

Sensory-Motor Behavior of Free-Flying FM Bats during Target Capture

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Introduction

Insectivorous bats face the formidable task of localizing and intercepting small, rapidly flying insect prey while the bat itself is on the wing. This task is successfully accomplished hundreds of times over a single evening in capture sequences lasting less than one second (Griffin, Webster, and Michael 1960). To understand the dynamic sensory processing and motor control underlying this complex task, our research focused on vocal-motor behavior of free-flying FM bats during sonar-guided localization and interception of targets.

In the laboratory, we recorded and analyzed the flight and vocal behavior of bats trained to intercept stationary tethered insects. The stationary-target paradigm has the advantage that the bat has complete control of its behavior during capture and does not need to compensate for the movement of the target. This advantage might reveal fundamental capture strategies used by bats during more complex captures of naturally moving insects.

We studied two species of bat, *Myotis septentrionalis* and *Eptesicus fuscus*. Both species use broadband frequency-modulated (FM) signals for echolocation and hunt insects on the wing. However, *M. septentrionalis* also gleans insects from surfaces (Miller and Treat 1993) and can eliminate sonar vocal emissions during the final portion of gleaning captures (Faure, Fullard, and Dawson 1993). In addition, *M. septentrionalis* is smaller in size (Kalcounis and Brigham 1995) and exhibits greater maneuverability in the lab. These factors suggest that *M. septentrionalis* may show greater flexibility in echolocation behavior than *E. fuscus*. Here, we compare the coordinated vocal-motor behaviors of these two bat species in an insect-capture task and consider whether sonar-target localization and motor planning early in the capture sequence determine behavior in the final stages of the sequence.

Materials and Methods

Five echolocating, big brown bats (*E. fuscus*) and six northern long-eared bats (*M. septentrionalis*) were trained to capture tethered mealworms in a large flight chamber (6.4 × 7.3 × 2.5 m) lined with acoustical

foam. Mealworms were suspended by monofilament line within a 5.3 m diameter target area in the center of the room. On each trial, bats were released from a consistent location, facing away from the target. They typically searched the room in a circular or figure-8 path for several seconds before localizing and capturing the target. Once bats achieved a consistent capture rate of nearly 100%, we carried out high-speed audio and video recording of their capture behavior.

Experiments were carried out using long wavelength lighting (Plexiglas no. 2711 and Bogen filter no. 182) to preclude visual orienting by the bat (Hope and Bhatnagar 1979). Two Gen-locked, high-speed video cameras (Kodak MotionCorder, 640 × 240 pixels, typically 240 Hz frame rate and $\frac{1}{240}$ s shutter speed) recorded target position, bat flight path, and target-capture behavior. A spatial calibration frame (2.2 × 1.9 × 1.6 m) was placed in the center of the room and filmed by both cameras prior to each session. These images were used in later calculation of the three-dimensional position of the bat, target, and microphones. We placed the target at random locations throughout the target area but recorded only captures that were within the calibrated portion of this space.

Echolocation signals were transduced using two ultrasonic microphones (UltraSound Advice SM1, spectral variation ± 5.5 dB from 10 to 100 kHz) placed within the calibrated area and recorded on the direct channels of a high-speed tape recorder (Racal Store-4, 30 ips). An additional FM channel recorded TTL synchronization pulses corresponding to the start of each video frame and gated to the end of video acquisition. The S/N ratio of the audio recordings was good during captures within the calibrated area, but it deteriorated at greater distances and when the bat was oriented away from the microphone.

ANALYSIS

A commercial motion analysis system (Peak Motus) was used to digitize selected points in each frame for both camera views and to calculate the three-dimensional location of marked points. The accuracy of the system typically was within $\pm 0.5\%$ (approximately ± 1.5 cm for the largest calibrated area). All audio channels were dig-

itized at $\frac{1}{4}$ recording speed (National Instruments AT-MIO-16-1, effective sampling rate 240 kHz/channel). Custom software trimmed the digitized audio data to correspond to the first and last frame of video acquisition, and output files were exported to a digital signal-processing program (Sona-PC, Waldman). The time and frequency structure of the first harmonic of the emissions was determined from sonograms (approximately 80 μ s time resolution, 470 Hz frequency resolution) and downloaded to a spreadsheet for further analysis. Off-line analyses correlated audio and video data and tracked changes in vocal-motor behavior with the relative position of the sonar target.

Results

Behaviors used to capture stationary tethered targets were similar to interfemoral membrane and wingtip catches used by vespertilionid bats capturing flying insects in the field (Webster and Griffin 1962). Both *E. fuscus* and *M. septentrionalis* captured tethered targets using a coordinated movement of the head, wing, and body to scoop the insect into the uropatagium (a pouch formed by the membrane between the tail and hind legs).

Biosonar behavior is divided into *search*, *approach*, and *terminal* phases (Griffin, Webster, and Michael 1960), based on the acoustic emission patterns of the bat as it approaches a target. During captures of stationary tethered insects, the vocal behavior of *E. fuscus* exhibited these characteristic changes in spectrum, inter-pulse interval (IPI), and pulse duration, culminating in a “terminal buzz” with an average minimum IPI of approximately 6.0 ms. The substrate-gleaning behavior used by *M. septentrionalis* lacks a terminal phase (Faure, Fullard, and Dawson 1993). However, while capturing stationary targets in the laboratory, *M. septentrionalis* also exhibited an approach and terminal phase in its vocal emission pattern (average minimum IPI of approximately 5.2 ms). This suggests that the stationary-target capture paradigm taps into the natural behaviors used for aerial hawking captures by both species. One striking difference in the vocal emission patterns of the two species (fig. 3.1) was that the terminal buzz was much longer for *E. fuscus* (mean \pm s.e.m. = 229.9 \pm 12.1 ms) than for *M. septentrionalis* (134.5 \pm 3.3 ms). Note also that the final echolocation pulse in the terminal buzz occurred before target contact, preceding contact on the average by 30 ms for *E. fuscus* and 25 ms for *M. septentrionalis*. A similar termination of the buzz just prior to contact has been reported in other species (e.g., Kalko 1995).

We observed stereotyped patterns in the IPI of both species while approaching and capturing stationary targets. Fig. 3.1 shows IPI functions for seven trials in which an individual *E. fuscus* intercepted tethered targets (3.1A) and seven trials for an individual *M. septen-*

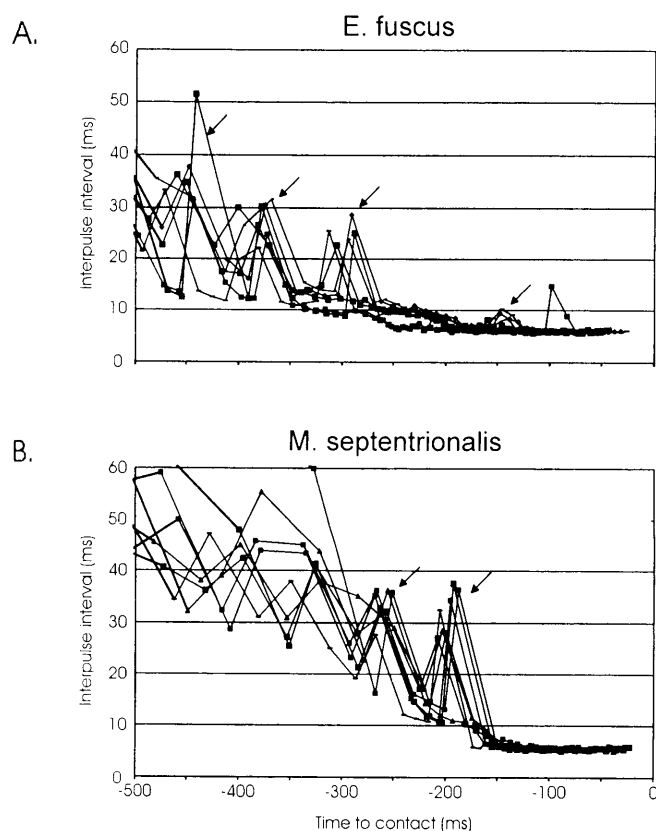


Fig. 3.1. Interpulse interval (IPI) functions for (A) seven trials in an individual *E. fuscus* and (B) seven trials for an individual *M. septentrionalis* while intercepting stationary tethered targets. The terminal buzz was defined as those IPIs less than twice the observed minimum IPI for each trial, which was shorter in *M. septentrionalis* (average onset 160 ms) than in *E. fuscus* (average onset 250 ms). Arrows indicate consistent increases in the IPI functions of both species (PEGs).

trionalis (3.1B). In each sequence, the target was at a different point in the room and the bat approached the target from a different location. However, peaks in the IPI functions, or pulse emission gaps (PEGs), occurred at consistent times during the late approach stage of the vocal sequence (arrows). PEGs occurred at about 450, 375, 300, and 150 ms before target contact in the example shown for *E. fuscus* and at about 250 and 200 ms before contact in the examples for *M. septentrionalis*. Note that the final PEG for *E. fuscus* occurred during the longer terminal buzz of this species. Similar breaks in vocal emission during the terminal phase have been reported by Schnitzler et al. (1987) in *Pipistrellus kuhli*.

In addition, both species appear to use a stereotypical pattern in their wing-beat cycle during the last approximately 400 ms of the capture sequence. Fig. 3.2 shows a raster plot of wing-beat timing relative to target contact for 13 target captures from *E. fuscus* and 13 target-capture trials from *M. septentrionalis*. In general, wing-beat frequency was lower for *E. fuscus* than for *M. septentrionalis*—13 Hz and 14.2 Hz, respectively.

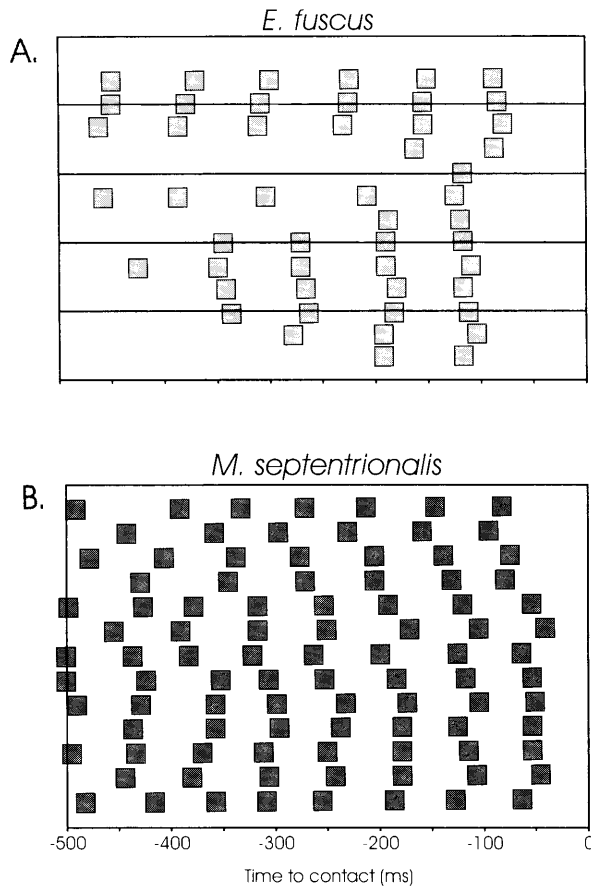


Fig. 3.2. Raster plot of wing-beat timing relative to target contact for (A) 13 target captures from an individual *E. fuscus* and (B) 13 trials in an individual *M. septentrionalis*. Single trials are shown along each row, with each symbol representing the timing of the bottom of a wing stroke. We used a different lens for the video recordings of the *E. fuscus* and the bat was in view for a shorter period before capture, decreasing the number of data points per trial.

However, for the *E. fuscus* shown in fig. 3.2A, wing beats do not appear to be randomly distributed; rather, they exhibited a consistent pattern across trials, suggesting that the bat used stereotypical wing-beat patterns to approach the target. The different pattern in the top four trials and the bottom nine trials suggests that *E. fuscus* might use two different, but stereotyped, strategies to capture stationary targets. For *M. septentrionalis* (fig. 3.2B), a columnar pattern also emerged about 300–400 ms before target contact, again regardless of target position or angle. While larger sample sizes would permit a more rigorous analysis, these data, particularly for *E. fuscus*, show that wing gait is not randomly distributed in the last 300–400 ms before contact.

Fig. 3.3 shows the timing of pulse emission gaps relative to wing-beat cycle in an individual *E. fuscus*. Almost all PEGs occurred during the second half of the wing-beat cycle, during the downward phase of the wing

stroke. These findings are consistent with work in *Phyllostomus hastatus* (Suthers, Thomas, and Suthers 1972), demonstrating that inspiration occurs during the downward portion of the wing cycle and exhalation on the upward phase. This relationship might be expected to produce gaps in vocal output synchronized with wing cycle, as has been observed in other species (Schnitzler and Henson 1980). Therefore, the stereotypy of the wing cycle before target capture demonstrated above could produce consistent respiratory patterns and, consequently, pulse emission gaps in the late approach phase of target capture.

A third consistent motor pattern is the bat's control of its range relative to the target during the final stages of capture. Fig. 3.4 shows the distance of *E. fuscus* (fig. 3.4A) and *M. septentrionalis* (fig. 3.4B) to the target as a function of time. Both species control their velocity relative to the target in the final 300–400 ms before contact. *E. fuscus* approached the target at about 3.2 m/s during the final portion of the capture. For *M. septentrionalis*, the relative velocity during this same period was about 2 m/s. Lee et al. (1995) calculated the function τ (estimated time of contact based on distance and velocity) for two *E. fuscus* catching stationary tethered targets. This estimate was accurate throughout stationary-target captures (their fig. 3E and 3F), suggesting that a constant capture velocity was maintained in these sequences as well (Lee et al. 1992).

The beginning of terminal buzz for *M. septentrionalis*

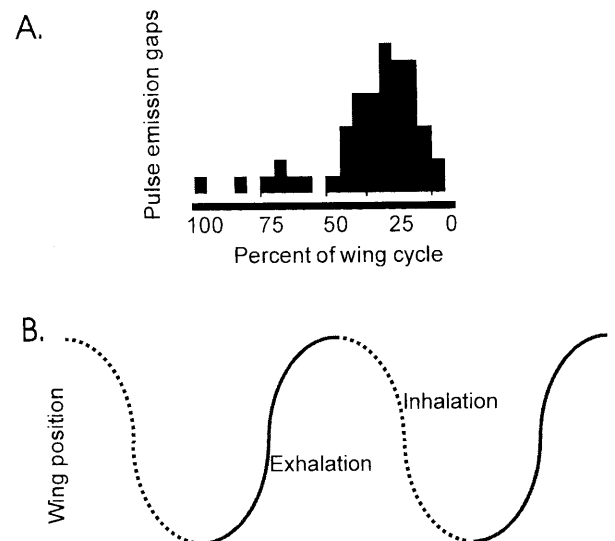


Fig. 3.3. A: Timing of pulse emission gaps at a function of wing cycle (defined as the time between the bottom of wing strokes) in an individual *E. fuscus*. The majority of PEGs were during the second half of the wing cycle, or during the downward portion of the stroke. B: The sinusoid shows the relationship between wing cycle and respiratory cycle (Suthers, Thomas, and Suthers 1972) on the same time scale.

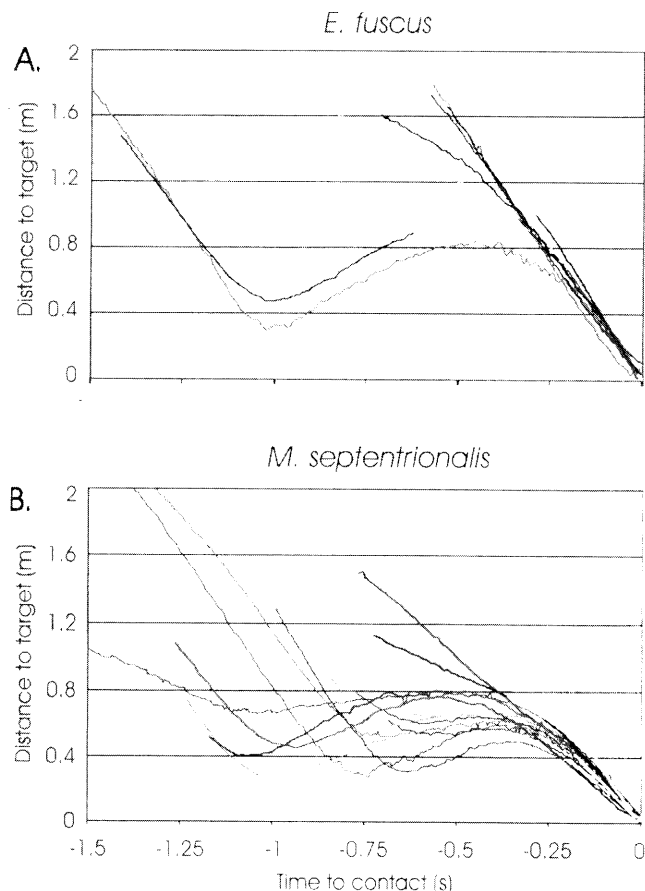


Fig. 3.4. Target range as a function of time to contact for (A) an individual *E. fuscus* and (B) three *M. septentrionalis* as determined from three-dimensional reconstruction of the flight path during target capture. A consistent linear portion and slope is present in each of these curves immediately before contact, indicating that a consistent relative velocity is maintained in the final stage of the capture sequences. Note that *M. septentrionalis* is capable of higher relative velocities than used during the final portion of the capture, exhibiting relative velocities of over 3 m/s in the early portion of some sequences.

averaged about 160 ms before contact (fig. 3.1B), well after the beginning of the constant relative velocity phase. Likewise, the beginning of the terminal buzz for *E. fuscus* averaged about 250 ms, also after constant relative velocity was initiated. Given the relative velocities of the two species and the timing of their terminal buzz, the distance from the target at buzz onset works out to about 32 cm for *Myotis septentrionalis*, similar to that observed by Webster (1962) in *Myotis lucifugus*. However, *Eptesicus fuscus* began the buzz at a much greater range, about 82 cm. Based on the maximum pulse emission rate of around 167 Hz for *E. fuscus* and 192 Hz for *M. septentrionalis*, the two species travel about 1.9 and 1.0 cm/pulse between pulses, respectively, during the buzz. Therefore, the rate at which acoustic information is acquired by *M. septentrionalis* is higher than for *E. fuscus*, measured in terms of both time and distance.

Discussion

We showed that acoustic information available to the bat prior to the onset of the terminal buzz is sufficient not only to induce changes in vocal emission pattern, but also to adjust wing gait and relative velocity. Our working hypothesis is that both *E. fuscus* and *M. septentrionalis* generate a motor plan for target capture about 400 ms prior to contact, presumably to coordinate scooping the target into the interfemoral membrane with a favorable wing-beat phase. Preparatory adjustments in tail position before contact have been observed in *Myotis lucifugus* (Webster and Griffin 1962) and in several pipistrelle species (Kalko 1995). These behaviors suggest that bats may calculate the time to contact to initiate preparatory movements at the correct point in the capture sequence. Webster and Griffin (1962) also argued that calculating a motor plan before target contact would be necessary to position the bat at the location of a moving target. Other investigators have suggested that echolocating bats might update spatial information on an echo-to-echo basis, orienting toward the last known target position until collision (e.g., Masters, Moffat, and Simmons 1985). If the motor patterns shown above are in fact anticipatory adjustments for capture at a favorable wing-beat phase, this would indicate that the bat can calculate location and wing phase at least 400 ms in the future. However, the observed pattern might also emerge as a result of the bat controlling its relative velocity or direction to the target (i.e., without planning *per se*). Experiments that might shed light on this problem would determine if the stereotyped motor behaviors are also present during capture of a moving target and when the bat must either predict, or adjust for, changing spatial relationships introduced by the target.

The pulse emission gaps demonstrated above are similar to those shown by Turl and Penner (1989) in the beluga, *Delphinapterus leucas*. PEGs in the sonar emissions of stationary beluga were longer than the two-way travel time of the signal to the target, thus allowing echoes to return without overlapping with outgoing sonar pulses—a potentially confounding factor in echo information processing. Fig. 3.5A shows how echoes returning from targets within an “inner window” can overlap with the end of the outgoing pulse. Echoes returning from targets outside an “outer window” can temporally overlap with later sonar emissions.

Fig. 3.5B shows the IPI and sonar pulse duration for a stationary-target capture by *E. fuscus*. The ranges within an “overlap-free” window based on these acoustic data are shown in fig. 3.5C. The actual target range during this trial, determined from three-dimensional reconstruction, is within the overlap-free window except during the final 60 ms (18 cm), where overlap occurs in the inner window. Note that the PEGs at approximately 450, 380, and 300 ms before target contact have a large

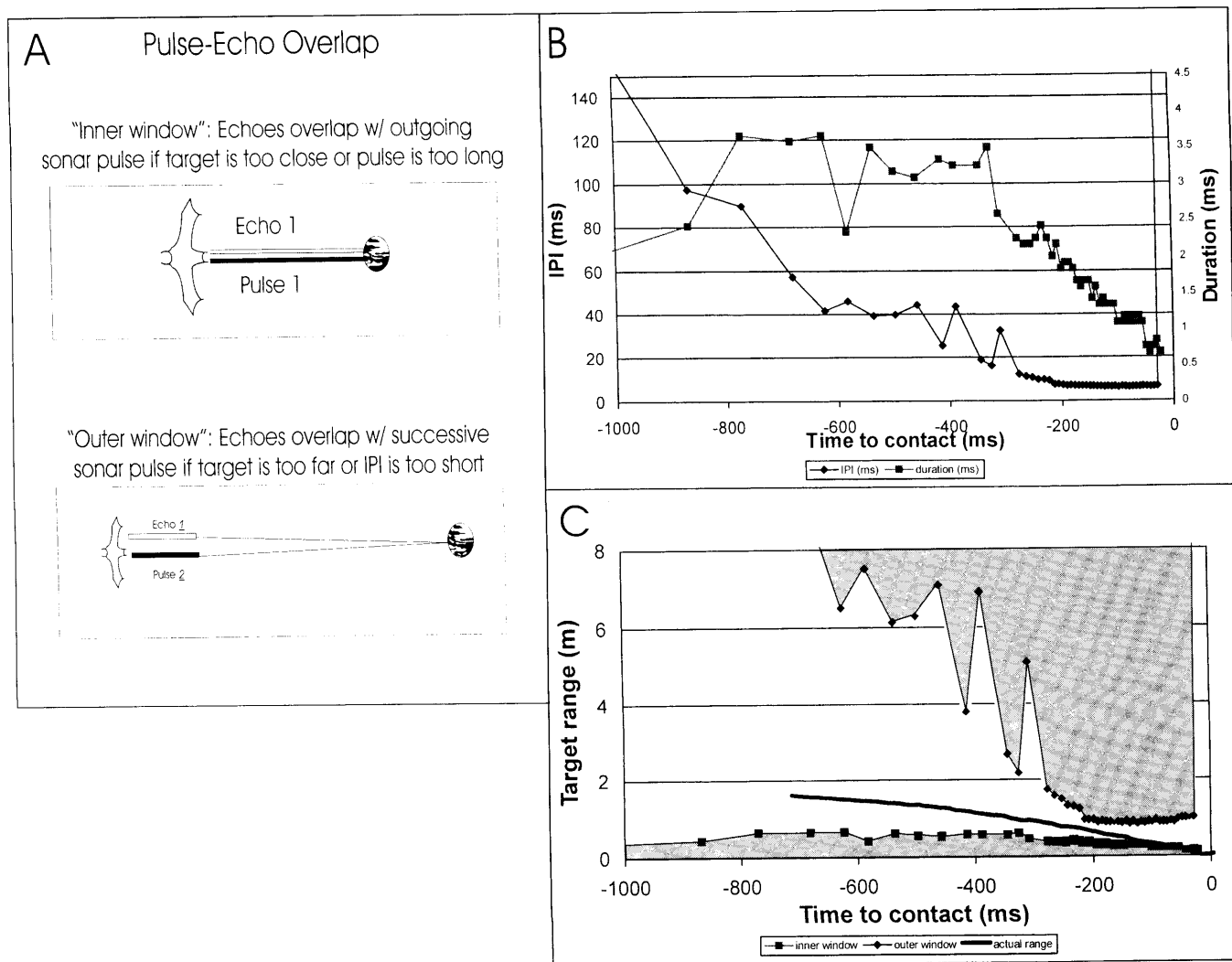


Fig. 3.5. *A*, inner window: Pulse-echo overlap can occur when targets are closer than the two-way travel time of a given pulse. The inner window is determined by the sonar pulse duration. *A*, outer window: Echoes from targets farther than the "outer window" can temporally overlap with later sonar emissions. The outer window is determined primarily by IPI and duration of the echolocation pulses. *B*: IPI and sonar pulse duration for a representative stationary-target capture by *E. fuscus* showing PEGs at about 450, 380, and 300 ms before target contact. *C*: Target ranges between the inner and outer window shown for acoustic data in *B*. Shaded areas show target ranges at which pulse/echo overlap is possible. Distance of the bat to the target for this trial is also shown.

influence on the outer window, producing periodic increases in the maximum target distance without overlap. These periodic increases in IPI might influence the perceptual system of the echolocating bat. For example, brief increases in the operating range of the biosonar system caused by PEGs might be useful in localizing more distant targets, allowing the bat to establish figure/ground relationships before the effective range of the system is diminished during the terminal buzz (fig. 3.5C).

The common features in the motor patterns of *E. fuscus* and *M. septentrionalis* described above are produced by modifying underlying behaviors that differ in detail.

The most striking differences between the two species are the emission rate during the terminal buzz, the terminal buzz duration, and the relative velocity during the final stages of target capture. The difference in emission rate (or IPI) between *E. fuscus* and *M. septentrionalis* might be explained by size differences between the two species. For example, smaller pipistrelle species have vocal emission patterns with shorter IPIs (Kalko 1994). Moreover, given the coupling between wing-beat cycle and vocalization and the higher wing-beat rate in *M. septentrionalis*, one might expect higher vocalization rates in this species.

The difference in terminal buzz duration could be explained by different target detection ranges in the two species, with a later detection in *M. septentrionalis* giving rise to a shorter terminal buzz. However, we showed that stereotypical wing-beat and velocity control emerge at roughly the same time in the capture sequence of both species. This suggests that the later terminal buzz in *M. septentrionalis* is not due to later detection. Estimates of the vocal emission levels suggest that the two species could receive echoes of similar intensities (Kick 1982; Miller and Treat 1993), which also argues against the idea of late detection in *Myotis septentrionalis*. Terminal buzz duration is labile within a number of species, varying dramatically from trial to trial (Schnitzler et al. 1987). Here, we showed differences in the buzz duration of two bat species capturing targets under identical conditions, suggesting that species-specific characteristics of biosonar systems also influence terminal buzz duration.

It is difficult to interpret any relative advantage of the more rapid approach and longer terminal buzz used by *E. fuscus* or the slower approach and shorter terminal buzz of *M. septentrionalis*. This is due, in part, to having little information about the function of the terminal buzz. The higher emission rate of the terminal buzz must be useful in increasing both the temporal and spatial information flow in the biosonar system. This might help the bat in fine control of its flight behavior before contact, especially if control of flight behavior is accomplished by monitoring acoustic variables related to relative velocity and location (Lee et al. 1995). From our data, it appears that *M. septentrionalis* puts a premium

on the information conveyed by this acoustic behavior. Both the lower flight speed and higher emission rate of *M. septentrionalis* served to increase the pulse density per unit distance during the terminal buzz to twice that of *E. fuscus*. This would provide more detailed information during the final few hundred milliseconds before contact, and it also might compensate for the shorter buzz duration in this species.

In summary, we made a direct comparison of the vocal-motor capture behavior of two FM bat species capturing targets under identical conditions. These comparisons revealed a set of stereotypical behaviors used by echolocating bats for capturing insect prey. Early motor behaviors included patterning of the wing-beat cycle, a coincident pattern in biosonar vocalization pattern, and a period of constant relative velocity. These behaviors emerged about 300–400 ms before target contact in both species and could be evidence for an early motor plan for target capture. Future experiments will explore the question of motor planning further, focusing on the influence of target movement on these behaviors.

Acknowledgments

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Biosonar Pulse Production in Odontocetes: The State of Our Knowledge

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Introduction

The story of the evolution and diversification of odontocetes is primarily one about the development of echolocation/biosonar. The development of echolocation was arguably the preeminent adaptive advantage that allowed odontocetes to diversify into the oceans of the world. The apparatus that supports the biosonar function can be divided into sound-generation and sound-

reception components, one no less important than the other. In this chapter, we focus on toothed whale sound-generation components. In some species, these tissue components constitute a system that is capable of producing sounds that approach the finite limit of acoustic intensity in water (Griffin 1980) and may border on the potential to cause tissue damage (Norris and Møhl 1983).

In this summary of odontocete biosonar signal generation, we outline the current primitive understanding of