

J. R. Barber · K. A. Razak · Z. M. Fuzessery

## Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat *Antrozous pallidus*

Received: 23 January 2003 / Accepted: 26 September 2003 / Published online: 15 October 2003  
© Springer-Verlag 2003

**Abstract** A tenet of auditory scene analysis is that we can fully process only one stream of auditory information at a time. We tested this assumption in a gleaning bat, the pallid bat (*Antrozous pallidus*) because this bat uses echolocation for general orientation, and relies heavily on prey-generated sounds to detect and locate its prey. It may therefore encounter situations in which the echolocation and passive listening streams temporally overlap. Pallid bats were trained to a dual task in which they had to negotiate a wire array, using echolocation, and land on one of 15 speakers emitting a brief noise burst in order to obtain a food reward. They were forced to process both streams within a narrow 300 to 500 ms time window by having the noise burst triggered by the bats' initial echolocation pulses as it approached the wire array. Relative to single task controls, echolocation and passive sound localization performance was slightly, but significantly, degraded. The bats also increased echolocation interpulse intervals during the dual task, as though attempting to reduce temporal overlap between the signals. These results suggest that the bats, like humans, have difficulty in processing more than one stream of information at a time.

**Keywords** Auditory scene analysis · Echolocation  
Gleaning bat · Sound localization

J. R. Barber · K. A. Razak · Z. M. Fuzessery (✉)  
Department of Zoology and Physiology,  
University of Wyoming,  
Laramie, WY 82071 USA  
E-mail: zmf@uwyo.edu  
Tel.: +1-307-7664207  
Fax: +1-307-7665625

J. R. Barber  
Department of Biology, Wake Forest University,  
P.O. Box 7325, Winston-Salem, NC 27109 USA

K. A. Razak  
Department of Biology, Georgia State University,  
24 Peachtree Center Ave., Atlanta,  
GA 30303 USA

### Introduction

An essential role of the central auditory system is the parsing of a complex acoustic environment into discrete auditory objects. This process, termed auditory scene analysis, involves grouping of components of a complex wave into perceptual representations of auditory objects based on attributes such as frequency, harmonic relationships, temporal structure and location. The association of a sequence of sounds with one auditory object is termed auditory stream segregation (Bregman 1990). All vertebrates examined, from fish to humans, have the capacity for auditory scene analysis (Yost 1991; Wisniewski and Hulse 1997; MacDougall-Shackleton et al. 1998; Fay 1998). A basic tenet of this construct is that we are able to fully attend to only one stream at a time, but we are able to rapidly shift attention between streams, proportional to the differences in their attributes (Duncan et al. 1997; Joseph et al. 1997; Duncan 1998; Luck and Ford 1998; Giard et al. 2000; Hopfinger et al. 2000; Marois et al. 2000).

This apparent limitation in attending to more than one auditory stream presents an interesting dilemma for one functional group of auditorily specialized animals, the gleaning bats. Gleaners use echolocation for general orientation, but most employ passive listening to detect and locate terrestrial prey (Bell 1982; Marimuthu and Neuweiler 1987; Ryan and Tuttle 1987; Anderson and Racey 1991; Faure and Barclay 1994). Most gleaners are capable of hovering over their prey, and can bring both echolocation and passive listening to bear on prey analysis (Marimuthu and Neuweiler 1987; Neuweiler 1990; Anderson and Racey 1991; Faure et al. 1993; Faure and Barclay 1994; Schmidt et al. 2000). Others, however, are unable to hold position and repeatedly scan with echolocation, and must therefore rely more on passive listening. Such is the case with the pallid bat, the subject of this study. It uses echolocation to avoid obstacles, and attends selectively to prey-generated noise bursts to locate prey (Bell 1982; Fuzessery et al. 1993). Thus, while hunting, the

pallid bat must attend to two streams of auditory information. Since the bat echolocates at a rate of 10–35 pulses  $s^{-1}$ , it is likely these streams will occasionally overlap in time.

The question we address here is whether the pallid bat is capable of simultaneous “dual stream” processing, or whether, like humans, it experiences a deficit in processing two concurrent inputs (e.g., Duncan et al. 1997). Several adaptations of the pallid bat suggest it may be capable of dual-stream processing. The acoustic attributes of the two streams are distinct. The echolocation pulse is a downward, frequency-modulated (FM) sweep from 60 to 30 kHz, while lower-frequency noise bursts are used for prey detection and localization (Brown 1976; Bell 1982; Fuzessery et al. 1993). These sounds will typically be spatially discrete for a flying bat listening for prey, with echoes originating along the bat’s flight path, and sounds from terrestrial prey emanating from the lower sound field. The frequency-dependent directionality of the external ears enhances this spatial segregation (Fuzessery 1996).

The pallid bat’s central auditory system appears to have evolved to segregate the processing of echolocation and prey-generated sounds. It is characterized by an extreme response selectivity for these signals, particularly the echolocation pulse, that is unusual, even among bats. Over 50% of neurons in the inferior colliculus tuned to the echolocation pulse respond selectively to this signal, while a third respond almost exclusively to it (Fuzessery 1994). This is in contrast to four other species of bats, in which less than 5% of neurons in the inferior colliculus respond selectively to the echolocation pulse (Suga 1965, 1969; O’Neill 1985). A similar degree and prevalence of selectivity is also present at the cortical level of the pallid bat (Razak and Fuzessery 2002). We have suggested (Fuzessery 1994) that these extreme forms of selectivity act as biological filters that segregate the neural pathways serving echolocation and the passive detection and localization of prey. In effect, the pallid bat can be thought of as having two parallel auditory systems designed for dual stream processing.

To test this assertion, the present behavioral study forced the bats, to the extent possible, to process both auditory streams within a narrow time window of 300–500 ms. This was accomplished by requiring the bats to echolocate a wire array while receiving a single noise burst from one of 15 speaker locations within the time window. The bats had to avoid the wires and land on the correct speaker to receive a food reward. A previous study indicated that pallid bats have remarkably accurate open-loop passive sound localization abilities, with an angular resolution estimated at  $\pm 1^\circ$  (Fuzessery et al. 1993), but nothing is known of their echolocation acuity. In the present study, we first tested their passive sound localization and echolocation acuities separately, and used these data as controls for their performance in a combined echolocation and passive localization task (termed the “dual task”). We found a decrement in their dual task performance, and will suggest that, like hu-

mans, the pallid bat has difficulty processing two concurrent streams of information. To mitigate this problem, the bat modifies its echolocation behavior to reduce the temporal overlap of the two signals.

## Materials and methods

Pallid bats were mist-netted in Arizona and held in a 6.7×4.9×3.4 m flight room in the Animal Care Facility of the University of Wyoming. For 3 months prior to training the bats were allowed to hunt crickets that had been raised on Purina Rat Chow to indirectly provide nutrients. The bats were kept on a reversed 10 h dark, 14 h light cycle using a single 60 W incandescent bulb. A fluorescent ceiling light covered with transparent red Plexiglas was illuminated at all times. All tests were conducted 2–4 h into the dark cycle. A total of 13 bats were used for these experiments. The *Principles of Laboratory Animal Care* (NIH publication No. 85-23, revised 1985) were followed.

### Wire avoidance and echolocation acuity

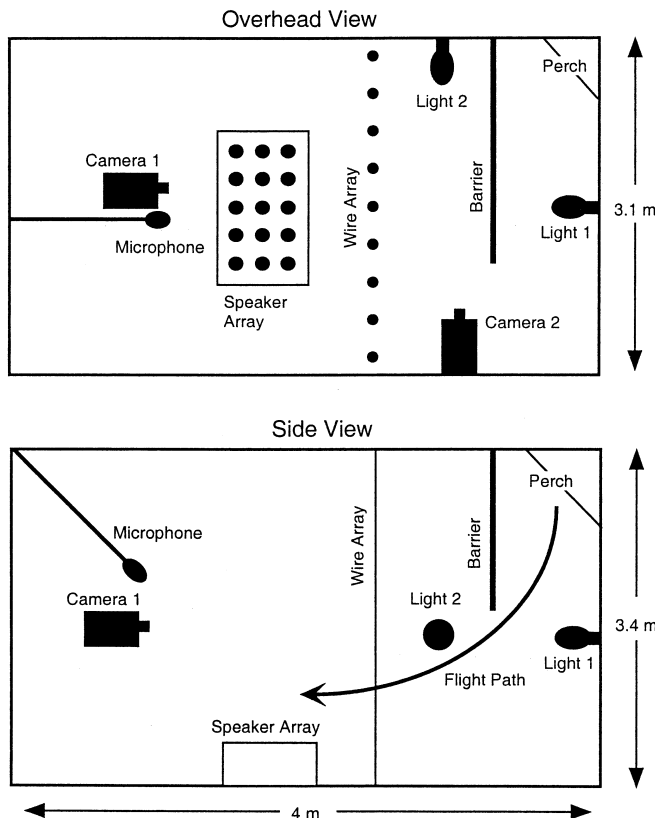
The echolocation acuity of nine bats, in two groups of four and five bats, were tested at different times, using the wire avoidance paradigm developed by Griffin (1958) and later modified by Schnitzler and Henson (1980). The bats were introduced to the experimental room for several days before data collection, and were therefore familiar with it. Each bat was tested individually for its ability to avoid an array of wires. The bats were trained to fly from one side of the room to the other, through an array of wires, for approximately 30 min to obtain access to mealworms. Only flights that started from the perch side of the room (see perch position in Fig. 1) were scored for data collection.

Five vertical wires were attached to a 2.5 m×3 m aluminum frame placed in the center of the room. The frame was hung from the ceiling on a sliding-door track to allow up to 60 cm lateral movement. The wires were spaced 48 cm apart, slightly bigger than the wingspan of an adult pallid bat. To ensure that the bats were not memorizing wire locations, the entire frame was moved before each test flight (Jen and Kamada 1982). Wire avoidance was coded according to Griffin’s (1958) original definitions. If a bat successfully avoided or lightly brushed a wire with no obvious change in flight path or speed, it was scored as a miss. If a bat contacted a wire with a noticeable change in flight path or speed it was scored as a hit. The percentage of trials in which the bat successfully avoided the wires was used as the obstacle avoidance metric (percentage avoidance). The first group of four bats was tested in order on 4.0-, 1.2-, 0.75-, 0.55-, 0.4-, 0.3-, and 0.1-mm-diameter wires. To obtain more information at intermediate wire diameters, the second group of five bats was tested in order on 1.2-, 0.75-, 0.55-, 0.4-, and 0.3-mm-diameter wires. At least 150 data points were collected for each bat on each wire diameter with the exception of the 4-mm wire where 50 data points were collected per bat. Each wire diameter was in place for 2–5 days.

### Dual task training

A third group of four bats, not used in the preliminary wire avoidance tests, was first trained to localize speaker-generated noise bursts. This task was then combined with the wire avoidance to produce what we term the “dual task”, in which the bats had to echolocate and avoid the wire array while locating a speaker emitting a single noise burst in order to obtain a food reward.

The passive sound localization task required considerable training because pallid bats do not readily approach speaker-generated sounds (Fuzessery et al. 1993) or accept dead prey. The bats had to be operantly conditioned to go to an activated speaker to obtain a freshly killed mealworm placed near the speaker. This was accomplished by first allowing the bats to hunt live crickets. A speaker was then placed in a corner of the room where crickets



**Fig. 1** Two views of the experimental room during the dual task experiment, showing the locations of the wire array that had to be avoided through echolocation, and the 5×3 array of 15 speakers, one of which had to be located through passive sound localization. As shown in the side view, a bat dropped from the perch, and flew under a Plexiglas barrier while the two cameras were active. The Plexiglas barrier was present only during the dual task trials and the associated wire avoidance control. One of the first few echolocation pulses were picked up by the microphone, which triggered the noise burst from one of the speakers, and simultaneously activated the two lights (LEDs) that served to locate the bat's position in three-dimensional space when the speaker was activated. This information was then used to reconstruct the bat's angular resolution in the passive sound localization task

accumulated. A noise burst (25 ms duration, 1–25 kHz bandwidth) was produced from the speaker each time a bat approached the corner, and the bats associated the sound with food. The live crickets were gradually replaced with anesthetized crickets until only anesthetized crickets surrounded the speaker. Once the bats were routinely localizing the speaker to obtain food, the speaker was gradually moved over several days to the center of the room. The food reward was then switched to freeze-killed mealworms.

To incorporate the echolocation task, the bats were trained to start all flights from a wire mesh perch, pass through the aluminum frame that would later hold the wire array, and locate one of an

array of 15 speaker locations (Fig. 1). During this period, a Plexiglas acoustic barrier was hung from the ceiling between the perch and the aluminum frame (Fig. 1). The purpose of this barrier was to reduce the time window in which the bats could echolocate the wires to 300–500 ms. During the dual task, the bat dropped from the perch, and as it cleared the barrier, its echolocation pulses triggered a noise burst from the speaker, which presented the bat with both streams of information within this narrow time window. The bats used the sound generated by moving the wire array, the last step for the experimenter in preparing for another trial, as the cue to begin each experiment. Due to variability in the intensity of the first few echolocation pulses, the timing of the triggered speaker output varied slightly, making it difficult for the bats to predict the exact timing of the noise burst.

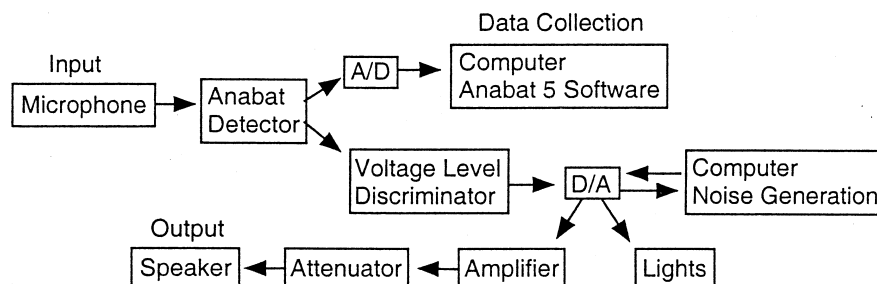
Passive sound localization controls are based on 80–110 trials. All dual-task experiments are based on 80–115 trials with the exception of those trials involving 0.08 mm wire which are based on 60–80 trials. Wire avoidance controls are based on 80 trials each.

### Experimental design and equipment

As shown in Fig. 2, the output of the microphone of an Anabat II Bat Detector served to trigger a single speaker output when the echolocation pulses of a bat dropping from the Plexiglas barrier were first detected, and to record all subsequent echolocation pulses and the output of the speaker. To trigger speaker output, the microphone output was sent to a Tucker Davis Technologies (TDT) SD1 spike discriminator that served to trigger a noise generation program from a computer via a TDT DA3-2 digital-to-analog converter. The output was amplified with a RCA SA-135 stereo amplifier and sent to a Sony Walkman speaker (1.5 cm in circumference) located in one of 15 evenly spaced locations in a 5×3 arrangement within a 1×1.6 m grid (Fig. 1). The grid was constructed of sheet-rock board with 1-inch holes drilled for the speaker positions. The speakers were recessed in rubber corks that were placed in the holes from under the sheet-rock board to hide the speaker wires. The speaker inserts (excluding the speaker itself) and the grid were covered in the same plastic material to provide uniform reflective properties. The second output of the microphone recorded all sound in the room via an Anabat II Bat Detector and a ZCAIN interface with a PC computer running Anabat5 software (Fig. 2).

The noise generation program produced 1 to 100 kHz random Gaussian noise with a 1-ms rise/fall time. After filtering the sound through the Sony Walkman speaker we recorded a stimulus of 1–28 kHz at the relative position of the bat in the task. Intensity was recorded to be greater than 65 dB at all possible positions the bats received the noise burst. All durations of noise bursts had 1-ms rise/fall times.

**Fig. 2** A schematic of the instrumentation used to detect and record echolocation behavior, trigger the noise burst from 1 of 15 speakers, and also trigger the lights that located the bat's position in three-dimensional space when the speaker was activated. Details of the instrumentation are provided in Materials and methods



Several precautions were taken to prevent giving the bats extraneous cues to use in wire avoidance and speaker localization. Only one Walkman speaker was used to generate the noise burst to preclude the possibility that the bats might use individual differences in frequency-response curves as a localization cue. The remainder of the speaker positions were occupied by dummy speakers identical to the active speaker to preclude echolocation of the speaker. The active speaker was repositioned (according to a random number table) after each trial, as was the wire array, to prevent the bats from using spatial memory. A single mealworm was placed near the speaker as a food reward. To eliminate the possibility that the bats might echolocate the mealworm, dummy mealworms made of rolled duct tape coated in mealworm paste, were placed more distant from the speaker. The use of vision to obtain food was eliminated or greatly reduced by conducting the experiments in red light (600–725 nm). Bell and Fenton (1986) reported that the pallid bat could detect only 460 to 590 nm wavelengths at 10–15 cm, and a previous study of the pallid bat reported that time to capture and success rate do not differ when the bats are hunting crickets in red light versus complete darkness (Fuzessery et al. 1993). The bats were allowed no more than 15 mealworms a day to maintain a high level of motivation to perform the tasks.

Wire avoidance performance was measured as described above. Sound localization acuity was measured by determining angular resolution from the bat's position at the time of noise burst onset, the position of the active speaker, and the bat's landing position. These three locations formed a triangle, and the angular separation between the speaker and landing locations, measured at the location of the bat, provided the calculation of angular resolution. The bat's *X*, *Y*, *Z* position at this time was reconstructed by two 8-mm Sony TRV37 video cameras (Fig. 1). Camera 1 obtained *X*, *Y* positional information and camera 2 captured the bat's *Y*, *Z* position. A numerical grid was marked in 5-cm increments on the wall opposite each camera to provide reference. The video cameras marked the time of occurrence of the noise burst via two LED lights on opposite walls from the cameras. The LEDs were illuminated by the output of the D/A converter that also triggered speaker output (Fig. 2). Finally, the bat's landing position on the speaker array was determined by the displacement of a fine layer of chalk dust.

The sound analysis software used in this study (Anabat 5) allowed real-time recording of 15 s sonograms with good sensitivity to both sonic and ultrasonic frequencies. Anabat uses a zero-crossing system to compute frequency where the number of times the waveform crosses 0° phase is counted and frequency is computed. This methodology inherently loses information about intensity and harmonics. Therefore, we did not quantify any frequency parameters of echolocation behavior. However, because temporal parameters were of most interest, this limitation was acceptable.

Repeated-measures ANOVAs and two-tailed paired *t*-tests were performed in SPSS 11.0 for Windows.

#### Data collection and analysis

Wire diameter and noise burst duration were gradually decreased to test for effects of task difficulty on dual-stream processing. It was assumed that shorter duration noise bursts, which would preclude updating through closed-loop sound localization (e.g., Populin and Yin 1998), would make the task more difficult. Wire avoidance controls (no noise burst present—see earlier description of wire-avoidance acuity) were conducted on 0.75, 0.55, 0.3, and 0.08-mm diameter wire. Sound localization controls (no wires present) utilized 1- to 28-kHz noise of 100, 50, and 25 ms duration. Dual task data was collected from largest to smallest wire diameter, starting with 1–2 days of 100 ms noise bursts, followed by 50 ms, and then by 25 ms. In addition, 1–2 days of data were collected at a given wire diameter in which all noise burst durations were randomly presented, prior to changing the wire diameter. Visually comparing means showed no difference between random and non-random presentation of noise burst duration, therefore the data was combined for analysis. Sound localization control data was collected first, followed by dual-task and wire avoidance control data.

Individual echolocation pulse duration, pulse train duration, and interpulse interval (IPI) were measured using Anabat5 software. This software was also used to determine the presence of overlap between returning echoes and the speaker-generated noise burst at the position of the bat, taking into account the approximate travel times of echolocation pulses and speaker output from the sources to the microphone.

All statistical comparisons were done in SPSS 11.0 for Windows using repeated-measures ANOVAs and paired *t*-tests.

## Results

### Wire-avoidance behavior

The preliminary echolocation acuity studies, conducted with the two groups of bats not used in the dual-task study, revealed that pallid bats can detect wires as small as 0.3 mm in diameter (Fig. 3). Percentage avoidance at 0.3–0.1 mm wire diameters dropped from 75.5% to 56.8%. A sharp inflection in the performance function is more obvious in the echolocation acuity of the four bats used in the dual task studies (Fig. 3). Qualitatively, in contrast to larger diameters, the contacts at 0.1 mm diameter wires were often direct hits that knocked the bats out of the air, as though they were simply unable to detect the wires. We therefore place the lower limit of detection between the diameters of 0.3 and 0.1 mm. As in previous wire avoidance studies (reviews by Griffin 1958; Schnitzler and Henson 1980), individual variability was high.

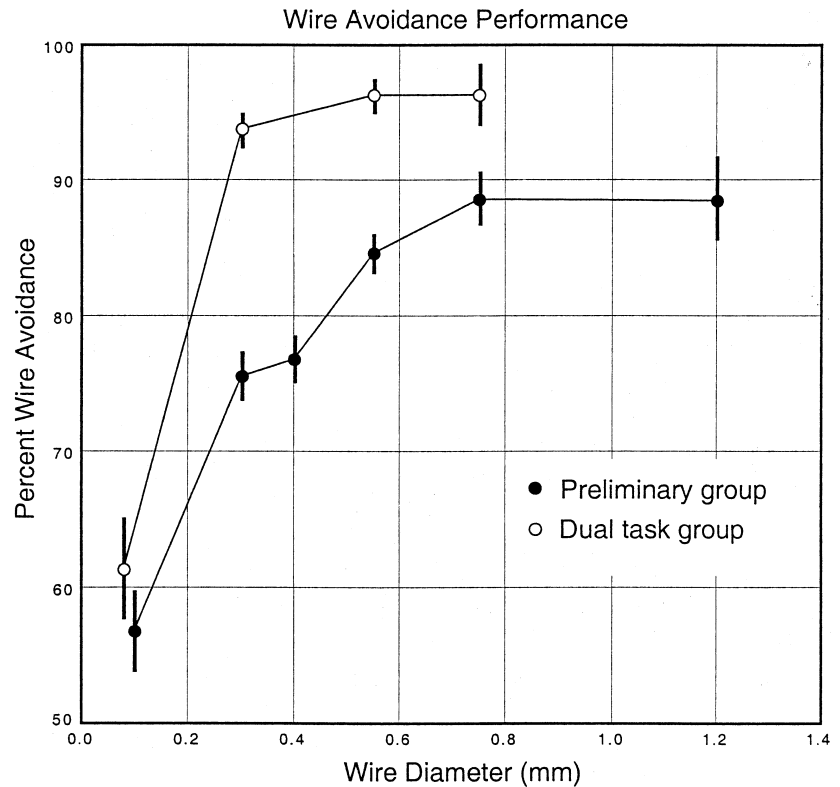
A learning effect was also apparent in the first two groups of bats tested for echolocation acuity. This is seen in the reduction in standard error of performance as wire diameter was reduced (Fig. 3). Since the bats were tested in order of decreasing diameter, this trend in variance presumably reflects an increase in task proficiency. The small variance seen at the largest diameter (4 mm: SE = 0.71, not shown in Fig. 3) does not fit this trend, and is likely due to the fact that such a large diameter wire presented no challenge.

The third group of bats, those used in the dual task study, achieved better mean wire avoidance scores than did the first two groups, with values of  $\geq 90\%$  at wire diameters down to 0.3 mm. Why might their scores be higher? A Plexiglas barrier in front of the perch from whence the bats began their flight was present only in the dual task study. Its purpose was to limit the time available for echolocating the wire array. This may have forced the dual task group to pay more attention to the wire avoidance task, increasing their performance. Alternatively, given that there can be considerable individual variation in performance in wire avoidance studies, the four bats used in the dual task wire avoidance control may simply have been better at this task.

### Passive sound localization controls

The passive sound localization task was designed to be challenging even for an animal that relies on passive

**Fig. 3** The mean wire avoidance performance of the nine bats used in the two preliminary echolocation acuity tests (*filled circles*), and four bats that would subsequently used in the dual task (*open circles*). The vertical bars represent standard error. Not shown on this graph is that the mean score for the preliminary group at the largest wire diameter of 4.0 mm was 98% avoidance. The performance of both groups dropped to around 60% at wire diameters of 0.08 or 0.1 mm, indicating that the bats were operating at a chance level, and unable to detect wires of this diameter



listening for prey detection. A startling slap to the speaker grid was used to teach the bats that landing and searching for the reward was not permissible; only a landing on the speaker would produce a food reward. However, they were successful if any part of their body touched the mealworm. A landing bat encompassed an area of approximately  $7 \times 10$  cm, considerably larger than the 1.5 cm speaker. However, even with this enlarged area of success, the bats acquired a food reward in only 34% of passive sound localization trials.

Control passive sound localization accuracy and variance for the group were quite similar at all noise burst durations tested:  $2.0 \pm 0.6$  (mean  $\pm$  SD) at 100 ms,  $2.2 \pm 0.9$  at 50 ms, and  $2.6 \pm 1.3$  at 25 ms (no statistical difference in angular resolution; repeated-measures ANOVA:  $F_{2,6} = 0.91$ ,  $P = 0.73$ ). This consistency across noise burst duration suggests a ceiling effect, and that the additional spatial information contained in longer signals was not necessary for accurate localization. This assumption is supported by a previous study (Fuzessery et al. 1993) reporting that the pallid bat is capable of similar accuracy given only a single 10–25 ms sound.

#### Dual-task performance

##### Wire avoidance

Mean wire-avoidance performance under the dual-task condition revealed that there was a slight (7%) average increase in wire contacts relative to controls at the

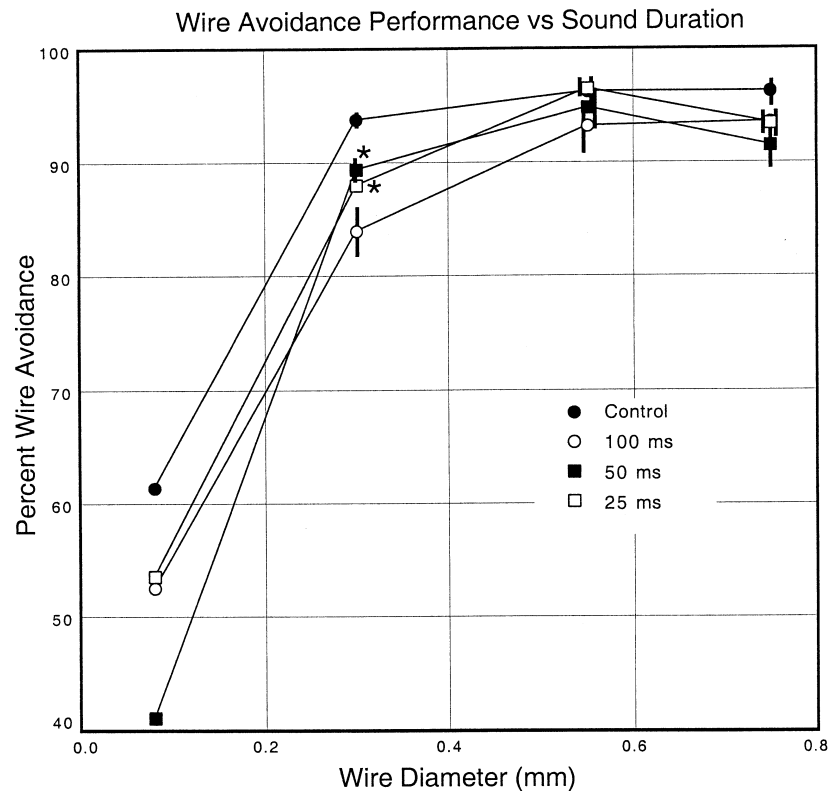
smallest detectable wire diameter of 0.3 mm (Fig. 4). We assume that any differences in performance at the smallest diameter tested (0.08 mm) were due to chance, since the bats appeared unable to detect wires of this diameter under control conditions.

As discussed below, the duration of the noise burst had a significant effect on the bats' ability to accurately locate the speaker under dual task conditions, but it did not appear to have an effect on their ability to avoid wires. A repeated-measures ANOVA revealed no main effect of noise burst duration ( $F_{3,9} = 1.84$ ,  $P = 0.211$ ) and no interaction effect ( $F_{6,18} = 0.68$ ,  $P = 0.668$ ). The main effect of wire diameter was nearly significant ( $F_{2,6} = 4.84$ ,  $P = 0.056$ ). We conclude that noise burst duration did not decrease wire avoidance performance in the dual task study, but that a trend exists indicating a decrease in wire avoidance performance with decreasing wire diameter.

##### Passive sound localization

A repeated-measures ANOVA revealed a main effect of both noise burst duration ( $F_{2,6} = 9.94$ ,  $P = 0.012$ ) and wire diameter ( $F_{3,9} = 16.23$ ,  $P = 0.001$ ) on the passive sound localization performance when the bats were required to simultaneously negotiate the wire array and localize the speaker (Fig. 5). The interaction term was also significant ( $F_{6,18} = 4.32$ ,  $P = 0.007$ ) and Tukey's HSD post hoc tests indicated that angular resolution values for 100 ms noise burst duration were significantly different from control at all wire diameters ( $P < 0.01$ ).

**Fig. 4** The mean wire-avoidance performance of the four bats used in the dual task experiment under four conditions: wire avoidance only (*filled circles*), and wire avoidance when locating a speaker emitting a 100 ms (*open circles*), 50 ms (*filled squares*) and 25 ms (*open squares*) noise burst. The *asterisks* indicate where performance was significantly poorer than control, which occurred only in the dual task, at 0.3 mm wire diameter in conjunction with 25 and 50 ms noise bursts. Performance at the same wire diameter with a 100 ms noise burst produced a greater difference in means experimental and control, but the variance in experimental group was large, resulting in a lack of significant difference



Compared to control, angular resolution values at 50 ms noise burst duration were  $P < 0.01$  at 0.75 mm wire and  $P < 0.05$  at 0.55 mm wire diameter and not significant at the 0.3 mm wire diameter. Finally, angular resolution values for 25 ms noise burst duration were not significantly different across wire diameters.

It is important to note that a learning effect appears to be present in the data, resulting in the seemingly counterintuitive result that the bats had the most difficulty at the larger diameter wires (Fig. 5). The bats were tested first at the largest wire diameter of 0.75 mm, and last at the smallest diameter of 0.3 mm, and appeared to become more proficient at the dual task with time and experience.

In addition to the changes seen in passive sound localization accuracy, measures of variance in passive sound localization trials also increased in the dual task. Mean SDs more than doubled compared to controls for 100 ms ( $SD \pm 1.68$ ; control  $SD \pm 0.63$ ) and almost doubled for 50 ms ( $SD \pm 1.47$ ; control  $SD \pm 0.94$ ) bursts. However, as with mean angular resolution values, there was less change in mean variance for the 25 ms burst ( $SD \pm 1.02$ ; control  $SD \pm 1.29$ ) compared to controls.

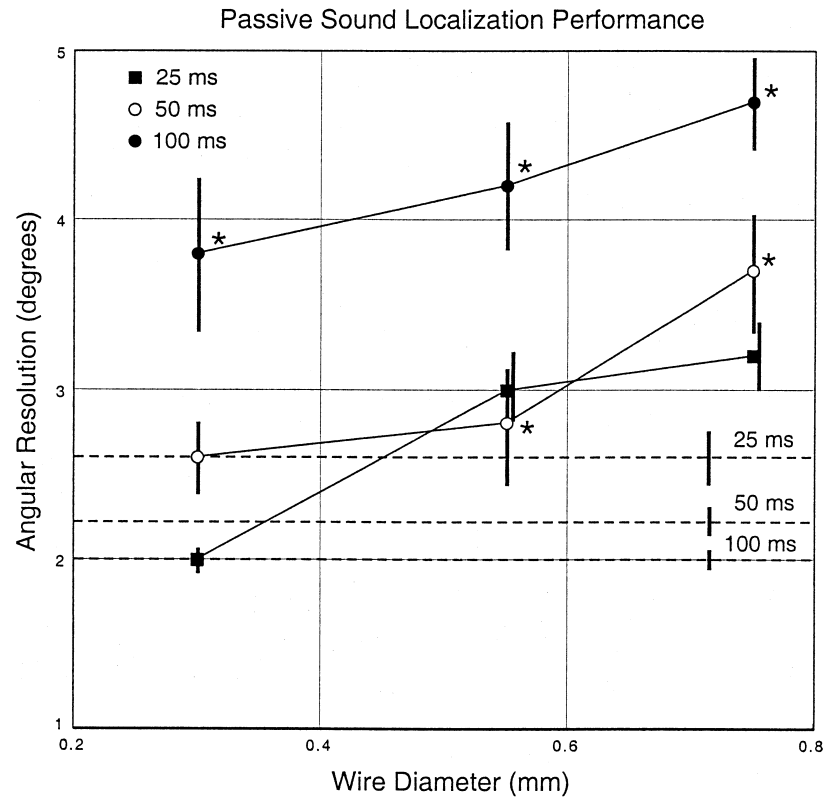
This increase in the variability of passive sound localization performance in the dual task is due to an interesting feature in the results. There was a marked “step-function” in performance. For all combinations of wire diameters and noise-burst durations, the bats were able to perform as accurately as they did in the control condition in some trials, but in other trials, they landed a considerable distance from the speaker. This suggests

that sometimes they acquired the requisite spatial information, and sometimes they did not. This step-function in performance perhaps explains why the bats were still successful in acquiring a food reward in ~25% of dual-task trials. Whether or not they acquired this information was not related to their wire avoidance success (paired  $t$ -test,  $P = 0.34$ ), so it is not simply the case that when they had difficulty negotiating the wires, they also had difficulty locating the speaker.

#### Echolocation behavior

Temporal parameters of echolocation behavior under the three test conditions (wire avoidance only, passive sound localization only, or the dual task) were analyzed to determine whether the bats were changing their echolocation behavior to optimize performance (Fig. 6, Table 1). For example, pulse duration in bats has been reported to show task-dependent changes (e.g., Simmons et al. 1979; Schmidt et al. 2000), specifically a shortening of the pulse when interrogating obstacles or prey. In the present study, echolocation pulse duration changed little between wire-avoidance controls ( $1.4 \pm 0.23$  ms), sound localization controls ( $1.3 \pm 0.23$  ms), and dual task trials ( $1.5 \pm 0.26$  ms) and did not change systematically as the bats approached either the wires or the speaker platform. While a repeated-measures ANOVA showed a significant difference ( $F_{2,6} = 6.52$ ,  $P = 0.031$ ) in pulse duration across conditions, Tukey's HSD post hoc tests revealed that

**Fig. 5** Passive sound localization performance in terms of angular resolution, as a function of wire diameter and noise burst duration. *Vertical bars* indicate standard error. *Asterisks* indicate a significant difference from controls (passive sound localization only). The *dashed lines* indicate the control values for angular resolution at the three noise burst durations; the *vertical bars* indicate standard errors during control tests. Note that performance was significantly poorer at the longest noise burst duration (100 ms) at all wire diameters, but that there was no significant difference in performance at the shortest duration (25 ms) at any wire diameter



difference to be carried by a disparity between dual-task trials and passive sound localization control trials ( $P < 0.05$ ). Thus, the bats produced slightly longer echolocation calls when the wires were present, whether involved in the dual-task or not.

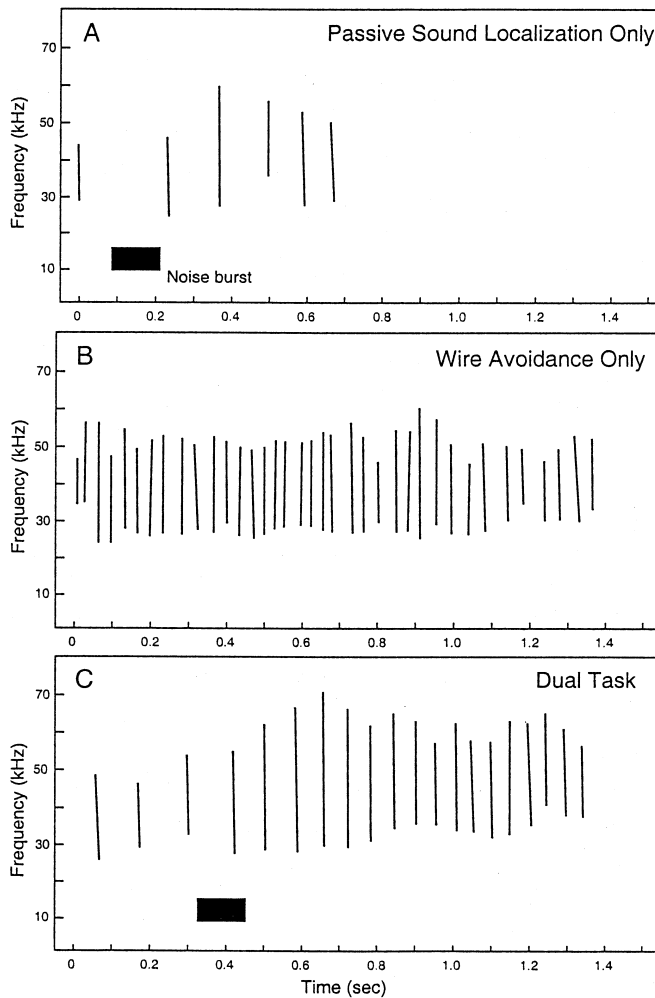
A second parameter of interest was the duration of the train of echolocation pulses (bout) emitted during a trial (Fig. 6). This parameter can indicate to what temporal extent echolocation is being used to image the environment. The duration of the entire echolocation bout gradually increased from passive sound localization controls ( $1160 \pm 450$  ms), to wire avoidance controls ( $1380 \pm 230$  ms), to dual-task conditions ( $1580 \pm 320$  ms). A repeated-measures ANOVA showed a significant difference in bout duration across conditions ( $F_{2,6} = 36.13$ ,  $P = 0.0001$ ). Tukey's HSD post hoc tests revealed this difference to lie between passive sound localization control trials and both wire avoidance controls and dual-task conditions ( $P < 0.01$ ). No other comparisons were significant. This increase in bout duration suggests that passive sound localization controls were the least reliant on echolocation, and that dual task and wire avoidance control conditions required more use of the biosonar system.

The most pronounced temporal change was seen in the average IPI of the echolocation bout. Previous studies have shown that bats modulate their pulse rate (or IPI) for different acoustic tasks (Simmons et al. 1979; Schnitzler and Henson 1980). When the bats were asked to localize the active speaker with no wires present, they

produced an average IPI of 110 ms or a pulse rate of  $9.1 \text{ pulses s}^{-1}$  (Table 1, Fig. 6A). Echolocating wires alone, the bats produced a much smaller average IPI of 30.3 ms or a pulse rate of  $33 \text{ pulses s}^{-1}$  (Table 1, Fig. 6B). When passive sound localization and wire avoidance were combined in the dual task, the bats produced an intermediate average IPI of 69.2 ms or  $14.5 \text{ pulses s}^{-1}$  (Table 1, Fig. 6C). A repeated-measures ANOVA on IPI showed a main effect of noise burst duration ( $F_{3,9} = 151.75$ ,  $P = 0.0001$ ) and wire diameter ( $F_{4,12} = 27.05$ ,  $P = 0.0001$ ) as well as a significant interaction effect ( $F_{12,36} = 39.87$ ,  $P = 0.0001$ ). Thus, the bats generated different IPIs at different noise burst durations and at each wire diameter (Table 1). All Tukey's HSD multiple comparison tests of dual-task data, whether compared to wire avoidance controls or passive sound localization controls, were significant at  $P < 0.01$ . Therefore, the bats produced significantly different pulse rates in these different acoustic environments.

A finer analysis of dual task sonograms reveals two distinct IPI groups within the echolocation bouts. The IPI for the first five pulses averaged 120 ms, then, shortly after receiving the noise burst, the IPI was decreased to 40 ms for the remainder of the bout. In other words, it appeared that the bats were initially increasing the IPI in order to create a temporal gap in which to receive the noise burst.

If increasing the time between emitted pulses is a strategy to allow processing of two near simultaneous sounds, are the bats trying to prevent the speaker-gen-



**Fig. 6** Representative echolocation behavior during the three test conditions of passive sound localization only (A), wire avoidance only (B), and both combined in the dual task (C). These records were produced by Anabat 5 software. For clarity, the echolocation pulses and the noise bursts were then drawn over with vertical lines and filled boxes. See also Table 1 and text

erated noise and returning echoes from temporally overlapping? With a 120 ms IPI, a 100 ms noise burst is likely to overlap with echoes more often than a 25 ms noise burst, and possibly explain why the bats were more successful when presented with short-duration sounds in the dual task. However, a comparison of performance means between those trials when the sounds overlapped and those when they did not showed no obvious relationship between temporal overlap of echoes and the noise burst with either sound localization accuracy (paired *t*-test,  $P=0.78$ ) or obstacle avoidance performance (paired *t*-test,  $P=0.15$ ). Therefore, the recordings do not provide direct evidence that temporal overlap of the two signals is responsible for the observed processing deficits in passive sound localization. However, it was impossible to determine if this measure of temporal overlap corresponded with perceptual overlap for the bat.

**Table 1** The intervals between echolocation pulses (IPIs) emitted by the four bats used in the dual task experiment

Condition	Interpulse intervals						
	<i>N</i>	Bat 1	Bat 2	Bat 3	Bat 4	Mean	SD
Sound localization							
100 ms duration	45	114	122	122	122	120	4
50 ms duration	42	110	105	109	110	109	2.38
25 ms duration	84	95	82	107	112	99	13.39
Wire avoidance							
0.75 mm diameter	80	30	35	32	27	31	3.37
0.55 mm diameter	80	31	31	29	29	30	1.15
0.3 mm diameter	80	32	32	30	25	30	3.3
0.08 mm diameter	80	32	29	35	26	30	3.87
Dual task							
0.75 mm/100 ms	76	76	82	90	75	81	6.9
0.75 mm/50 ms	76	51	68	71	66	64	8.91
0.75 mm/25 ms	74	60	73	76	72	70	7.04
0.55 mm/100 ms	91	64	86	80	68	74	10.25
0.55 mm/50 ms	79	55	81	67	71	69	10.75
0.55 mm/25 ms	23	50	72	74	80	69	13.11
0.3 mm/100 ms	98	65	71	81	75	73	6.73
0.3 mm/50 ms	96	60	71	67	58	64	6.06
0.3 mm/25 ms	85	50	72	67	73	65	10.66
0.08 mm/100 ms	74	58	60	89	67	68	14.2
0.08 mm/50 ms	79	58	68	71	62	65	5.85
0.08 mm/25 ms	70	57	63	69	57	61	5.74

Sound localization: IPIs when the bats were only passively locating the speaker at different noise burst durations (ms)

Wire avoidance: echolocation behavior when only avoiding wires of four different diameters (mm)

Dual task: when the bats were avoiding wires of different diameter and localizing noise bursts of different durations

## Discussion

The primary question addressed in this study is whether the pallid bat is capable of processing two streams of acoustic information simultaneously, or whether it is subject to a fundamental limitation imposed by a basic tenet of auditory scene analysis—namely, that only one auditory object can receive full attention at a time. These two streams of information are processed within what can be considered two parallel auditory systems (Fuzessery and Hall 1996; Razak and Fuzessery 2002), a feature that might allow the bat to circumvent processing limitations. To test this, the bats were forced to process and act upon the information provided by echolocation and passive listening within a narrow time window of 300–500 ms.

A conservative interpretation of the results is that the bats were capable of rapidly switching attention between these two auditory streams, but were not capable of true simultaneous processing. First, the bats' ability to locate the wire array did not degrade significantly, although there was a trend suggesting that as the echolocation task became more difficult, and required greater attention, performance suffered.

Second, performance in the passive sound localization component of the task was affected by both the duration of the speaker-generated noise burst and the diameter of the wire they had to avoid. Although there



was considerable individual variation, the greatest decrement in accuracy occurred at the longer duration noise bursts. At the shortest noise-burst duration (25 ms), their individual passive sound localization performances were not significantly different from controls. It follows that if the bats were most successful when using the shortest duration noise bursts, and these bursts were least likely to temporally overlap with the echolocation stream, then it is reasonable to conclude that temporal overlap interfered with passive sound localization performance.

Third, the bats dealt with the dual task by what we interpret as an attempt to reduce temporal overlap in the two auditory streams. They decreased their echolocation pulse rates at a time when they would be receiving the information needed to both avoid wires and locate the speaker. This resulted in an average increase in interpulse intervals from 30.3 ms during echolocation controls, to 69.2 ms during the dual task. This behavior is the opposite of the increase in echolocation pulse rate reported when bats are using only echolocation to resolve targets (e.g., Simmons and Stein 1980), but similar to the behavior observed when bats are both echolocating their environment and passively listening for prey (Barclay et al. 1981). These results suggest that pallid bats, like humans (e.g., Duncan et al. 1997), have difficulty extracting complete information about more than one auditory object at the same time.

In the following discussion, we first compare the echolocation and passive sound localization abilities of the pallid bat with those of other species. We then place the results within the context of auditory scene analysis and suggest their implications.

#### Echolocation and passive sound localization acuity

The gleaning bats, those that take prey from substrates, are a diverse group, both in terms of taxonomy and the sensory information that they may use to detect and locate prey (Fiedler 1979; Barclay et al. 1981; Bell 1982; Neuweiler 1984; Bell and Fenton 1986; Marimuthu and Neuweiler 1987; Ryan and Tuttle 1987; Grant 1991; Faure and Barclay 1994; Schmidt et al. 2000). They typically have larger pinnae than closely related species that rely on echolocation to capture prey, a feature which suggests that their external ears are modified for the amplification of lower frequencies generated by their prey (Coles and Guppy 1986; Guppy and Coles 1988; Coles et al. 1989; Orbist et al. 1993; Fuzessery 1996). Bats are notoriously flexible in their foraging behavior; and most gleaners probably use either or both echolocation and passive listening while hunting. Echolocation may play a more important role in detecting prey when the substrate is acoustically uncluttered; passive listening may be more important when background clutter masks prey-generated echoes (Neuweiler 1984; Arlettaz et al. 2001). While the pallid bat appears particularly dependent upon passive listening for prey acquisition, it

should be noted that, at least under laboratory conditions, they will take flying prey, but using capture techniques that mimic pinning terrestrial prey to the ground (Johnston and Fenton 2001). What information was used to capture aerial prey in this study is not clear. We have observed hungry pallid bats occasionally investigate small inanimate objects (bolts) on a bare floor, a task that could have been accomplished only with echolocation. Whether echolocation is used for the localization of prey under natural conditions is unclear.

These caveats regarding flexible foraging strategies aside, behavioral studies of gleaning species suggest that they are capable of highly accurate passive sound localization. Unfortunately, this accuracy has rarely been quantified, which precludes comparisons with present results. A previous behavioral study (Fuzessery et al. 1993) of the pallid bat suggested that its open-loop localization acuity approaches  $\pm 1^\circ$  angular resolution, based on the bats' ability to land within 8 cm of the source of a single 10 to 20 ms noise transient from  $\sim 5$  m away. Present results, which provide a more quantitative three-dimensional analysis, indicate a similar average angular resolution of  $\pm 2.3^\circ$ . Other studies of passive sound localization acuity in bats have used a very different psychophysical paradigm in which bats were required to make left/right choices to indicate their ability to resolve angular separation (e.g., Heffner et al. 2001). Results in two species that are not strictly gleaners yielded estimates of  $10^\circ$  and  $14^\circ$  of resolution in the horizontal plane (Koay et al. 1998; Heffner et al. 2001). Given the differences in experimental protocol, it is difficult to make direct comparisons. Since present results were derived from a paradigm that reflected the naturally occurring condition in which the pallid bat has evolved to perform, we suggest that this species has one of the most accurate open-loop passive sound localization abilities reported. However, based on the wealth of less quantitative, but nonetheless compelling, results obtained from other gleaner species, the pallid bat is probably not unusual in its localization ability (Fiedler 1979; Barclay et al. 1981; Bell 1982; Neuweiler 1984; Ryan and Tuttle 1987; Marimuthu and Neuweiler 1987; Grant 1991; Faure and Barclay 1994; Schmidt et al. 2000).

The echolocation acuity of the pallid bat, as measured in the present study, is similar to that of other vespertilionid species, including those that probably rely exclusively on echolocation to capture flying insects (myotis species), as well as those that glean, such as *Plecotus auritus* (Table 2). It is possible that the pallid bat has better echolocation acuity than measured with our paradigm because the obstacle avoidance task is also a measure of agility. Pallid bats are relatively clumsy fliers, and coupled with the short time and distance available to them to avoid wires in the present study, these factors may have contributed to an underestimation of their echolocation acuity.

Along with the other vespertilionids that have been tested, the pallid bat's ability to detect fine wires is less

**Table 2** Minimum avoidable wire diameters as obtained from the obstacle avoidance paradigm for a variety of microchiropteran species

Species	Diameter	Reference
<i>Antrozous pallidus</i>	0.1–0.3 mm	This study
<i>Artibeus jamaicensis</i>	0.175 mm	Griffin and Novick (1955)
<i>Asellia tridens</i>	0.05–0.065 mm	Gustafson and Schnitzler (1979)
<i>Carollia perspicillata</i>	0.175 mm	Griffin and Novick (1955)
<i>Glossophaga soricina</i>	0.175 mm	Griffin and Novick (1955)
<i>Macrotus mexicanus</i>	0.19 mm	Griffin and Novick (1955)
<i>Megaderma lyra</i>	0.06–0.08 mm	Möhres and Neuweiler (1966)
<i>Myotis lucifugus</i>	0.26 mm	Curtis (1952); Griffin (1958)
<i>Myotis oxygnathus</i>	0.2 mm	Konstantinov et al. (1967)
<i>Noctilio leporinus</i>	0.21 mm	Suthers (1967)
<i>Pipistrellus hesperus</i>	0.21 mm	Suthers (1967)
<i>Plecotus auritus</i>	0.2 mm	Konstantinov et al. (1967)
<i>Rhinolophus euryale</i>	0.05 mm	Schnitzler (1968); Konstantinov et al. (1967)
<i>Rhinolophus ferrumequinum</i>	0.05–0.08 mm	Schneider and Möhres (1960)
<i>Rhinolophus mehelyi</i>	0.05 mm	Schnitzler (1968); Konstantinov et al. (1967)

Some values are given as ranges because bats performed above chance at one value, below at another, and no intermediate diameters were tested

than that of specialized echolocators, like the rhinolophids and hipposiderids, or the megadermids (Table 2). Differences in the echolocation acuity of these species may result from differences in pulse spectrum. For example, the megadermids are also gleaners, and capable of resolving prey on substrates solely with echolocation (Fiedler 1979; Marimuthu and Neuweiler 1987; Schmidt et al. 2000). The higher frequencies and multiple harmonics of their more sophisticated echolocation pulses would presumably allow detection of smaller diameter wires.

#### Auditory scene analysis

Auditory scene analysis is the extraction of an auditory object from the acoustic background by unique spectral, temporal, and spatial attributes of that object. This process appears to be present in all animals (Bregman 1990; Hulse et al. 1997; Wisniewski and Hulse 1997; Fay 1998, 2000; MacDougall-Shackleton et al. 1998). Research on scene analysis and directed attention has focused on humans, and it has been well established that we are not able to focus full attention on more than one stream of information at a time, as long as the streams occur within one sensory modality (Duncan et al. 1997; Joseph et al. 1997; Duncan 1998; Luck and Ford 1998; Giard et al. 2000; Hopfinger et al. 2000; Marois et al. 2000). However, we can switch attention between streams, and the rapidity of this switching is directly related to the extent to which the streams are distinct in spectrum, temporal structure and location (Bregman 1990; Luck and Ford 1998; Marois et al. 2000). It has been suggested that this is related to the extent to which the objects must be processed through a common neural substrate (Luck and Ford 1998).

As mentioned in the Introduction, the various specializations of the pallid bat auditory system led us to suspect that this bat might be an exception to this perceptual limitation. Moreover, its hunting behavior suggests that it may routinely have to cope with processing two streams of information. Unlike other gleaners, such

as the megadermids, that can hover and effectively interrogate objects with echolocation, the pallid bat is only able to hold position in the air for two to three wingbeats in what resembles a flight “stall” (Bell 1982; Norberg and Rayner 1987). While hunting, the pallid bat remains in forward flight, using echolocation to avoid obstacles, while listening for prey-generated sounds. It has been observed to make repeated flights over prey while presumably passively listening and echolocating simultaneously (Orr 1954; Bell 1982; Johnston and Fenton 2001).

Such a division of labor requires attention to two streams of input while hunting. However, present results indicate that, as in humans, there is a transient impairment of processing when the inputs occur together in a short time window. In this case, the ability to accurately identify the locations of two auditory objects is degraded. The bats displayed relatively little decrement in locating and avoiding the array of wires using echolocation, but their ability to locate the activated speaker could be markedly disrupted. That passive localization appeared to suffer more than echolocation may simply be a question of the priority that the bats assigned to the dual task. The wires had to be successfully avoided first in order to receive the food reward, and perhaps equally important, it was not pleasant for the bats to hit the wires.

It is also likely that the passive localization task was more difficult in that it required a memorized image of speaker location. Given that the bats encountered the wire array within 500 ms, avoidance required an immediate motor response to the detected wire. In contrast, the flight to the speaker was delayed, and was also typically indirect. Speaker localization would therefore require formation of a three-dimensional internal representation of space.

The conditions that degraded performance were not the same for echolocation and passive listening. A slight increase in wire contacts occurred, as might be expected, with increasing task difficulty. The duration of the passive sound cue did not affect echolocation performance (Fig. 4). In contrast, the duration of the noise burst from

the speaker affected passive sound localization at any wire diameter, with performance decreasing with increasing sound duration (Fig. 5). There were individual differences as to the degree of the duration effect but individual variability is inherently high in behavior studies and perhaps amplified in this study due to the 'real-world' nature of our paradigm. Requiring the bats to perform such a complicated in-flight task summed variability from at least three sources; flight ability, echolocation acuity, and passive sound localization acuity.

However, it is also important to note that the bats' ability to locate the speaker under dual task conditions was often as accurate as observed under the control condition, i.e., the bats landed directly on the target. This suggests a step-function in performance; sometimes the bats obtained the required spatial information, and sometimes they did not. Thus, the presence of two auditory streams sometimes interfered with the extraction of information from at least one stream.

The bats' change in echolocation behavior in response to the dual task condition suggests that temporal overlap caused this inference. Pallid bats flying about an uncluttered room typically emit pulses at a rate of around 10 pulses  $s^{-1}$  (Fuzessery et al. 1993). In the present study, when dealing only with avoiding the wire array, the bats increased this rate to an average of 33 pulses  $s^{-1}$ , presumably to maximize information about wire location within the 300–500 ms available after leaving the perch. An increase in pulse emission rate is common among bats when presented with obstacles (Simmons et al. 1979; Simmons and Stein 1980). When dealing only with passively locating a speaker, the average pulse rate was 9 pulses  $s^{-1}$ . This increase in interpulse interval (decrease in pulse rate) presumably served to create a wider time window in which to receive and process the speaker signal without interference from returning echoes.

In the dual task condition, pulse emission rates were intermediate (14 pulses  $s^{-1}$ ) when measured over the entire flight from perch to speaker. However, the rate changed during the flight. For the first 3–5 pulses, prior to negotiating the wires and receiving the speaker output, the rate was 8 pulses  $s^{-1}$ , similar to that observed under passive localization control. Once past the wires, the rate increased to 25 pulses  $s^{-1}$ , similar to the wire-avoidance control. This post-wire rate increase may have been used to scan the substrate for landing.

We interpret this change in echolocation behavior as a compromise strategy for obtaining sufficient spatial information about both wire location and speaker location. It would appear that the bats preferred not to receive echoes and speaker output at the same time. By expanding the interpulse interval from approximately 30 ms, as observed in the wire-avoidance task, to 120 ms, as observed in the dual-task condition, more time was allocated to receiving a signal from the speaker without interference from returning echoes. This suggests that the bats were attempting to reduce the prob-

ability of temporal overlap in the two streams of information. However, we found no obvious relationship between temporal overlap, and performance in wire avoidance or passive sound localization. This inability to provide direct evidence for the temporal overlap hypothesis may be due simply to the fact that we had no way of knowing how attention was distributed across the three to five echoes emitted before reaching the wire array, or how many echoes the bats needed to fully image the wire array. It is quite possible that the bats acquired sufficient information about the wires from one of these echoes, and that temporal overlap between the single noise burst and other echoes was not consequential to wire avoidance. If true, then it would be anticipated that passive sound localization would be more likely to suffer than echolocation, and the results indicate this to be the case.

These results seem consistent with those of studies of auditory attention in humans. Two near-simultaneous inputs cannot be processed with the same accuracy as they can be individually. The time-course of this phenomenon has been termed the 'attentional blink' (Duncan et al. 1997; Duncan 1998; Giard et al. 2000; Marois et al. 2000). The decrement in reporting the second stimulus is thought to be a result of a limitation in retrieval or access from short-term memory given interference from categorically similar information in the same short-term memory buffer. If these two objects compete for retrieval, such that the object remaining in the short-term memory buffer is lost before it can be consolidated to more permanent forms of memory and acted on, only the object chosen for retrieval will be accurately located.

If we apply this hypothesis to the pallid bat, several assumptions must be made. First, deficits in the acquisition of information could occur even without temporal overlap in the two auditory objects. Second, the bats assigned first priority to acquiring spatial information about the wire array. Third, the bats' attention was captured by the noise burst for its entire duration, and that the spatial information had to be placed in short-term memory in order to land on the speaker. Finally, the occurrence of an echo competing for the same memory substrate would interfere with the retention of information needed to locate the speaker. This could explain the bats' own responses to this situation, i.e., increasing interpulse interval to reduce interference.

This may explain why the longer duration noise bursts impaired the bats' ability to locate the speaker. Burst duration per se was not a factor, since the bats performed similarly at all three durations when performing only passive sound localization. This suggests that only the information in a 25 ms (or less) noise burst was needed for optimal localization performance. One can imagine a case in which a 25-ms burst occurred between echoes, and the bat acquiring and retaining the information needed to locate the speaker because there was no interference. One can also imagine a case in which a 100 ms noise burst begins at the same time as

the 25 ms burst (relative to the timing of echoes), but the burst persists longer and overlaps with an echo. The echo may, in effect, backward mask the preceding segment of the noise burst and erase it from memory.

If these assumptions are correct, then they suggest that, like humans, the pallid bats experience a neural “bottleneck” because the same neural tissue is required to process both streams of spatial information (Marois et al. 2000). Therefore, although physiological studies suggest that the pallid bat primary auditory pathway has evolved specializations that should maximize the separation of the processing of echolocation and passive listening required under dual-task conditions, there is ultimately a convergence of these pathways that precludes true simultaneous dual-stream processing. The data do, however, suggest that the pallid bat is capable of rapid attentional switching between auditory objects.

In conclusion, it appears that processing two sounds close in time comes with a cost, even in species with discrete neural pathways dedicated to their processing. The pallid bat appears to mitigate this cost by decreasing its echolocation pulse rate to allow more time for the uninterrupted reception and processing of prey-generated noise. It is interesting that every gleaner examined to date exhibits a similar lack of “terminal buzz” (a systematic increase in pulse rate as a bat nears its prey; Griffin 1958) when using passive acoustic cues to localize prey (Fiedler 1979, *Megaderma lyra*; Grant 1991, *Nyctophilus gouldi* and *N. geoffroyi*; Faure et al. 1993, *Myotis septentrionalis*; Faure and Barclay 1994, *Myotis evotis*; Fuzessery et al. 1993, *Antrozous pallidus*; Arlettaz et al. 2001, *Myotis myotis* and *Myotis blythii*). This low pulse rate behavior cannot be solely attributed to the risk of warning prey, as the same behavior is seen in gleaners that feed on prey deaf to ultrasound (Barclay et al. 1981, *Trachops cirrhosus*; Ryan and Tuttle 1987, *Cardiaderma cor*). Therefore, given the limited processing capacity of sensory systems, decreasing echolocation pulse rate when navigating complex environments in order to concurrently listen for prey sounds may be a common strategy of gleaner bats.

**Acknowledgements** We are most grateful for the assistance in statistical analyses provided by Ken Gerow and Mark Leary, the software programming by Glen McLelland and Willard Wilson, and editorial comments by Mali Yenisey and Terri Zumsteg. We also appreciate the considerable time and effort contributed by two anonymous reviewers. This research was supported by grants to Z.M.F. from the National Science Foundation (IBN-9828599) and the National Institutes of Health (R01 DC00054).

## References

- Anderson EM, Racey PA (1991) Feeding behavior of captive brown long-eared bats, *Plecotus auritus*. *Anim Behav* 42:489–493
- Arlettaz R, Jones G, Racey PA (2001) Effect of acoustic clutter on prey detection by bats. *Nature* 414:742–745
- Barclay RMR, Fenton MB, Tuttle MD, Ryan MJ (1981) Echolocation calls produced by *Trachops cirrhosus* (Chiroptera: Phyllostomatidae) while hunting for frogs. *Can J Zool* 59:750–753
- Bell GP (1982) Behavioral and ecological aspects of gleaning by a desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav Ecol Sociobiol* 10:217–223
- Bell GP, Fenton MB (1986) Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macroptes californicus* (Chiroptera: Phyllostomidae). *Anim Behav* 34:409–414
- Bregman AS (1990) Auditory scene analysis. MIT Press, Cambridge, MA
- Brown P (1976) Vocal communication in the pallid bat, *Antrozous pallidus*. *Z. Tierpsychol* 41:34–54
- Coles RB, Guppy A (1986) Biophysical aspects of directional hearing in the Tamar wallaby, *Macropus eugenii*. *J Exp Biol* 121:371–394
- Coles RB, Guppy A, Anderson ME, Schlegel P (1989) Frequency sensitivity and directional hearing in the gleaning bat, *Plecotus auritus* (Linnaeus) 1758. *J Comp Physiol A* 165:269–280
- Curtis WE (1952) Quantitative studies of echolocation in bats (*Myotis l. lucifugus*), studies of vision in bats (*Myotis l. lucifugus* and *Eptesicus f. fuscus*) and quantitative studies of vision in owls (*Tyto alba pratincola*). PhD Thesis, Cornell University, Ithaca, NY
- Duncan J (1998) Converging levels of analysis in the cognitive neuroscience of visual attention. *Philos Trans R Soc Lond Ser B* 337:1307–1317
- Duncan J, Martens S, Ward R (1997) Restricted attentional capacity within but not between sensory modalities. *Nature* 387:808–810
- Faure PA, Barclay RMR (1994) Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behavior of the long-eared bat, *Myotis evotis*. *J Comp Physiol A* 174:651–660
- Faure PA, Fullard JH, Dawson JW (1993) The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis* are relatively inaudible to moths. *J Exp Biol* 178:173–189
- Fay RR (1998) Auditory stream segregation in goldfish (*Carassius auratus*). *Hear Res* 120:69–75
- Fay RR (2000) Spectral contrasts underlying auditory stream segregation in goldfish (*Carassius auratus*). *JARO* 1:120–128
- Fiedler J (1979) Prey catching with and without echolocation in the Indian false vampire (*Megaderma lyra*). *Behav Ecol Sociobiol* 6:155–160
- Fuzessery ZM (1994) Response selectivity for multiple dimensions of frequency sweeps in the pallid bat inferior colliculus. *J Neurophysiol* 72:1061–1079
- Fuzessery ZM (1996) Monaural and binaural spectral cues created by the external ears of the pallid bat. *Hear Res* 95:1–17
- Fuzessery ZM, Hall JC (1996) The role of GABA in shaping frequency tuning and selectivity for FM sweep direction in the inferior colliculus. *J Neurophysiol* 76:1059–1073
- Fuzessery ZM, Buitenhoff P, Andrews B, Kennedy JM (1993) Passive sound localization of prey by the pallid bat (*Antrozous p. pallidus*). *J Comp Physiol* 171:767–777
- Giard M, Fort A, Mouchetant-Rostaing Y, Pernier J (2000) Neurophysiological mechanisms of auditory selective attention in humans. *Front Biosci* 5:84–94
- Grant JDA (1991) Prey location by two Australian long-eared bats, *Nyctophilus gouldi* and *N. geoffroyi*. *Aust J Zool* 39:45–56
- Griffin DR (1958) Listening in the dark. Yale University Press, New Haven
- Griffin DR, Novick A (1955) Acoustic orientation of neotropical bats. *J Exp Zool* 130:251–300
- Guppy A, Coles RB (1988) Acoustical and neural aspects of hearing in the Australian gleaning bats, *Macroderma gigas* and *Nyctophilus gouldi*. *J Comp Physiol A* 162:653–668
- Gustafson Y, Schnitzler HU (1979) Echolocation and obstacle avoidance in the hipposiderid bat *Asellia tridens*. *J Comp Physiol* 131:161–167
- Heffner RS, Koay G, Heffner HE (2001) Sound localization in a new-world frugivorous bat, *Artibeus jamaicensis*: acuity, use of binaural cues, and relationship to vision. *J Acoust Soc Am* 109:412–421

- Hopfinger JB, Buonocore MH, Mangun GR (2000) The neural mechanisms of top-down attentional control. *Nat Neurosci* 3:284–291
- Hulse SH, MacDougall-Shackleton SA, Wisniewski AB (1997) Auditory scene analysis by songbirds: stream segregation of birdsong by European starlings (*Sturnus vulgaris*). *J Comp Psychol* 111:3–13
- Jen HS, Kamada T (1982) Analysis of orientation signals emitted by the CF-FM bat, *Pteronotus p. parnellii* and the FM bat, *Eptesicus fuscus* during avoidance of moving and stationary obstacles. *J Comp Physiol* 148:389–398
- Johnston DS, Fenton MB (2001) Individual and population-level variability in diets of pallid bats (*Antrozous pallidus*). *J Mammal* 82:362–373
- Joseph JS, Chun MM, Nakayama K (1997) Attentional requirements in a 'preattentive' feature search task. *Nature* 387:805–807
- Koay G, Kearns D, Heffner HE, Heffner RS (1998) Passive sound-localization ability of the big brown bat (*Eptesicus fuscus*). *Hear Res* 119:37–48
- Konstantinov AI, Sokolov BV, Stosman JMA (1967) Comparative research on bat echolocation sensitivity. *DAN SSSR* 175:1418
- Luck SJ, Ford MA (1998) On the role of selective attention in visual perception. *Proc Natl Acad Sci USA* 95:825–830
- MacDougall-Shackleton SA, Hulse SH, Gentner TQ, White W (1998) Auditory scene analysis by European starlings (*Sturnus vulgaris*): perceptual segregation of tone sequences. *J Acoust Soc Am* 103:3581–3587
- Marimuthu G, Neuweiler G (1987) The use of acoustical cues for prey detection by the Indian false vampire bat, *Megaderma lyra*. *J Comp Physiol* 160:509–515
- Marois R, Chun MM, Gore JC (2000) Neural correlates of the attentional blink. *Neuron* 28:299–308
- Möhres FP, Neuweiler G (1966) Die Ultraschallorientierung der Großblatt-Fledermäuse (Chiroptera-Megadermatidae). *Z Vergl Physiol* 53:195–227
- Neuweiler G (1984) Foraging, echolocation and audition in bats. *Naturwissenschaften* 71:446–455
- Neuweiler G (1990) Auditory adaptations for prey capture in echolocating bats. *Physiol Rev* 70:615–641
- Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos Trans R Soc Lond Ser B* 316:335–427
- O'Neill WE (1985) Responses to pure tones and linear FM components of the CF-FM biosonar signal by single units in the inferior colliculus of the mustached bat. *J Comp Physiol A* 157:797–815
- Orbist MK, Fenton MB, Eger JL, Schlegel PA (1993) What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. *J Exp Biol* 180:119–152
- Orr RT (1954) Natural history of the pallid bat, *Antrozous pallidus* (Le Conte). *Proc Calif Acad Sci* 28:165–246
- Populin LC, Yin TCT (1998) Behavioral studies of sound localization in the cat. *J Neurosci* 18:2147–2160
- Razak KA, Fuzessery ZM (2002) Functional organization of the pallid bat auditory cortex: emphasis on binaural organization. *J Neurophysiol* 87:72–86
- Ryan MJ, Tuttle MD (1987) The role of prey-generated sounds, vision, and echolocation in prey localization by the African bat *Cardiaderma cor* (Megadermatidae). *J Comp Physiol A* 161:59–66
- Schmidt S, Hanke S, Pillat J (2000) The role of echolocation in the hunting of terrestrial prey—new evidence for an underestimated strategy in the gleaning bat, *Megaderma lyra*. *J Comp Physiol A* 186:975–988
- Schneider H, Möhres FP (1960) Die Ohrbewegungen der Hufeisenfledermäuse (Chiroptera-Rhinolophidae) und der Mechanismus des Bildhörens. *Z Vergl Physiol* 44:1–40
- Schnitzler HU (1968) Die Ultraschall-Ortungslaute der Hufeisen Fledermäuse (Chiroptera-Rhinolophidae) in verschiedenen Orientierungs-situationen. *Z Vergl Physiol* 57:376–408
- Schnitzler HU, Henson OWJ (1980) Performance of airborne animal sonar systems. 1. Microchiroptera. In: Busnel RG, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York, 109–181
- Simmons JA, Fenton MB, O'Farrell MJ (1979) Echolocation and the pursuit of prey by bats. *Science* 203:16–21
- Simmons JA, Stein RA (1980) Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *J Comp Physiol A* 135:61–84
- Suga N (1965) Analysis of frequency-modulated sounds by auditory neurons of echolocating bats. *J Physiol (Lond)* 179:26–53
- Suga N (1969) Classification of inferior colliculus neurons of bats in terms of responses to pure tones, FM sounds, and noise bursts. *J Physiol (Lond)* 200:555–574
- Suthers RA (1967) Comparative echolocation by fishing bats. *J Mammal* 48:79–87
- Wisniewski AB, Hulse SH (1997) Auditory scene analysis in European starlings (*Sturnus vulgaris*): discrimination of song segments, their segregation from multiple and reversed conspecific songs, and evidence for conspecific song categorization. *J Comp Psychol* 111:337–350
- Yost WA (1991) Auditory image perception and analysis: the basis of hearing. *Hear Res* 56:8–18