Versatility of biosonar in the big brown bat, *Eptesicus fuscus*

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Abstract: Infrared cameras and ultrasonic microphones were used to record big brown bats (*Eptesicus fuscus*) flying in natural conditions at night while they hunted for insects. As expected, bats avoided obstacles while flying through vegetation and intercepted flying prey in the open. But bats also appeared to capture insects near and possibly on the ground and near or in vegetation, flew low over water to drink, and pursued each other in aerial "dogfights." In less than a minute, the same bat often used echolocation for several different tasks, showing a wider repertoire of sonar-guided behavior than revealed by previous observations limited to seeing bats flying against the evening sky or being photographed in fixed fields-of-view.

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1. Introduction

The big brown bat, *Eptesicus fuscus*,[1] transmits short-duration ultrasonic frequency-modulated (FM) sounds at frequencies of about 20 to 110 kHz to locate its prey, orient to objects, and perceive their shape and location.[2-4] These animals have evolved technologically interesting wideband processing techniques for representing objects from their echoes.[5] Big brown bats perceive the distance to objects from the delay of echoes.[4,6] They exhibit surprisingly fine delay acuity and can determine the delays of multiple, overlapping echoes by processing a time-frequency representation of the FM signals[4,7] with ~2 μs resolution of delay.[8] Such high delay acuity seems unnecessary if these bats were to use their sonar only to find and intercept individual flying insects in open areas where there are no competing echoes from clutter, particularly if identification of targets is not required to initiate pursuit.[4] These bats must encounter more complex situations where the presence of multiple targets or the need for target classification places a premium on high-resolution imaging.

It is difficult to observe bats while they deploy their sonar in many natural settings because they can be seen easily only when they fly silhouetted against the evening sky. Their dark fur makes them effectively invisible when they fly against a background such as vegetation or the ground. This limitation creates a bias in favor of watching bats only when they hunt for prey in the open. A variety of methods have been used to mark bats for observation, such as attachment of light tags or radio transmitters,[9] but these methods do not reveal details of how a bat maneuvers over short intervals of a few seconds at a time. Video cameras require illumination with bulky lights and power sources to watch bats in darkness. Even night-vision devices do not solve the problem of watching small, fast-flying bats against vegetation, although this method has been used for studying foraging by a large, ground-feeding species of bat.[10]

Our present understanding of how big brown bats use their sonar comes from visual field observations made in conjunction with extensive ultrasonic recording or use of acoustic "bat detectors,"[2,11,13] from laboratory photographic or video studies of interceptions staged before cameras,[14] and from photographs of bats in the field flying into the field-of-view of multiple strobe-flash cameras.[15,16] On this basis, big brown bats are assumed to belong to a "guild" of bat species that uses echolocation to pursue and capture insects flying in the open, but not to fly close to vegetation or the ground—either to find or to capture prey.[15,16] Nevertheless, big brown bats sometimes feed upon types of insects that do not fly and have to be taken from the ground.[1,7] Limitations of the usual methods of observation might explain why these bats appear to have a repertoire limited to aerial interceptions in the open. To overcome these limitations, we made recordings of the flight and acoustic behavior of bats with infrared cameras that are sensitive to the longer wavelength ("far") infrared signals given off by the animal's own body heat.[18]

2. Methods

A Raytheon PalmIR-250© thermal-imaging camera (spectral sensitivity 7-14 μm) was used to watch bats in flight, and video recordings were made with a Sony GV-A500 Video Walkman© Hi-8mm recorder. The ultrasonic sonar sounds of the bats were picked up with an Ultra-Sound Advice Mini-3 bat detector mounted on the camera for recording on one audio track of the videotape. This type of bat detector heterodynes the bat's ultrasonic broadcasts against a tuned frequency (here, 28-30 kHz) to deliver an audio display.[11] The first harmonic in the big brown bat's FM sounds was detectable over distances of 50-60 m, but most observations were made by moving to within 5-15 m of the bat. The system could store 1½ hours of video and audio data on one Hi-8mm videotape, and the camera, recorder, and bat detector were light enough to be carried for tracking bats through the viewfinder. A 25 mm or 50 mm lens proved best for following individual bats over spaces with dimensions of ~10-50 m. Recordings were examined the same night they were acquired to find specific events by playing the tape back on the Sony Video Walkman while listening to the heterodyned bat sounds. Flights were subsequently analyzed as MPEG video clips after digitizing them into a Pentium-II PC computer using a Pinnacle Systems Studio DC-10 video capture board with editing software.

We made recordings at several sites in Rhode Island and Nevada from mid-May to October 1999. Here, we report on Rhode Island sites where large numbers of May (June) beetles (Scarabidae) were emerging from the grass every evening to fly up into trees to feed and mate. Big brown bats are robust bats that feed mostly on larger insects.[1] They hunt May beetles extensively when they are "in season."

3. Results

This system proved superior for making observations of bat behavior at night because the bats are nearly always visible and can be followed for as long as they remain in line-of-sight out to 50-100 m or so. The bat detector gave early acoustic warning that bats were present and served to regulate the observer's vigilance with the camera. A total of 14 hours of recordings were accumulated at two sites where big brown bats could be observed reliably every evening for an hour beginning about one-half hour after sunset. At one site, near a school, big brown bats emerged singly or in pairs 30-45 minutes after sunset and flew about 50 m over the grass-covered school yard directly to a line of trees, night-after-night passing through the same location in the vegetation while in transit. Fig. 1a shows a single frame from a visible-light video recording made with a conventional 8-mm camcorder (Sony Model TR416) at its most sensitive setting to illustrate the difficulty of watching a flying bat at twilight. This bat is making a typical cruising flight on its way to pass through the trees. Fig. 1b shows an infrared recording of another bat emerging to follow the same path, also to pass through the trees. The corresponding video clips show each whole flight.

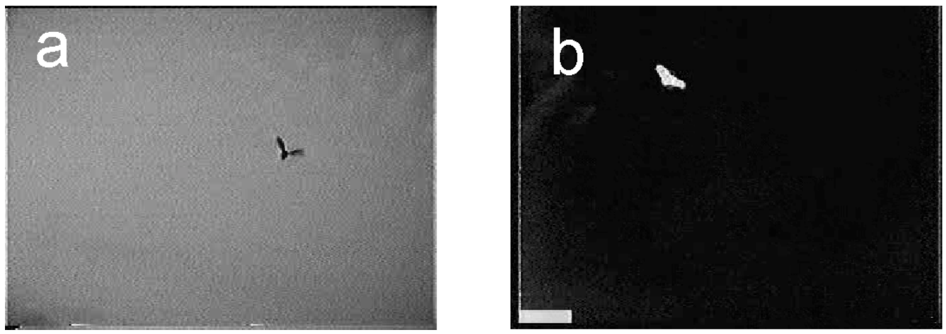

Fig. 1. Comparison of visible-light (a) and infrared (b) video frames showing a big brown bat in cruising flight from its roost to a feeding area (see Mms. 1-2).

Mm. 1. Visible flight (919 Kb)

Mm. 2. Infrared flight (639 Kb)

In the visible-light clip, the bat is a low-contrast object at best and cannot be seen after it has dropped below the tree line, whereas in the infrared clip it is a high-contrast object and remains visible even after it has flown lower than the tree line in the images.

Sometimes a bat flying out of the school maneuvered to capture a flying insect while it flew towards the trees, but most of the feeding was observed after these bats had emerged and flown away (whether these same bats returned to the school yard to feed is not known). Usually only one or two bats were present at a time, but on several occasions three or four bats appeared together. Then, approximately 90 minutes after sunset, bats were rarely seen, except for an occasional individual returning to the school or flying rapidly over the school yard. Just after sunset, adult May beetles (*Phyllophaga* sp.) emerged from the grass near the trees, flew up into the air, and then settled on the trees, presumably to feed on their leaves or to mate. Each night during the peak of the beetle season (late May to June), several trees at the edge of the schoolyard were enclosed by a cloud of hundreds of beetles hovering close to the vegetation or landing on the leaves. During their flight out of the grass, the beetles were vulnerable to midair interception by bats, as shown by the aerial capture in Fig. 2a and the associated video clip (Figs. 2a-f corresponds to Mms. 3-8). (Surprisingly, the beetles are visible in many of these recordings, possibly because they were warmed by their flight muscles.)

Mm. 3. Aerial (432 Kb)

Mm. 4. Near tree (444 Kb)

Mm. 5. In tree (754 Kb)

Mm. 6. Drinking (1,915 Kb)

Mm. 7. On ground (838 Kb)

Mm. 8. Dogfight (1,269 Kb)

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When searching for prey or cruising in an open area, big brown bats emit their FM sonar sounds at relatively slow rates of ~5 Hz, increasing the rate of emission to 20-30 Hz during approach and up to 150 Hz during the terminal stage of capture (audio track of Mm. 3).[2,11,12] The entire aerial maneuver lasts only a second, so these increases in repetition rate are very transient events. The beetles remained vulnerable to attack when they were flying in proximity to the vegetation as well as in the open, and bats sometimes pursued them quite near the trees to make interceptions (Fig. 2b and Mm. 4). The repetition rate of the sounds is higher for the bat flying near the tree line (audio track of Mm. 4) than for the bat flying in the open (Mm. 3).

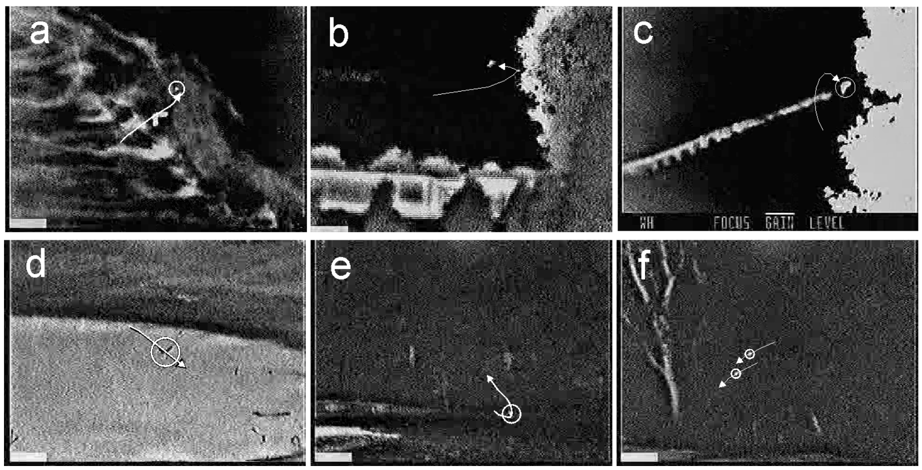

Fig. 2. Individual video frames from recordings of (a) an aerial interception in the open, (b) an aerial interception close to vegetation, (c) a capture made into vegetation with the bat emitting no detectable sounds during its approach, (d) a bat skimming over a pond to drink, (e) a capture on or near the ground, and (f) two bats chasing each other in a dogfight. Corresponding video clips are Mms. 3-8. The bat's location is circled where it is difficult to see in the frozen frame, and its track is shown by an arrow.

After May beetles flew into the vegetation and either landed on or hovered near the leaves, individual bats flew directly up to or even into the vegetation and appeared able to capture the insects (Fig. 2c). Sometimes the bat was seen dropping insect parts while flying away. These flights were distinguished from aerial pursuits of flying beetles or from transit flights through vegetation by the bat's apparent silence while flying towards the vegetation (audio track of Mm. 5). It is not known whether the bats actually ceased their sonar broadcasts altogether or just reduced the strength of emissions when they were approaching beetles in trees; in either case, their normally strong signals frequently dropped out of the recordings until they flew away from the vegetation. This occurred often for flights close to or into vegetation (Mm. 5) as distinct from ordinary aerial interceptions completed near vegetation (Mm. 4). The buzzing sounds of beetles flying among the leaves were audible through the bat detector, and we suppose the bats could hear the beetles and may have been guided by passive hearing. The bats might have reduced their emissions to reduce cluttering echoes or even to avoid alerting the beetles to their approach (suggestively, Mm. 5 shows beetles leaving the scene). Many insects that are active at night,[19,20] including at least one species of scarab beetle,[21,22] have evolved the capacity to hear the ultrasonic sounds of bats and take evasive action or other countermeasures. If May beetles do hear the sonar sounds of attacking bats and have evolved countermeasures, the bats may have adapted by reducing or eliminating the ultrasonic cues they offer the beetles during flights into vegetation.[20]

Big brown bats also were recorded while flying low over water to drink (Fig. 2d and Mm. 6), while flying low and possibly even contacting the ground to catch prey (Fig. 2e and

Mm. 7; in this case the observer heard the bat hit the ground), and even while pursuing each other in aerial "dogfights" (Fig. 2f and Mm. 8). In all of these situations, the bats emitted sonar sounds more or less continuously, at repetition rates that depended on how far away they were from the nearest surfaces. For example, when skimming low over water, the bat's sounds are produced at a steady, high rate until the bat flies up and away from the surface (audio track of Mm. 6; the strong background noise comes from ultrasonic-emitting insects in the vegetation around the pond). During what appeared to be attacks on insects on the ground, the bats did not become silent but instead continued to emit sonar sounds all the way down (audio track of Mm. 7). During bat-to-bat dogfights, both bats emitted sonar sounds that sometimes were audibly distinguishable from the bat detector output. Listening to the pattern of these differences suggests that the chasing bat and the chased bat might be emitting sounds in different temporal patterns (audio track of Mm. 8).

4. Conclusions

Big brown bats have often been observed pursuing insects in open areas,[2,13,15,16] and it is well established that they achieve airborne interceptions by sonar. If only one target is present, it is not difficult to conceive of how a bat can find and locate it from the well-isolated echoes this bat would receive. However, when several sources of echoes are present at about the same distance from the bat, the echoes will overlap to form a single, complex sound. The overlapping echoes would have to be separated by their arrival times and directions for the bat to perceive the objects individually.[4,7] This ability may be based on the processing of an expanded time-frequency representation developed in the bat's auditory midbrain.[5,7] The latency dispersion that creates neural delay lines in the big brown bat's inferior colliculus[23] integrates information about the timing of echoes with their spectral structure at a potential delay resolution at least down to 6-8 μs.[24]

Our infrared video observations reveal that big brown bats enter cluttered acoustic situations more often than would be expected if they belonged to a guild of aerial-feeding species whose echolocation is not capable of processing multiple echoes that overlap in time.[16] Hypotheses about echo that are processing based on the assumption that the bat's acuity of echo-delay perception is not better than 50-100 μs—which may be sufficient to account for interception of single airborne targets—have to be revised to accommodate the higher acuities implied by the bat's successful completion of more complex acoustic tasks, such as flights through vegetation, capture of prey near vegetation, and possibly capture of prey directly on vegetation or the ground. The scope of echo processing needed to guide bats through high-speed aerial dogfights (*e.g.*, Mm. 8) is a positive embarrassment for most current thinking about auditory coding of echoes. The video records also reveal that bats fly and maneuver very violently in many situations, exposing the vestibular system to high linear and angular accelerations. The full role of inertial sensing in conjunction with sonar to guide big brown bats through rapid maneuvers in the dark has not been determined, but we do know that disturbing vestibular input in blindfolded bats affects their obstacle-avoidance behavior.[25] These animals have evolved a well-developed nonvisual spatial sense whose receiver system and interactions with inertial sensing are likely to be of technological interest.

Acknowledgments

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