesh, 1.5×1.5 cm holes). The nets spanned the height and width of the flight room (Fig. 1A). The first net opening (area, 0.27 m<sup>2</sup>) was placed close to the ground on one side of the room, while the other net opening (area, 0.51 m<sup>2</sup>) was placed close to the ceiling on the other side of the room. The bats were trained to catch insects (*Tenebrio molitor* larvae) tethered and hanging from the ceiling by monofilament fishing line (Berkley Trilene, 0.9 kg test, 0.13 mm diameter). The tethered insect was hung 0.76 m behind the second net and towards the middle of the room. This setup required the animals to navigate through the lower net opening, ascend and turn through the corridor, navigate through the second net opening, turn towards the tethered insect, and finally make insect capture.

### Data recordings

We recorded 94 animal flight trials for each bat over a period of four consecutive days. Two ultrasound-sensitive microphones (UltraSound Advice, SM2 microphone with SP2 amplifier) were used to record the wideband sonar emissions (band-passed between the frequencies of 10 and 100 kHz, Wavetek-Rockland Dual Hi/Lo Filter) and recorded digitally (National Instruments PCI-6122, sampling rate 250 kHz). A set of 10 motion-tracking cameras (Vicon MX T40) tracked reflective markers placed on the bats at 300 Hz. Motion-tracking data were downloaded to a computer running Vicon Nexus software and exported to MATLAB (MathWorks) for further analysis. A set of markers, reflective tape cut into 6.35 mm diameter circles, were attached to the wings of the bats. On each wing, markers were placed at the thumb joint, the base of the wing near digit five, and at the wing tip on both the dorsal and ventral sides (Fig. 1B). Markers were fixed to the bat using tape adhesive and were replaced each day they fell off. A hemispherical marker was also attached to the body but was not reliably recorded by the motion-tracking system and was not used in analysis. Data synchronization was achieved using a trigger switch that broadcast a transistor-transistor logic (TTL) signal to each system. Each system was configured with an 8 s rolling buffer aligned to the onset of the TTL pulse.

We did not analyze a set of trials in which there were tracking problems, reducing the total number of trials from 94 for each bat to 86, 85 and 78 for bats 1, 2 and 3, respectively. Trials in which the bats did not fly directly between the first net opening and the second net opening (indirect flight) were excluded from analysis. These trials were excluded if the time to cross the nets was larger than 1 s.d. above the median time and if the flight speed was below 2 s.d. of the median speed. Direct flights comprised 81.4%,

81.2% and 75.6% of trials for bats 1, 2 and 3, resulting in 70, 69 and 59 trials analyzed per bat.

### Sound analysis

Recordings of sonar vocalizations were analyzed using custom-written MATLAB software. Vocalization peak intensities were identified from a squared and smoothed (200 point moving average) version of the time waveform using the MATLAB findpeaks function with a threshold that adapted to the noise floor of each recording. Echoes were automatically excluded when the ratio between peaks differed by a magnitude of five or higher and the interval between pulse and echo was below 15 ms. The waveforms and spectrograms of the vocalizations were visually inspected for accurate inclusion in the data set.

The call onsets and offsets were identified using custom-written software which searched for changes in energy. The sonar calls were high passed for onset markings, or low passed for offset markings (Butterworth filter, frequency cutoff at 30 kHz for both). Vocalizations with a pulse interval (PI) below 10 ms (terminal buzz phase) or with a low signal to noise ratio (adapted to the noise floor of each recording and the intensity of the previous call) did not have onsets or offsets marked and were excluded from duration analysis. We visually inspected and corrected the markings using spectrograms. Onset and offset times were used to calculate call duration.

The end frequency of each FM sonar call was automatically extracted from the last half of each call. A squared, smoothed frequency spectrum was calculated (smoothing: 20 point moving average). Values outside 10–40 kHz were ignored in order to suppress harmonics, echoes and background noise. The end frequency was determined by an adaptive amplitude threshold crossing on the squared, smoothed spectrum values. Frequency markings were visually verified using spectrograms.

Sound groups were identified as clusters of sounds, surrounded by calls with larger intervals (PI>1.2 times the mean interval of the sound group). For call pairs, or doublets, the variation in PI is not used as a means for inclusion, but for three or more sounds, call groups were characterized by the additional criterion of stable PI (<5% variation). Vocalizations occurring with pulse intervals outside the range 10–100 ms were not examined for sound group inclusion. The methods for identifying sound groups are the same as used by Moss et al. (2006). Sound groups with three calls present were termed triplets.

Echolocating bats that use FM sonar signals reduce call duration with object distance to avoid pulse–echo overlap (Kalko and Schnitzler, 1989). We calculated the pulse–echo overlap zone (Kalko and Schnitzler, 1993), also referred to as the inner window (Wilson and Moss, 2004), as the boundary distance from the bat in which object echoes would return to the bat after the bat has completed emitting its pulse, and is defined as:

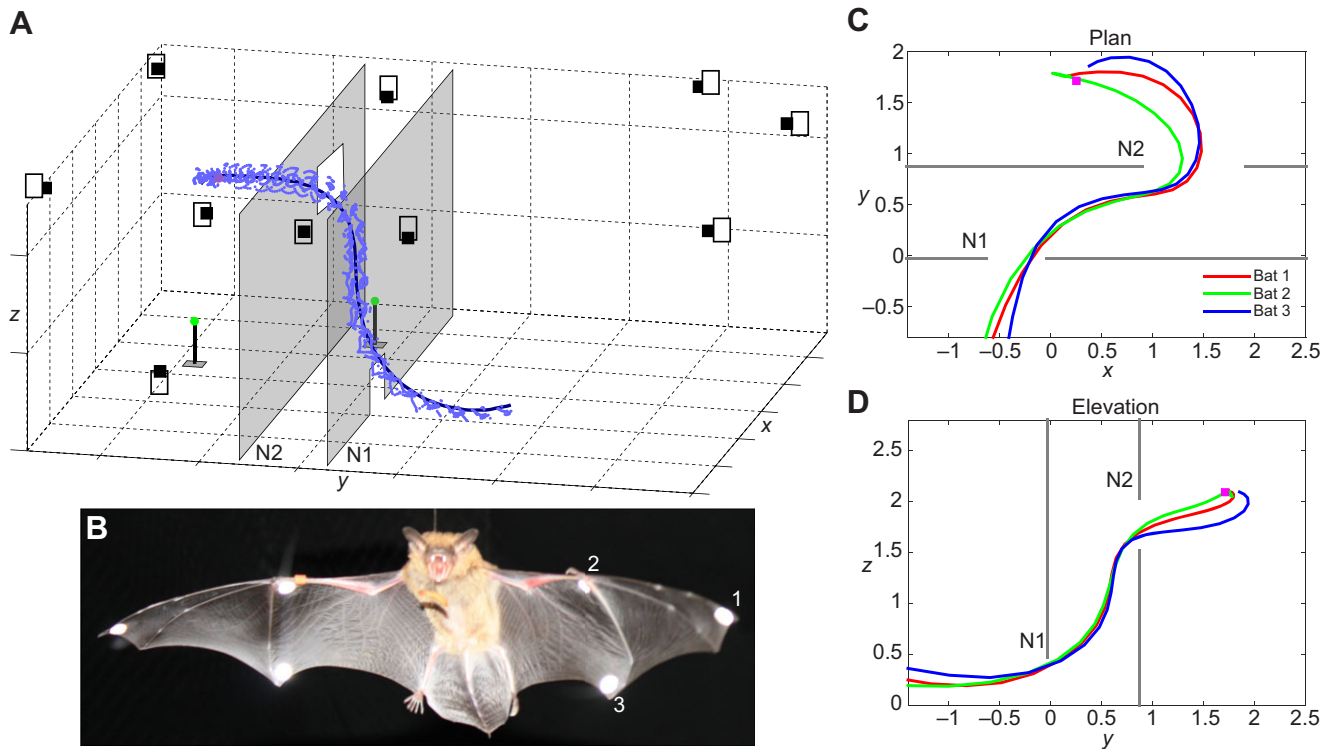
$$\frac{d \times c}{2},$$

where  $d$  is the sonar pulse duration,  $c$  is the speed of sound (we used a constant 344 m s<sup>−1</sup>), and dividing by two accounts for the two-way travel time of the pulse.

### Flight path analysis

Motion-tracking data were used to calculate flight trajectories. For each frame, we calculated a centroid from the recorded reflections of the markers on the bats. We smoothed these centroid data using a 60 point moving average weighted by the number of reflections recorded within each frame. After smoothing, small gaps in the trajectories, due to missing reflections, were spline filled. Wingbeat oscillations were removed when calculating speed, turn rate and climb rate using a low-pass Butterworth filter (cutoff frequency 6 Hz, order 6 with zero phase). The instantaneous speed of the bat was calculated as the distance traveled by the bat between each frame. The instantaneous turn rate was calculated as the difference in angular flight direction, along the  $x/y$  plan projection, between each frame and smoothed using a 60 point moving average. The instantaneous climb rate was calculated as the difference in elevation between each frame.

For wingbeat calculations, the unsmoothed centroid was filtered with a 15 point moving average, weighted by the number of reflections recorded within each frame. The altitude values in this smoothed centroid were band-pass filtered (Butterworth filter, cutoff frequencies 6 and 20 Hz, order 12 with zero



**Fig. 1. Schematic diagram of the flight room with example trajectory, reflective marker locations on the wing, and plan and elevation views of averaged trajectories.** (A) Ten motion-tracking cameras (black and white rectangles) were placed around the room with approximate camera aim indicated. Reflective markers on the wings of the bat return reflections to the camera system, which determines 3D coordinates (light blue). A smoothed centroid calculated from the positions of the markers (dark blue) represents the bat's trajectory through the flight room. Two nets (gray) with openings separate the room. The first net, labeled N1, has an opening near the floor, while the second net, labeled N2, has an opening near the ceiling. Ultrasound-sensitive microphones were mounted on the floor (green circles) and the tethered insect was placed after the second net (magenta-colored circle). 3D positions of the objects in this schematic diagram were extracted from the motion-tracking system. (B) Photo of the bat in flight during insect capture showing reflective markers on the ventral side of the wing. Markers were placed at the wing tip (1), near the thumb joint (2) and at the base of the wing near digit five (3). Markers on the dorsal side of the wing are present but not visible in this photo. (C,D) Data were aligned in time to the first net crossing and 3D positions were averaged along 0.1 s time bins for bats 1, 2 and 3 (plotted as red, green and blue lines). Net positions are plotted as gray lines and labeled N1 and N2 for first and second nets. The tethered insect position is shown as a magenta square. Data are plotted as plan projection in C or elevation projection in D.

phase) in order to isolate wingbeat oscillations. We determined the locations of the wingbeat peaks and troughs using the findpeaks MATLAB function. An instantaneous phase of the wingbeat was calculated from the analytic signal (Hilbert transform of the smoothed and band-pass filtered altitude data) and was used for aligning the vocalization times to the phase of the wingbeat.

To calculate the Strouhal number ( $St$ ), we measured wingtip amplitude from labeled motion-capture data, after correcting for the climb angle, along complete wingbeat cycles. A total of 63 wingbeat cycles were analyzed from bats 1 and 2. The instantaneous flight speed and wingbeat rate were used in the calculations as well. Bat 3's motion-capture data had large gaps and were not used.

### Statistics

For statistical analysis of trajectory data, sound group percentage and sonar pulse parameters, we used the lmer method in the lme4 package in R to construct a linear mixed model for statistical analysis of the repeated measures. We used the CircStat Toolbox for MATLAB (Berens, 2009) to calculate the relative phase angle and confidence intervals between the wingbeat cycle and sonar vocalizations. We used 0.05 s bins aligned to each net crossing when performing the cross-correlation between sound group percentage and turn rate.

### RESULTS

Three bats completed a series of 94 trials each, over four test days, flying to a food reward through a corridor of parallel nets spanning the width of the experimental test room (Fig. 1A). In each trial, the bat entered the corridor through an opening low to the ground,

climbed to the end of the corridor, where it flew through a second net opening close to the ceiling, and then captured a tethered insect (Fig. 1C,D). We analyzed trials in which the bat flew directly between the two net openings, resulting in 70, 69 and 59 trials for bat 1, 2 and 3, respectively.

### Flight behavior

On average it took the bats  $0.80 \pm 0.03$  s to pass through the corridor between the two nets (Table 1). In this amount of time, the bats traveled an average of  $2.37 \pm 0.01$  m, climbed  $1.32 \pm 0.02$  m, and flew at an average speed of  $2.79 \pm 0.10$  m s<sup>-1</sup>.

The bats adjusted trajectory behavior as they passed through the net corridor to capture the tethered insect (Fig. 2). Flight speed changed with time to net crossing (linear mixed effects model, Wald Chi square test,  $\chi^2_{20}=36,167$ ,  $P<0.001$ ) (Fig. 2A). At 0.25 s before the first net crossing, the bats reached their peak flight speed, at  $4.15$  m s<sup>-1</sup> (95% CI 4.06, 4.24). The bats decreased flight speed in the corridor by  $-2.13$  m s<sup>-1</sup> between 1.05 s before the second net crossing and 0.15 s after the second net crossing ( $z=-70.173$ ,  $P<0.001$ , Tukey correction). Once past the second net opening, the bats increased speed to capture the tethered insect.

The bats made two turns, with turn rates exceeding  $100$  deg s<sup>-1</sup>, during the task in order to navigate the net openings and reach the tethered insect (Fig. 1C). The average turn rate in between the nets was  $130.1 \pm 2.8$  deg s<sup>-1</sup> (Table 1), and turn rate was not constant

Table 1. Flight behavior measures of the bats crossing between the nets

Bat	1	2	3	Mean
Number of trials	70	69	59	
Time (s)	0.86±0.01	0.78±0.01	0.76±0.04	0.80±0.03
Distance traveled (m)	2.38±0.01	2.35±0.01	2.37±0.01	2.37±0.01
Elevation change (m)	1.33±0.01	1.35±0.01	1.28±0.01	1.32±0.02
Speed (m s <sup>-1</sup> )	2.78±0.02	2.96±0.02	2.63±0.02	2.79±0.10
Turn rate (deg s <sup>-1</sup> )	127.5±2.8	135.7±3.1	127.1±2.8	130.1±2.8
Climb rate (m s <sup>-1</sup> )	1.55±0.02	1.71±0.02	1.43±0.02	1.56±0.08
Wingbeat rate (Hz)	11.7±0.0	10.9±0.0	11.1±0.1	11.2±0.2

Values are means±s.e.m.

(linear mixed effects model, Wald  $\chi^2_{20}=3468.5$ ,  $P<0.001$ ) (Fig. 2B). The bats approached the first net at a low turn rate of  $61.1\text{ deg s}^{-1}$  (95% CI 53.0, 69.3), at 0.45 s before the first net crossing. Turn rate increased by  $80.5\text{ deg s}^{-1}$  between 0.45 s before the first net crossing and 0.15 s after the first net crossing ( $z=14.626$ ,  $P<0.001$ , Tukey correction). Turn rate then rapidly decreased by  $94.6\text{ deg s}^{-1}$  in between the nets, from 0.15 s after the first net crossing to 0.45 s after the first net crossing ( $z=-17.219$ ,  $P<0.001$ , Tukey correction). Then, as the bats approached the second net opening, turn rate increased by  $187.7\text{ deg s}^{-1}$  from 0.35 s before the second net

crossing to 0.05 s before the second net crossing ( $z=35.146$ ,  $P<0.001$ , Tukey correction), reaching a peak turn rate of  $207.5\text{ deg s}^{-1}$  (95% CI 199.9, 215.0). Turn rate remained above  $100\text{ deg s}^{-1}$  after the second net crossing.

The entrance and exit openings in the net corridor were offset in height, which required the bats to climb in elevation (Fig. 1D). The bats changed flight elevation by an average of  $1.32\pm0.02\text{ m}$  between the nets, which resulted in an average climb rate between the nets of  $1.56\pm0.08\text{ m s}^{-1}$  (Table 1). The bats altered climb rate in order to navigate the net obstacles and reach the tethered insect (linear mixed

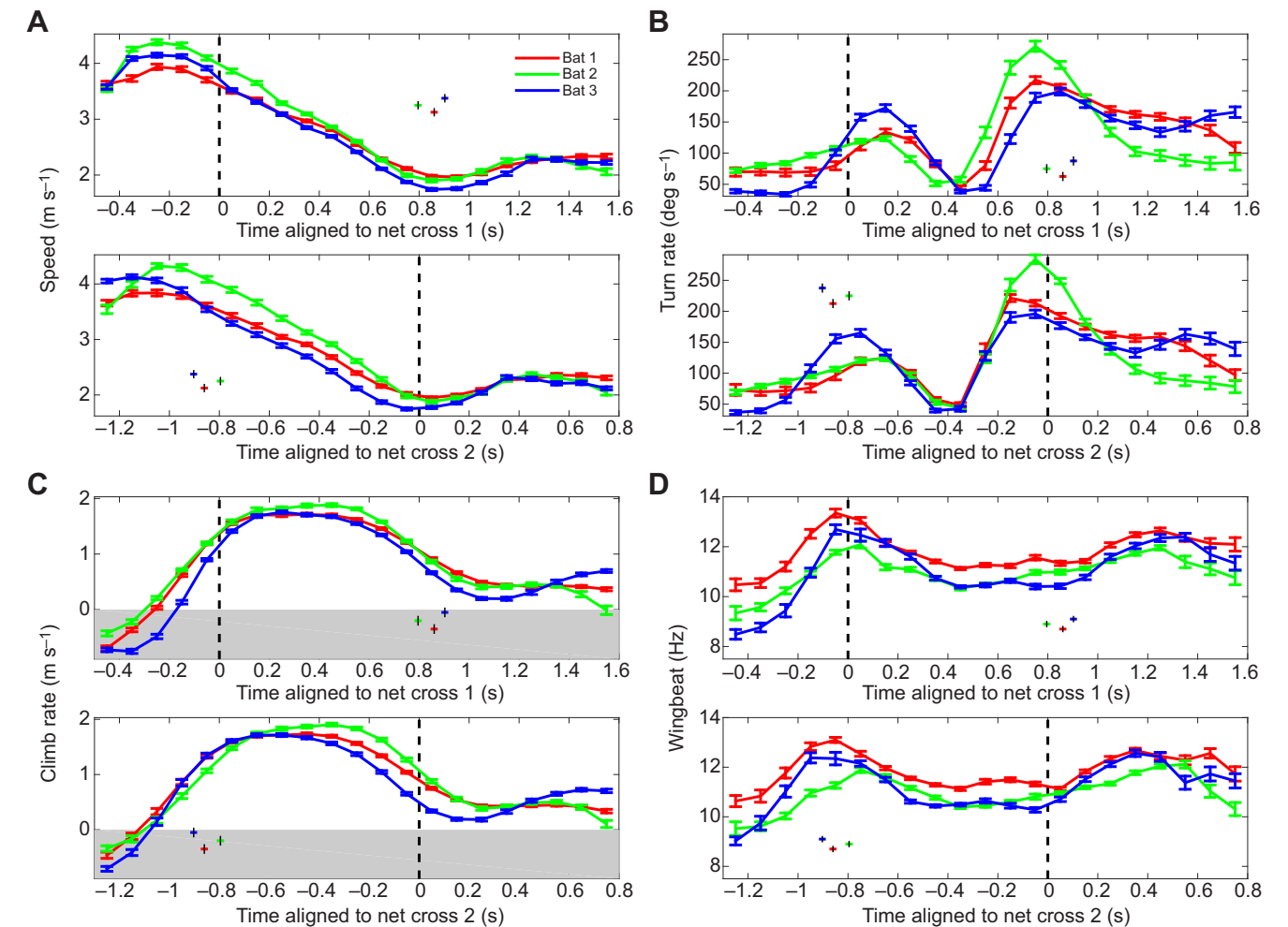


Fig. 2. Average flight measures across trials for each bat relative to net crossings. (A) Flight speed, (B) turn rate, (C) climb rate and (D) wingbeat rate. Across each measure, the top panel is aligned to the first net crossing and the bottom panel is aligned to the second net crossing. Data were averaged across trials along 0.1 s time bins, with bat 1 in red, 2 in green and 3 in blue. Values plotted are means±s.e.m. The aligned net crossing is shown at zero seconds with a dashed black line. The average net cross time of the other net crossing is represented as a short vertical line (black) with the s.e.m. represented as a horizontal line (color coded to each bat). In C, the shaded region is negative climb rate (diving).



effects model, Wald  $\chi^2_{20}=29,587$ ,  $P<0.001$ ) (Fig. 2C). Climb rate was initially negative as the bats approached the first net opening, with a value of  $-0.73 \text{ m s}^{-1}$  (95% CI  $-0.73, -0.51$ ), at 0.45 s before the net crossing. Climb rate increased by  $2.38 \text{ m s}^{-1}$  from 0.45 s before the first net crossing to 0.25 s after the first net crossing ( $z=87.204$ ,  $P<0.001$ , Tukey correction). As the bats navigated the second net opening, flight climb rate decreased by  $1.42 \text{ m s}^{-1}$ , from 0.45 s before the second net crossing to 0.25 s after the second net crossing ( $z=-44.583$ ,  $P<0.001$ , Tukey correction).

The average wingbeat rate of bats flying between the nets was  $11.2 \pm 0.2 \text{ Hz}$  (Table 1). Their wingbeat rate varied while navigating the nets (linear mixed effects model, Wald  $\chi^2_{20}=1950.4$ ,  $P<0.001$ ) (Fig. 2D). On the approach to the corridor, wingbeat rate was low at 9.5 Hz (95% CI 8.9, 10.1), at 0.45 s before the first net crossing. As the bats approached the first net opening, wingbeat rate increased by 3.1 Hz from 0.45 s before the first net crossing to 0.05 s before the first net crossing ( $z=25.663$ ,  $P<0.001$ , Tukey correction). Inside the corridor, wingbeat rate decreased by 1.9 Hz from 0.05 s after the first net crossing to 0.45 s after the first net crossing ( $z=-16.216$ ,  $P<0.001$ , Tukey correction). Wingbeat rate then increased by 1.6 Hz from 0.35 s before the second net crossing to 0.35 s after the second net crossing ( $z=13.659$ ,  $P<0.001$ , Tukey correction), as the bats prepared to catch the tethered insect.

### Strouhal number and related flight parameters

We examined the effect of changing flight parameters on force production and vortex flow. Our data show that as the bats navigated the nets and captured the tethered insect, wingbeat frequency varied from 9 to 13 Hz (Fig. 2D). However, wingbeat frequency and flight speed were not directly correlated (Fig. S1C).

Wingbeat frequency ( $f$ ), forward flight speed ( $U$ ) and wing amplitude ( $A$ ) determine the Strouhal number ( $St$ ),

$$St = \frac{fA}{U}, \quad (1)$$

a dimensionless number which describes oscillating flow mechanisms and predicts unsteadiness of the flow (Triantafyllou et al., 1991, 1993). Bats, birds and insects, as well as non-fliers such as bony fish, sharks and dolphins, tune their locomotion to a narrow range of Strouhal numbers, between 0.2 and 0.4, which is associated with efficient lift and thrust production during cruising (Taylor et al., 2003). However, non-cruising, maneuvering or slow speed flight occurs outside the range of favorable force production and Strouhal numbers, where unsteady flow may play a larger role (Norberg and Winter, 2006).

We measured the Strouhal number and found a mean of  $0.66 \pm 0.22$ , with values falling in an unfavorable range for force production (Fig. 3A), indicating that the bats experienced unsteady airflow. We measured Strouhal number relative to the net cross times, and found that  $St$  increased inside the corridor after the first net opening, then decreased after the bats passed the second net opening (Fig. 3B).

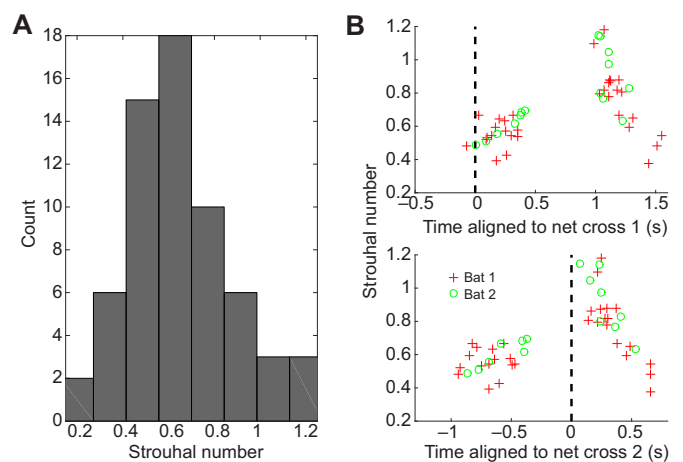
### Sonar behavior

Sonar PI is the time between sonar emissions and determines the rate of echo information flow. We examined PI as the bats navigated the net openings and found that PI varied with the time to net crossing (Fig. 4). Single trials (Fig. 4A) revealed that the bats emitted sonar sound groups, or clusters of vocalizations with a stable PI surrounded by calls with a larger PI, in large numbers prior to the first net crossing. Single trials also showed sound groups between the nets, as well as before the terminal buzz after the second net

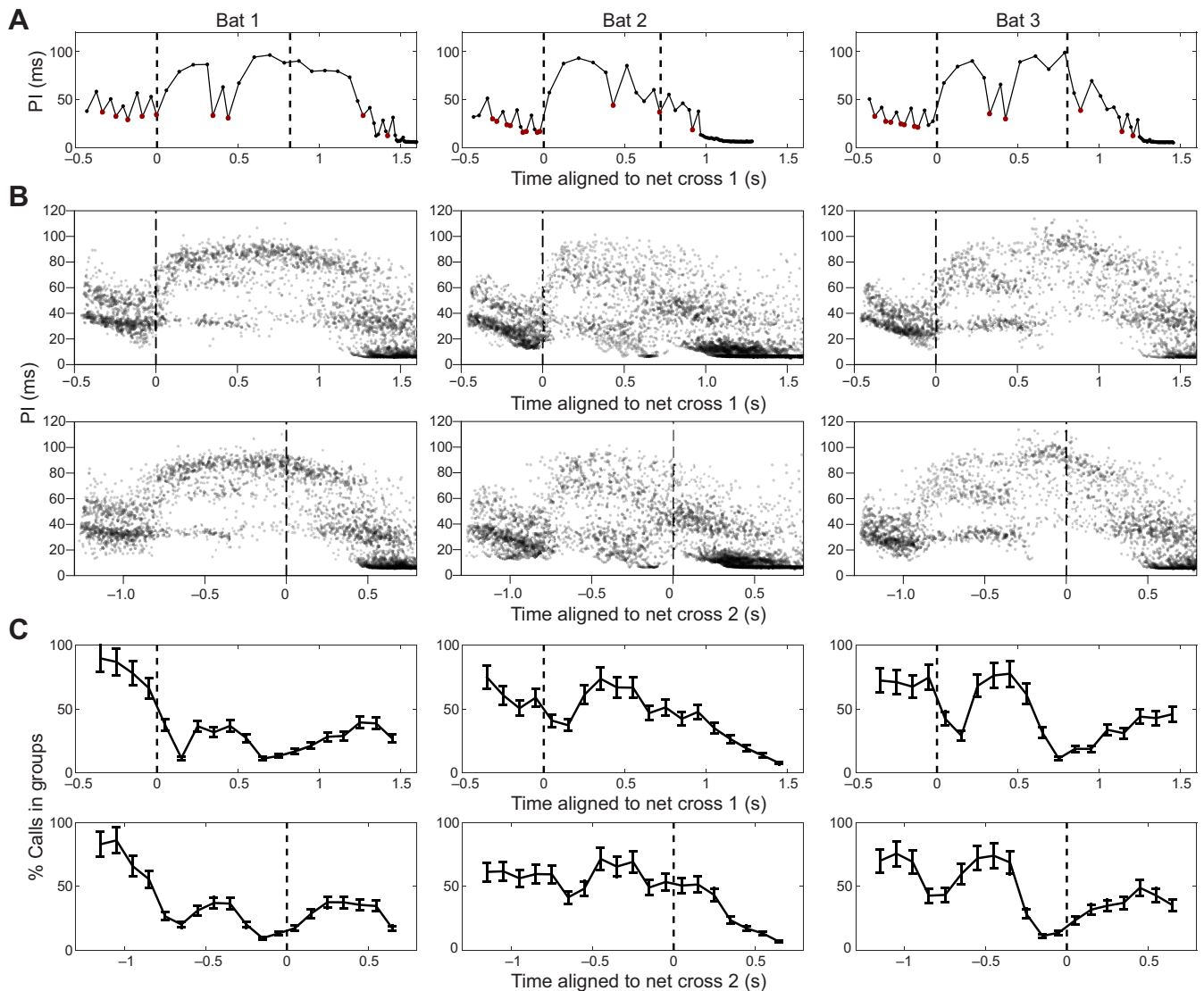
crossing (see Movies 1–3). Across trials (Fig. 4B), clusters of vocalizations with short PI and long PI are evident, which indicate sonar sound groups. There was also a trend of decreasing PI as the bats approached the first net opening. The timing of the terminal buzz occurred earlier in bat 2 than in bats 1 and 3. Bat 2 also produced a buzz group before the second net opening in 8.70% of trials, with an average pulse production rate before the second net opening in these trials reaching  $155.07 \pm 1.83 \text{ calls s}^{-1}$ . The percentage of calls in sound groups varied during the task (linear mixed effects model, Wald  $\chi^2_{20}=621.54$ ,  $P<0.001$ ), and was high prior to the first net crossing and in between the nets before the second net crossing (Fig. 4C).

The bats in this study altered the duration of their sonar sounds in relation to the distance to the net openings (linear mixed effects model, Wald  $\chi^2_{11}=677.7$ ,  $P<0.001$ ) (Fig. 5A). As the bats approached the first net opening, they used longer duration pulses of 2.9 ms (95% CI 2.6, 3.2) at 0.45 s before crossing net one. The bats decreased pulse duration by 0.4 ms from 0.45 s before the first net crossing to 0.15 s before the first net crossing ( $z=-9.633$ ,  $P<0.001$ , Tukey correction). Pulse duration then increased after crossing the first net by 0.2 ms, from 0.15 s before the first net crossing to 0.15 s after the first net crossing ( $z=6.180$ ,  $P<0.01$ , Tukey correction). As the bats approached the second net opening, pulse duration decreased by 0.6 ms, from 0.7 s before the second net crossing to 0.4 s before the first net crossing ( $z=-8.653$ ,  $P<0.001$ , Tukey correction). However, as the bats crossed the second net, pulse duration increased by 1.5 ms, from 0.4 s before the second net crossing to the time of the second net crossing ( $z=22.489$ ,  $P<0.001$ , Tukey correction). Pulse duration then decreased after crossing the second net as the bats prepared to capture the tethered insect.

We measured the end frequency of each sonar vocalization, excluding calls in the terminal buzz, and found that the bats adapted the frequency content of their sonar signals in the presence of the net obstacles (linear mixed effects model, Wald  $\chi^2_{11}=1016.9$ ,  $P<0.001$ ) (Fig. 5B). There was a difference in call end frequencies between the individual bats, with a maximum difference of 5.5 kHz, but the bats changed end frequency as they navigated the nets in a similar pattern to each other, decreasing near the first net opening, decreasing between the nets, and increasing after the first net crossing and during the approach to the second net opening. The bats had an average end frequency 0.45 s prior to the first net crossing of



**Fig. 3. Strouhal number during navigation of net openings.** (A) Count histogram of Strouhal number. (B) Strouhal number relative to each net crossing. Values for bats 1 and 2 are plotted (data for bat 3 were not used; see Materials and methods).



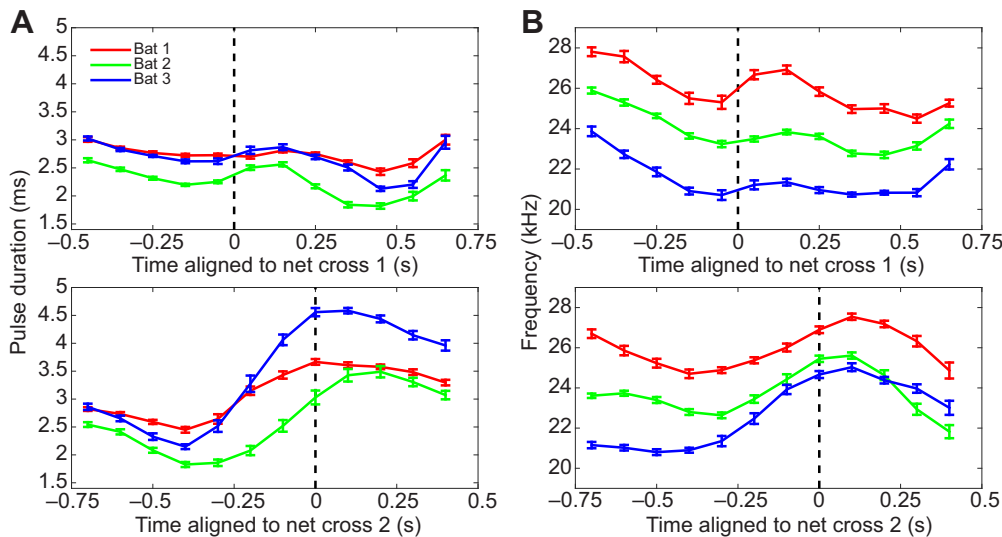
**Fig. 4. Pulse interval (PI) and sound group ratio relative to net crossings for each bat.** Left panels are bat 1, middle panels are bat 2 and right panels are bat 3. (A) An example trial sequence for each bat. The inner PI for each sound group is highlighted in red, with all other vocalizations in black. First and second net crossings are indicated with dashed black lines. (B) PI values plotted across all trials for each bat. (C) The proportion of calls in sonar sound groups plotted relative to each net crossing (bin size is 0.1 s and values are means  $\pm$  s.e.m.). The vertical dashed black line signifies the aligned net crossing (time 0).

25.8 kHz (95% CI 23.2, 28.3). The bats decreased end frequency from 0.45 s prior to the first net crossing to 0.05 s before the first net crossing by 2.7 kHz ( $z=-19.247$ ,  $P<0.001$ , Tukey correction). After crossing the first net opening, call end frequency increased by 1.0 kHz from 0.05 s before the first net crossing to 0.15 s after the first net crossing ( $z=6.977$ ,  $P<0.001$ , Tukey correction). The call end frequency decreased as the bats approached the second net opening, by 1.1 kHz from 0.7 s before the second net crossing to 0.4 s before the second net crossing ( $z=-6.058$ ,  $P<0.001$ , Tukey correction). The bats then increased end frequency before they crossed the second net crossing by 3.1 kHz, from 0.4 s before the second net crossing to 0.1 s after the second net crossing ( $z=17.204$ ,  $P<0.001$ , Tukey correction). After crossing the second net opening, as the bats prepared to capture the insect, call duration decreased. End frequencies of calls in sound groups were not different from single calls produced outside of sound groups. We also did not observe differences in end frequencies between calls within sound groups.

The pulse–echo overlap zone is the range in distance in which sonar emissions overlap with echo returns, calculated here relative to each net crossing (Fig. 6). When approaching the first net opening, bats did not reduce pulse duration with decreasing distance to the net. As a result, the bats experienced pulse–echo overlap with echoes from the net starting  $0.11 \pm 0.01$  s and  $0.43 \pm 0.03$  m prior to net crossing. As the bats approached the second net opening, pulse–echo overlap occurred earlier, starting  $0.22 \pm 0.02$  s before net crossing, but at approximately the same distance, at  $0.44 \pm 0.04$  m from net crossing.

#### Timing of sonar calls with wingbeat cycle

We calculated the relative timing of each sonar call with respect to the phase of the wingbeat for each bat (Fig. 7). We found that the timing of single echolocation signals occurred close to and before the end of the upstroke for each bat, at  $-31.6$  deg (95% CI  $-32.9$ ,  $-30.3$ ) in the wingbeat cycle. In sound groups with two calls (doublets), the first call occurred earlier, at  $-106.4$  deg (95% CI  $-124.6$ ,  $-88.2$ ), while



**Fig. 5. Pulse duration and frequency relative to each net opening.** (A) Pulse duration and (B) pulse end frequency are shown for bat 1 in red, 2 in green and 3 in blue. Data were averaged across 0.1 s time bins, and error bars are s.e.m. Top panels are aligned to the first net crossing; bottom panels are aligned to the second net crossing. Only data with a PI greater than 10 ms were included in this analysis. The vertical dashed black line signifies net crossing (time 0).

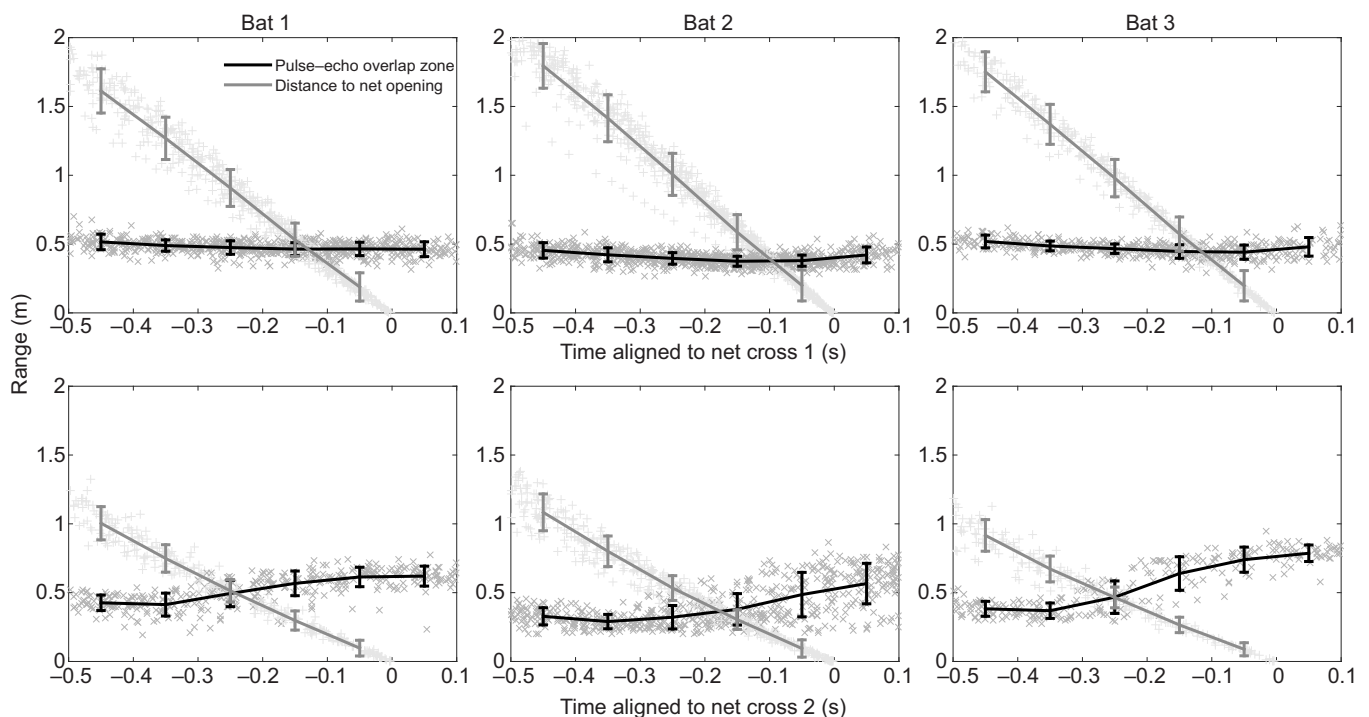
the second call in the doublet occurred later, at 20.4 deg (95% CI 8.7, 32.1). In sound groups with three calls (triplets), the first call occurred earlier, at -144.1 deg (95% CI -162.1, -126.1), close to the beginning of the upstroke. The middle call in the triplet occurred at -55.4 deg (95% CI -70.8, -40.0). The third call in the triplet occurred during the downstroke at 40.1 deg (95% CI 28.3, 51.9). There was variation in the specific timing of doublets and triplets between bats, but single calls had the least variation and occurred near the apex of the wingbeat cycle in all bats.

We examined the timing of calls relative to wingbeat phase either before or after the first net crossing for each bat (Fig. 8). Single calls were not emitted in large numbers before the first net opening, which

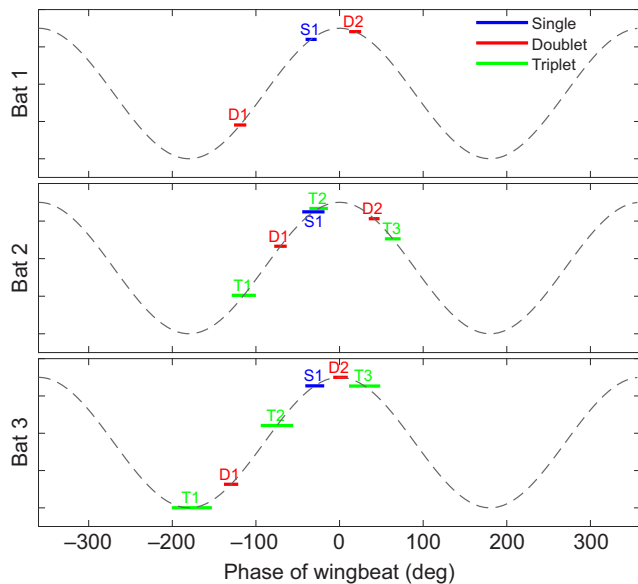
reduced our ability to characterize and compare the relative wingbeat phase for these calls. However, we did notice a trend in bats 1 and 2, with single calls occurring later in the wingbeat phase after the net crossing. Sonar calls in call doublets were also shifted to a later wingbeat phase after the net crossing, with the first call in doublets shifted from -128.6 deg (95% CI -147.0, -110.2) to -81.4 deg (95% CI -100.3, -62.5), and the second call in doublets shifted from -9.6 deg (95% CI -29.6, 10.4) to 47.3 deg (95% CI 30.5, 64.1).

#### Emission of sound groups relative to turn rate

We analyzed the temporal relationship between the percentage of calls in sound groups and each bat's turn rate (Fig. 9). During the



**Fig. 6. Pulse-echo overlap zone relative to the distance to net opening across multiple trials.** The pulse-echo overlap zone is the minimum distance an object can be to each bat without echoes from the net overlapping in time with produced pulses. Plotted are the mean pulse-echo overlap zone (black line) and the mean distance to the net opening (gray line) relative to each net crossing, with error bars as s.d. The top panels are the first net crossing and the bottom panels are the second net crossing. Left panels are bat 1, middle panels are bat 2 and right panels are bat 3. The individual values for each sonar call are also plotted: pulse-echo overlap zone as dark gray crosses and distance to net opening as light gray crosses.



**Fig. 7. Timing of sonar calls with respect to the phase of the wingbeat for each bat.** Top panel, bat 1; middle panel, bat 2; bottom panel, bat 3. Plotted separately are single calls (blue), sonar sound groups of two calls, or doublets (red), and sonar sound groups of three calls, or triplets (green). The span of the lines indicates 95% confidence intervals. For calls in sound groups, the call order is indicated with a number above each mean value. Triplets that did not meet requirements for a 95% confidence interval were not plotted (this occurred in bat 1). Terminal buzz calls were excluded. Non-buzz vocalizations were included from 0.5 s before the first net crossing to 0.075 s after the second net crossing for each trial.

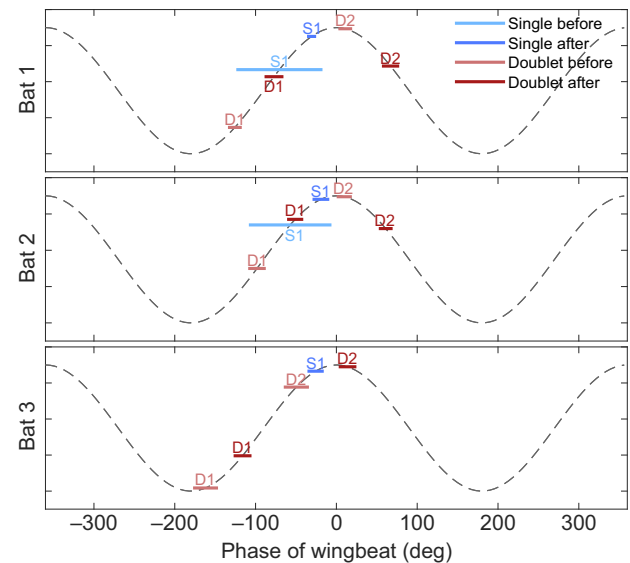
first net crossing, peak turn rate occurred 0.15 s after crossing, while peak percentage of calls in sound groups occurred 0.25 s before crossing. During the second net crossing, peak turn rate occurred 0.05 s before crossing, while peak percentage of calls in sound groups occurred 0.45 s before crossing. We compared turn rate and sound group percentage at these times and found the production of sound groups was high preceding each turn, but low during each turn (Table 2). We also cross-correlated the sound group percentage and turn rate and found the best correlation occurred at a time lag of 0.35 s for each bat and net crossing, except for bat 1 aligned to the second net crossing, which had a best lag of 0.3 s.

## DISCUSSION

This study investigated the coordination of flight and echolocation behaviors in the big brown bat, *E. fuscus*, as it negotiated a flight corridor to gain access to a tethered prey item. Bats made adjustments in flight speed, turn rate and climb rate, which coincided with adaptive changes in sonar behavior. In addition, bats adjusted the timing, duration and frequency of sonar vocalizations in relation to obstacle navigation and insect capture. In straight flight, bats produced sonar calls in phase with the upstroke of the wingbeat cycle, but that relationship changed when the bats navigated through openings in the net corridor.

### Strouhal number

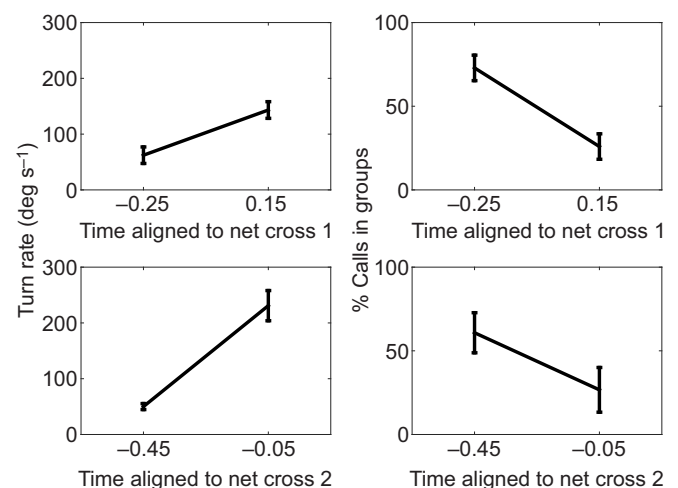
A study by Norberg and Winter (2006) showed that the nectar-feeding bat *Glossophaga soricina* achieved efficient Strouhal numbers at high flight speeds, but at low flight speeds, the Strouhal number increased to values that incur unsteady effects. In the same study, wingbeat rate was found to vary with flight speed at high flight speeds, but not at low flight speeds. While we found changes in wingbeat rate to coincide with obstacle navigation and



**Fig. 8. Timing of sonar calls with respect to the phase of the wingbeat before and after the first net crossing for each bat.** Plotted separately are single calls (blue) and sonar sound groups of two calls, or doublets (red). Calls before the net crossing have light shading and calls after the net crossing have dark shading. The span of the lines indicates 95% confidence intervals. For calls in sound groups, the call order is indicated with a number above each mean value. Single calls prior to the first net opening for bat 3 did not meet the requirements for confidence intervals and were not plotted. Triplets did not meet requirements for 95% confidence intervals along this time scale and were excluded from the analysis. The period of time for inclusion was 0.5 s on either side of the first net crossing.

maneuvering (Fig. 2D), flight speed and wingbeat rate were not strongly correlated (Fig. S1).

At low speeds, hovering-capable bat species produce a backwards flip of the wing tip (Norberg, 1970; Norberg and Winter, 2006), which has been suggested to generate lift (Norberg, 1976). These bat species have also been found to take advantage of a leading edge vortex to generate lift when flying at slow flight speeds (Muijres et al., 2008, 2014). In the present study, *E. fuscus* was never observed making a backwards flip of the wing tip, so this source of potential lift would not be available. While *E. fuscus* primarily forages in open space, it also hunts in cluttered environments, in and around vegetation, using adaptable pursuit strategies (Simmons,



**Fig. 9. Turn rate and percentage of calls in sound groups compared at their relative peak values.** Values are means  $\pm$  s.e.m.



**Table 2. Pairwise comparison of turn rate and percentage of calls in sound groups at peak times aligned to each net crossing**

	Time 1	Time 2	Estimated difference	z	P
Net cross 1, turn rate	−0.25	0.15 (peak)	78.0 deg s <sup>−1</sup>	14.203	<0.001
Net cross 1, sound group percentage	−0.25 (peak)	0.15	−32.0%	−6.574	<0.001
Net cross 2, turn rate	−0.45	−0.05 (peak)	182.0 deg s <sup>−1</sup>	34.085	<0.001
Net cross 2, sound group percentage	−0.45 (peak)	−0.05	−37.6%	−7.548	<0.001

Linear mixed effects model, Tukey correction. Time 1 for each net crossing was the time of peak sound group call percentage, while time 2 was the time of peak turn rate.

2005; Simmons et al., 2001). While maneuvering around obstacles, *E. fuscus* has been found to fly at slower speeds (Falk et al., 2014). Thus, unsteady flow effects, and alternative forms of generating lift, may occur when *E. fuscus* flies in different conditions.

**Adaptive sonar behavior**

The bats in the present study adjusted sonar behavior with respect to the net openings by altering the rate of overall call production, sonar sound group production, call duration and call end frequency (Figs 4, 5). By producing calls with shorter PI, such as when bats flew near the nets, they increased the rate of echo returns, which may have helped them localize the net openings. Previous research reported adaptations in pulse rate, duration and frequency during obstacle navigation (Jen and Kamada, 1982). In the present study, we report differences in the adaptive sonar behavior when navigating two obstacles in sequence. The PI of calls produced by bats approaching the second net opening was longer than that when approaching the first net opening. Additionally, the timing, call end frequencies and sonar sound durations were different between the two net crossings.

The two net crossings the bats encountered required different aerodynamic maneuvers. The different maneuvering requirements likely had an impact on the observed differences in sonar behavior. The second net opening was larger than the first net opening (0.51 m<sup>2</sup> area compared with 0.27 m<sup>2</sup>), which may have decreased localization requirements for the second net opening and reduced the need for a high pulse rate. The first net crossing occurred after a dive, as the bat entered the corridor from the open room, while the second net crossing occurred after a steep climb at slow flight speeds and high turn rates. Thus, it is not surprising that the echolocation behavior of the bats was different under these two conditions. For example, the flight speeds of the bats approaching the first net opening were approximately twice those of bats approaching the second net opening, which likely influenced rapid localization requirements at each net crossing. Once inside the net corridor, the bats could have relied more heavily on the nets as landmarks (Jensen et al., 2005). Their slower approach to the second net opening also allowed more time and reduced echo information requirements. Furthermore, the lower call rate of bats during the climb and turn within the corridor can be understood in terms of combined energetic costs of the flight and vocal motor behaviors.

**Sonar sound groups**

Bat echolocation sound groups, clusters of calls flanked by signals at longer intervals, are produced when animals encounter challenging sonar tasks requiring figure–ground segregation and accurate measurement of target position (Kothari et al., 2014; Moss et al., 2006). These sound groups are therefore hypothesized to support high-resolution sonar information (Moss and Surlykke, 2010). In this study, bats emitted sonar sound groups at relatively high incidence prior to navigating the first net opening and again between the nets, as they prepared to exit the second net opening

(Fig. 4). The shorter pulse intervals of sonar sound groups could allow the bat to sample spatial information with greater reliability (Moss et al., 2006), which would aid in navigation around obstacles.

Emitting sounds in phase with the expiration cycle of respiration is energetically advantageous (Speakman and Racey, 1991; Speakman et al., 1989), so even as the bats increased call production rate, they timed their call emissions, both within sound groups and for single calls produced outside of sound groups, with the rising phase of the wingbeat cycle (Fig. 7). Koblitz et al. (2010) and Wong and Waters (2001) reported similar patterning of calls with respect to the phase of the wingbeat cycle. Koblitz et al. (2010) also found that source levels varied with the wingbeat phase. We propose that patterning of sonar calls into groups allows bats to increase echo information flow without incurring large energy costs (Speakman and Racey, 1991).

**Duration adjustments and inner window with respect to net position**

As species of bats emitting FM sonar signals approach a target, they typically reduce the duration of their sonar sounds to avoid temporal overlap between their emitted pulses and returning echoes until the final phase of the terminal buzz (Kalko and Schnitzler, 1989; Schnitzler and Kalko, 2001). We found that as the bats navigated each net opening, they failed to reduce call duration to avoid overlap between their emitted sonar sounds and returning echoes from the nets (Fig. 6). In fact, the bats increased pulse duration when approaching the second net opening, which resulted in an overlap between pulse and net echo as early as 250 ms before the net crossing.

The increase in call duration prior to the second net crossing may reveal a shift in acoustic gaze to the insect behind the net. Longer duration calls are better suited for detection, as they return higher energy echoes. Previous studies found that bats navigating a single net opening, prior to capturing an insect, produced sound durations that overlapped with returning echoes from the net (Jensen et al., 2005; Surlykke et al., 2009). Surlykke et al. (2009) measured the aim of the sonar beam and reported that the bats directed their sonar beam on the more distant insect before they crossed the net opening while they experienced pulse–net echo overlap. Thus, as in the report by Surlykke et al. (2009), the bat’s failure to decrease call duration to avoid pulse–net echo overlap in this study may serve as an indicator that the animal shifted its attention to the more distant prey item beyond the second net crossing. We infer that during this segment of the trial, the bats may have relied on spatial memory for navigation.

**End frequency changes suggest changes in directionality**

Jakobsen and Surlykke (2010) found that foraging bats achieved a broadened sonar beam, and a widened field of view, by decreasing the frequency of their sonar calls during terminal buzz while keeping the effective sonar emitter size constant. Kloepper et al. (2014) found changes in mouth gape in a stationary bat trained to a

platform during target detection, but those changes did not contribute strongly to changes in sonar parameters. Kounitsky et al. (2015) found that as bats approached a pond in order to drink, and as they flew away toward open space, they adjusted mouth gape without changing peak frequency, which resulted in a narrowed sonar beam when approaching the pond and a widened beam when flying towards open space. However, all sound frequencies can contribute to the sonar beam. In the present study, we found fine-scale changes in sonar call end frequency that occurred as the bats maneuvered in flight around obstacles (Fig. 5B). Assuming a constant emitter size, 5.9 mm as reported by Jakobsen and Surlykke (2010) for *Eptesicus serotinus*, similar to *E. fuscus*, we estimated the beam width using a piston model (Strother and Mogus, 1970). As the bats approached the first net opening, they decreased end frequency of the FM sweep from 26.2 to 23.4 kHz, which, according to the model, would increase the half-amplitude angle of their sonar beam by 10 deg, from 51 to 61 deg. From the time the bats approached the second net opening to just after the second net crossing, the bats increased end frequency from 22.8 to 25.9 kHz, which would decrease the half-amplitude angle by 12 deg, from 64 to 52 deg. These results indicate that bats could manipulate their sonar beam width as they maneuver around obstacles by changing the frequency characteristics of their sonar calls. Detailed measurements of changes in mouth gape and sonar beam width across frequency are needed to fully characterize the fine scale adjustments of the sonar beam field of view and search volume.

### Timing of sonar calls in relation to wingbeat phase and net position

As discussed by Koblitz et al. (2010), the coordination of sound groups with the wingbeat cycle indicates that call timing is planned several tens or hundreds of milliseconds in advance of production. The present study confirms that sound groups occur at consistent phases of the wingbeat cycle (Fig. 7). However, we also found that the relative timing of calls in relation to the wingbeat cycle changed when bats negotiated the turn and climb around the first net opening (Fig. 8). These differences in vocal patterning could be related to wingbeat irregularities during maneuvering. The shift in call timing pattern with respect to the wingbeat cycle likely resulted in changes in echo intensity, which we could not measure directly in this study. The timing of sonar calls relative to the wingbeat cycle appears to be adaptable and possibly influenced by task requirements and corresponding flight kinematics.

### Timing of sonar sound groups in relation to turn rate

Bats consistently produced sound groups as they prepared to enter the flight corridor and in between the nets (Fig. 4C). The emission of sound groups at this stage of the task did not occur when bats were engaged in turns, but instead occurred before the turns (Fig. 9, Table 2). Cross-correlating the sound group production with turn rate produced the best correlation with turn rate lagged by 0.3–0.35 s. The production of sound groups has previously been implicated in trajectory behavior near obstacles with a delay of 100–300 ms (Falk et al., 2014). Here, we found evidence along the same time scale, indicating that bats may use sound groups for path planning and navigation around obstacles.

### Conclusions

As a bat navigates and forages in cluttered environments, it must make precise and rapid adjustments in flight kinematics and echolocation call features. By quantifying the motor behaviors of bats engaged in a navigation task, we discovered that flight

kinematics and echolocation call features were not only dependent on the spatial relationship between the bat and obstacles but also tightly coordinated to execute integrated motor planning of sonar-guided orientation.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

B.F., J.K. and C.F.M. designed the research; B.F. and J.K. performed the research; B.F. analyzed the data; and B.F. and C.F.M. wrote the paper.

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### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.122283/-DC1>

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