

The role of the external ear in vertical sound localization in the free flying bat, *Eptesicus fuscus*

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The role of the external ear in sonar target localization for prey capture was studied by deflecting the tragus of six big brown bats, *Eptesicus fuscus*. The prey capture performance of the bat dropped significantly in the tragus-deflection condition, compared with baseline, control, and recovery conditions. Target localization error occurred in the tragus-deflected bat, and mainly in elevation. The deflection of the tragus did not abolish the prey capture ability of the bat, which suggests that other cues are available used for prey localization. Adaptive vocal and motor behaviors were also investigated in this study. The bat did not show significant changes in vocal behaviors but modified its flight trajectories in response to the tragus manipulation. The tragus-deflected bat tended to attack the prey item from above and had lower tangential velocity and larger bearing from the side, compared with baseline and recovery conditions. These findings highlight the contribution of the tragus to vertical sound localization in the free-flying big brown bat and demonstrate flight adaptations the bat makes to compensate altered acoustic cues.

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I. INTRODUCTION

Echolocating bats produce ultrasonic vocalizations and listen to echo returns to localize prey items and obstacles. They rely on biological sonar to accurately localize insects in a dynamic acoustic environment in which predator and prey are in continuous motion. Sound localization in bats, like other mammals, is accomplished largely via auditory computations on direction-dependent acoustic signals. Horizontal sound localization depends on binaural comparisons, such as interaural level difference (ILD) and interaural time difference (ITD), while vertical sound localization relies largely on spectral cues generated by the external ear.

The external ear of echolocating bats serves as a receiver to collect sound and is important for localizing auditory targets. The external ear of most bat species consists of two major parts, the pinna and the tragus (Fig. 1). The tragus is a piece of skin that stands in front of the ear canal and may affect the incoming acoustic signal. The size of the tragus varies across bat species but is typically a prominent structure, particularly compared with other mammalian ears.

It is generally believed that the tragus can generate spectral cues for vertical sound localization. Spectral notches in the head-related transfer function (HRTF) are elevation dependent, as reported in several bat species [*Phyllostomus discolor* (Firzlaff and Schuller, 2003), *Pteronotus parnellii* (Firzlaff and Schuller, 2004), *Antrozous pallidus* (Fuzessery, 1996), *Eptesicus fuscus* (Aytekin *et al.*, 2004; Müller, 2004; Wotton *et al.*, 1995; Wotton and Jenison, 1997)]. Previous studies have shown that spectral cues produced by the external ear are important for vertical sound localization in humans (Batteau, 1967; Bloom, 1977; Carlile *et al.*, 2005; Fisher and Freedman, 1968; Middlebrooks and Green, 1991;

Oldfield and Parker, 1986) as well as other animal species (Heffner *et al.*, 1996; Parsons *et al.*, 1999).

Several studies have addressed the functional contribution of the tragus to elevation-dependent spectral cues. Grinnell and Grinnell (1965) removed the contralateral tragus of the ear of *Plecotus townsendii* and recorded the evoked potential from the inferior colliculus (IC). Wotton *et al.* (1995) measured elevation-dependent changes in acoustic signals at the tympanic membrane of the big brown bat, *E. fuscus*, both before and after tragus removal. These two studies each reported sound elevation effects of tragus deflection, which occur below the bat's eye-nostril plane. Aytekin *et al.* (2004) found that tragus removal produced no change in elevation-dependent spectral notches of the big brown bat's HRTF in the frequency range of 30 to 50 kHz, as Wotton *et al.* (1995) reported. Instead, they found that the tragus contributed to the gain and directionality of the HRTF at 70 to 90 kHz. A similar HRTF study on another species, *Phyllostomus discolor*, reported that tragus deflection produced a significant decrease in the depth of a spectral notch at about 55–60 kHz (Firzlaff and Schuller, 2003). All studies to date reported some degree of change in characteristics of the HRTF when the tragus is removed. However, the nature and extent of change varies across studies and bat species. No research findings suggest that tragus removal abolishes elevation-dependent spectral notches, indicating that other sources of spectral cues may play a role in vertical sound localization, even if they must be relearned following changes to the external ear.

Psychoacoustic experiments on *E. fuscus* have also suggested that the tragus contributes to vertical sound localization, particularly below the horizon. The bat's ability to discriminate vertical angle deteriorates when the tragus is deflected (Lawrence and Simmons, 1982). Vertical angle

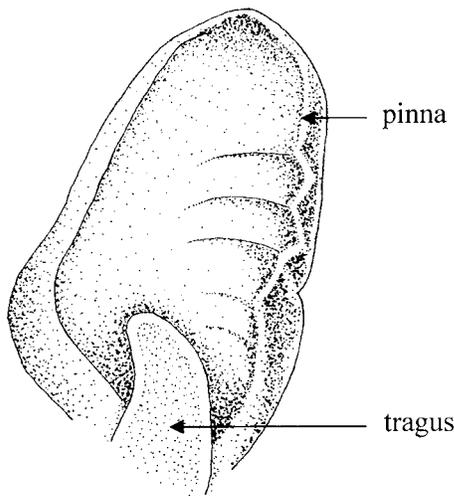


FIG. 1. Drawing of the external ear of *Eptesicus fuscus*, including the pinna and the tragus (drawn by Kweelen Lee).

acuity (VAA) in tragus-deflected bats is impaired for positions below the horizon, but not above the horizon (Wotton and Simmons, 2000). While past studies on the role of the tragus on vertical sound localization are suggestive, none have directly examined its importance in natural behaviors, namely on the precise localization required for insect capture.

Another question that remains to be answered is the extent to which an animal can adapt to modifications of the external ear that alter the acoustic cues used for vertical sound localization. Plasticity of sound localization has been studied in a broad range of animal species, including humans. Several studies demonstrate that plasticity can take place in adulthood, as long as a sufficient practice period is allowed (Hofman *et al.*, 1998; King *et al.*, 2000; Knudsen *et al.*, 1994; Linkenhoker and Knudsen, 2002; Van Wanrooij and Van Opstal, 2005). In addition, the degree and time period of adaptation in spatial hearing depends on the sound localization task.

There are two purposes of this study, first to investigate the influence of tragus deflection on prey capture behavior, with a particular emphasis on target localization in the vertical plane, and second to measure adaptive motor behaviors in response to changes in the acoustic cues believed to contribute to vertical sound localization.

II. METHODS

A. Experimental animals

Six big brown bats, *E. fuscus*, were used in the experiment. They were housed in an animal colony room at the University of Maryland, College Park, MD. The temperature and humidity in the facility were maintained at 24–28 °C and 30–50%, respectively. The light/dark cycle was reversed and maintained at 12 h, with lights off at 7:00 am so that bats were run in experiments during their active period. Bats were housed in small groups with two to four individuals in one cage, with free access to fresh water. They were maintained at approximately 80% of *ad lib* feeding weight and ate only

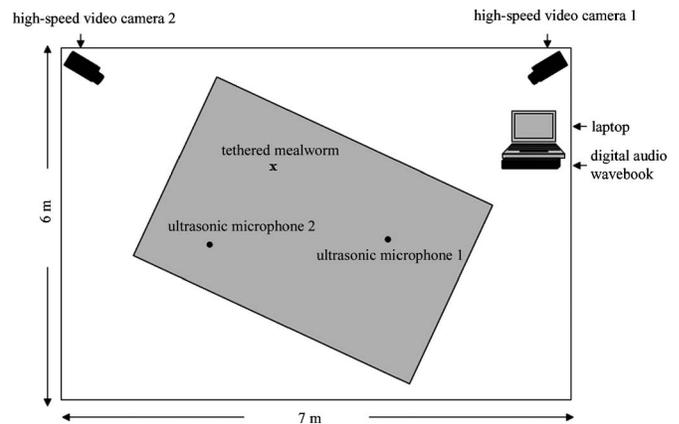


FIG. 2. Schematic of setup for video and sound recordings of tethered prey capture by echolocating bats. Two high-speed IR cameras (Kodak Motion-Corder Analyzer, 240 frames per second) were mounted in the room to permit 3D reconstruction of the bat's flight path. Video recordings were synchronized with audio recordings taken with two ultrasonic microphones delivering signals to an IOTech Wavebook.

when they successfully took tethered mealworm during experimental trials.

B. Behavioral experiment

Experiments were run between May and September when *E. fuscus* were most active. All the experimental trials were conducted in a large carpeted flight room (7 × 6 × 2.5 m³) with walls and ceiling lined with acoustic foam (Fig. 2). In order to eliminate the bat's use of visual cues, long-wavelength lighting (>650 nm) was used as the only light source in the flight room (Hope and Bhatnagar, 1979). Each bat was trained inside the flight room to catch tethered mealworms hung in random locations from the ceiling and with different string lengths (0.5, 0.75, 1, 1.25, and 1.5 m) to present insect prey at variable elevations. The data collection began after the bat performed the task at a minimum success rate of 75%.

C. Data collection

1. Audio recordings

Two ultrasonic microphones (UltraSound Advice, London) were placed on the floor to pick up vocalizations of the bat and stored digitally in a Wavebook (IOTech, sample rate 250 kHz per channel). These audio recordings were analyzed off-line using a custom MATLAB program to measure spectral and temporal features of echolocation calls produced by the bat performing the insect capture task.

2. Video recordings

Two high-speed video cameras (Kodak MotionCorder Analyzer, Model 1000, 240 frames per second) were mounted on two corners of the flight room to capture the motion of the flying bat. Video recordings from these two cameras were then digitized and analyzed off-line using commercial hardware and software (Peak Performance Technologies and MATLAB) to reconstruct the 3-D flight path of the bat.

3. Audio-video synchronization

Audio and video recordings were end-triggered simultaneously by the experimenter when the bat made or attempted contact with the mealworm and the preceding eight seconds of data were stored.

D. Tragus manipulation

Alteration of acoustic signals received at the bat's tympanic membrane was accomplished by gluing the tragus forward to the side of the head by Vetbond (3M) or Prosthetic Adhesive (Ben Nye). The glue was applied every day before the experiment started and served to hold down the tragus for approximately three hours (two hours after completion of experimental trials). There were four distinct experimental conditions: baseline, control, tragus-deflection, and recovery. Each condition was run over four successive days, except the control condition, which was run one day, and the entire experiment involved a total of 13 test days for each bat.

The behavioral task was identical in all four conditions. The baseline condition tested the prey capture performance of the individual bat with unmanipulated external ears. In the control condition, a drop of water was applied to the tragus, using the same procedures as the tragus-deflection condition without actually gluing down the tragus. The purpose was to determine if any change in the prey capture performance could be attributed to disturbance created by touching the bat's external ear. The tragus-deflection condition examined changes in the bat's prey capture performance when both tragi were glued down. The recovery condition was run after both tragi came up and documented the bat's behavior after the experimental manipulation to the external ears. The position of the tethered mealworm was changed every trial to prevent the bat's use of spatial memory rather than echolocation to perform the insect capture task.

E. Data analysis

Several parameters acquired from audio recordings were used to measure the bat's vocal behavior and are listed as follows: (1) spectral features of echolocation calls: start frequency (the highest frequency of the fundamental), end frequency (the lowest frequency of the fundamental), and bandwidth (the frequency range of the entire fundamental); (2) temporal features of echolocation calls: duration (the duration of the fundamental) and pulse interval (the time interval between the onset of two successive calls); and (3) terminal buzz duration, defined as the sound segment prior to insect capture or attempted capture with pulse intervals less than 8 ms.

Previous studies have shown that the tragus may play a role in vertical sound localization; thus the analysis of motor behavior was emphasized in the plane of elevation. Flight behavior was measured from video recordings and the following parameters were used: (1) trial time: from the moment the bat took off to when the bat made contact with the mealworm, (2) the elevation offset between the bat and the prey [Fig. 3(a)], (3) the tangential velocity of the bat in the vertical plane (side view) [Fig. 3(b)], and (4) the bearing in the vertical plane [Fig. 3(c)]. The bearing is the angle be-

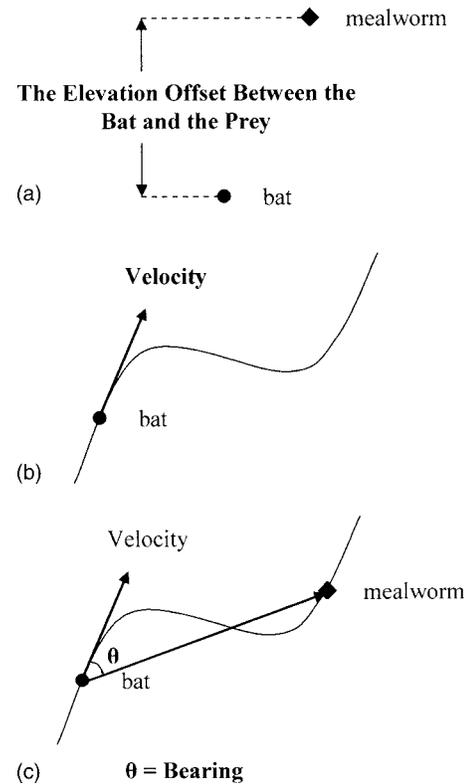


FIG. 3. Measurements of adaptive motor behavior. (a) The elevation offset between the bat and the prey; (b) the velocity of the bat from the side view; and (c) the bearing from the side view.

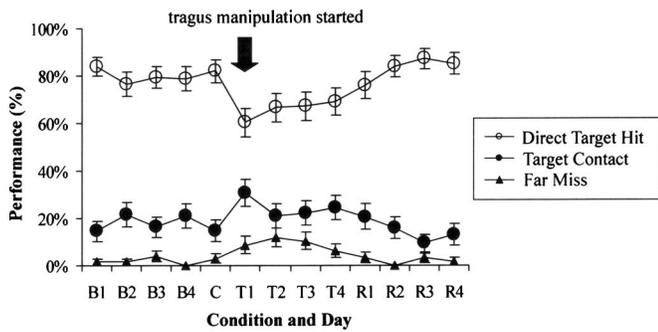
tween two vectors, which are the vector of the bat's tangential velocity and of the bat-worm vector (vector from the bat to the mealworm). The first vector represents the actual direction the bat is heading, and the second one is the direction from the bat to the worm.

All vocal and motor behavior analyses were carried out for trial segments within one second before contact with the tethered mealworm. In addition, only the vocal and motor behaviors of the direct target hit trials were included to study adjustments of these behaviors following the tragus manipulation. Repeated measurement ANOVA was used to test statistical differences in data across conditions. Bonferroni adjustments were used to correct for additive errors associated with multiple tests in *post-hoc* analyses, e.g., $0.05/n$, where $n=10$.

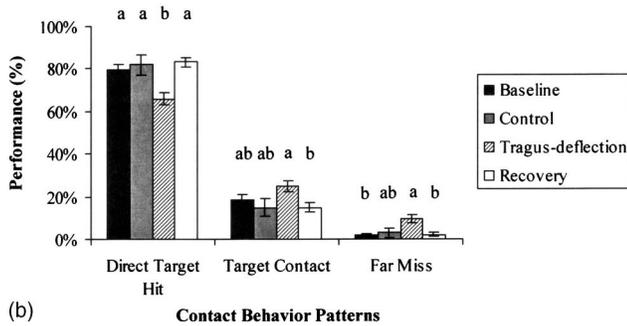
III. RESULTS

A. Performance

Three insect capture behavior patterns were categorized from video recordings, i.e., direct target hit, target contact, and far miss. Direct target hit was the most typical pattern in the prey capture behavior. The bat approached the mealworm and used its tail membrane to scoop up the mealworm. Target contact was recorded when the bat attempted insect capture with a body part other than the tail membrane (such as left/right wing, mouth, etc.). The bat may successfully consume the tethered mealworm or drop it in the contact behavior described above, but in either case the bat made physical contact with the target. Far miss occurred when the bat failed



(a) (B-baseline, C-control, T-tragus-deflection, R-recovery)



(b) Contact Behavior Patterns

FIG. 4. Prey capture performance. (a) Prey capture performance under different conditions over repeated test days. The open circle summarizes direct target hits, the closed circle shows target contacts, and the closed triangle shows far misses. The x axis represents the conditions (B as baseline, C as control, T as tragus-deflection, and R as recovery) and the number refers to test days 1 to 4. (b) Prey capture performance under different conditions. The letters above the histograms represent the rank of the performance. The same letter means no significant difference.

to hit the actual target. The first pattern characterizes the bat's precise localization of its prey. The second and third patterns show localization errors of different magnitudes.

The prey capture performance of all six bats is shown in Fig. 4. The Fisher exact test (Zar, 1996) was used to analyze the performance change across days and conditions. Within the same condition, there is no significant difference in performance across different days [$p > 0.05$, Fig. 4(a)]. Direct target hit is the most frequent behavior pattern across all four experimental conditions, and target contact and far miss trials increase in the tragus-deflection condition. The direct target hit trials remain at around 80% in the baseline condition. The performance of the control condition is comparable to that of the baseline condition. There is a drop in the percentage of direct target hit trials and a rise in target contact and far miss trials on the first day of the tragus deflection condition; performance in the tragus manipulation condition gradually returns to the baseline level. The percentage of direct target hits is higher on the first day of recovery compared with the tragus-deflection condition but lower than in baseline trials. The performance of the following three days of recovery data is similar to the baseline condition. Collapsing data across days, the percentage of direct target hit trials in the tragus-deflection condition is the lowest, and the percentages of target contact and far miss trials are the highest [Fig. 4(b)].

We also analyzed the interaction position of the bat with respect to the insect across conditions. The moment the bat

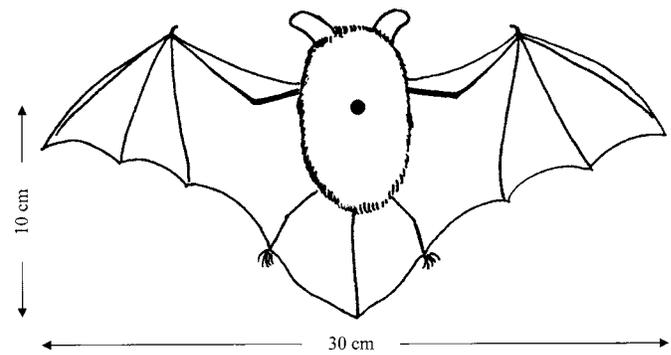


FIG. 5. The range of capture measurement in *E. fuscus*. The black dot on the bat's body is the center of the bat.

made contact with the mealworm is defined as interaction time. The bat's position at this time is referred to as the interaction position, and the distance between the bat and the prey at the interaction time is defined as the interaction distance. Because the bat can catch the mealworm using not only its tail membrane but also the wing, the range of capture is defined by the wingspan and body length of the bat (Fig. 5). The wingspan (30 cm) determines the horizontal range (x and y planes) and the length between the center of the body and the tip of the tail (10 cm) determines the vertical range (z plane) that the bat can reach. To examine in detail how the tragus manipulation influences interaction distance of the bat, the number of trials that exceed this range is shown in Table I across conditions. The interaction distance exceeds the range of capture in the z plane in significantly more trials when the tragus was glued down compared with baseline and recovery conditions. However, the tragus manipulation has no effect on the interaction distance in x and y planes.

B. Adaptive vocal behavior

The terminal buzz duration (Fig. 6) in both tragus-deflection and recovery conditions is significantly longer

TABLE I. The interaction distance under three different tragus conditions.

Dimension	Tragus condition	Trials exceed (x or $y > 15$ or $z > 10$)		p	Post hoc test
			%		
x plane	Baseline	2	0.74	n.s.	
	Tragus-deflection	3	1.14		
	Recovery	1	0.41		
y plane	Baseline	4	1.48	n.s.	
	Tragus-deflection	3	1.14		
	Recovery	1	0.41		
z plane	Baseline	3	1.11	<0.05	b
	Tragus-deflection	12	4.56		a
	Recovery	5	2.07		ab
Distance (3-D)	Baseline	3	1.11	<0.01	b
	Tragus-deflection	14	5.32		a
	Recovery	5	2.07		ab

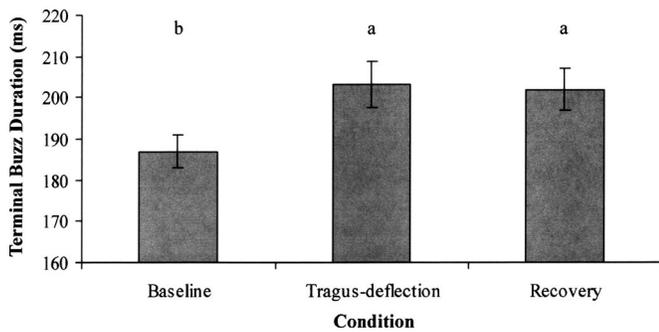


FIG. 6. Sonar buzz duration across the three different conditions, baseline, tragus-deflection, and recovery. The letter in the histogram represents the rank of the buzz length.

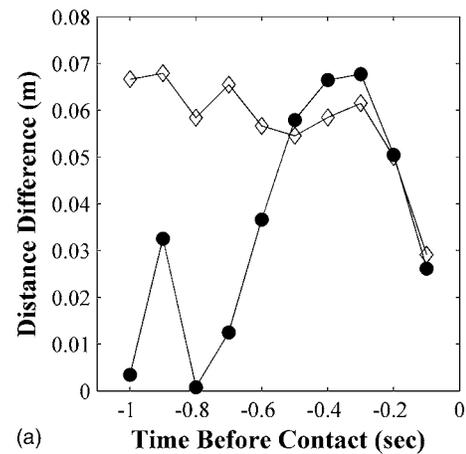
than in the baseline condition (one-way ANOVA, $p < 0.05$). The features of vocalizations were analyzed in 100-ms time blocks during the final 1000 ms before the bat captured the prey item. Only direct target hit trials were included in the analysis of adaptive vocal behavior to examine if the bat modified its echolocation calls in order to catch the prey successfully. No reliable pattern of change in the vocalizations emerged from these analyses when comparing the baseline, tragus-deflection, and recovery conditions.

C. Adaptive motor behavior

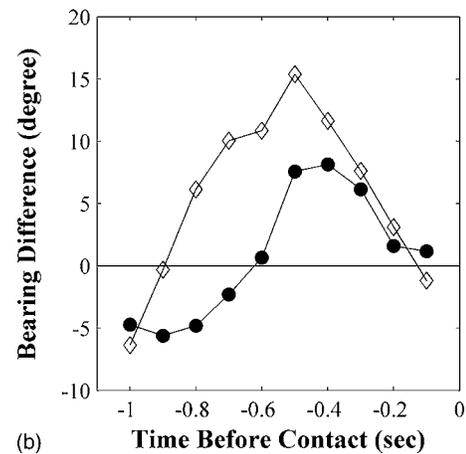
There is no significant difference in trial time from release to capture across baseline (17.78 ± 1.78 s), tragus-deflection (19.94 ± 2.42 s) and recovery conditions (16.84 ± 1.88 s). Although the tragus-deflection condition shows the largest average trial time compared with the other two conditions, the difference is not statistically significant (one-way ANOVA, $p > 0.05$).

The adjustment of distance (between the bat and the prey) and bearing in the tragus-deflection condition is shown in Fig. 7. The magnitude of adjustment is computed from the distance and bearing difference between baseline and tragus-deflection conditions (the mean distance/bearing in the tragus-deflection condition subtract by the mean distance/bearing in baseline condition). The distance [Fig. 7(a)] and bearing [Fig. 7(b)] differences in the vertical plane are similar to differences in the horizontal plane in the last half second, but show larger differences in the vertical plane than in the horizontal plane before 0.5 s before contact. The modifications of flight path in the tragus-deflection condition are more prominent in the vertical than the horizontal plane.

The bat tended to attack the mealworm from above when tragi were glued down. The elevation offset between the bat and the prey in the tragus-deflection trials is significantly larger than in the baseline condition during the entire last second before contact [Fig. 8(a)]. The recovery condition shows the smallest elevation offset between the bat and the prey and even smaller than the baseline condition for half the time segments (five out of ten time segments). The bat flew slower in the tragus-deflection condition [Fig. 8(b)]. In the tragus-deflection condition, the bat first shows higher side tangential velocity than in the baseline condition and lowers it and then raises it again in the last 0.1 s before contact. The side tangential velocity in the recovery condition shows no



(a)



(b)

FIG. 7. The adjustment of flight path in different planes in the tragus-deflection condition. (a) Distance difference and (b) bearing difference in the horizontal (closed circle) and vertical (open diamond) planes. The difference is computed from the difference between mean values in baseline and tragus-deflection conditions in every time segment.

significant difference compared with the baseline condition in most time segments, except three (0.7, 0.6, and 0.1 s before target contact, $p < 0.005$), and the differences between baseline and recovery conditions are not as large as the differences between tragus-deflection and recovery conditions. The bearing from the side view is larger in the tragus-deflection than in the baseline condition during 0.8 to 0.2 s before contact [$p < 0.005$, Fig. 8(c)]. The recovery of the bearing is not complete and, in three time segments (0.4 to 0.2 s before contact, $p < 0.005$), the bearing is significantly different from the baseline condition.

The prey capture performance dropped most dramatically on the first day of the tragus-deflection condition. Therefore, the motor behavior data from the first test day were analyzed in detail. The motor behavior of different attack patterns, direct target hit and target contact, was also compared here. Far miss trials were excluded from this analysis due to the small sample size. To simplify the description of the results on adaptive motor behaviors in the first day of tragus-deflection, we summarized the findings separately for the baseline condition direct target hit (B-DH) trials, the first day tragus-deflection condition direct target hit (1st T-DH) trials, and the first day tragus-deflection condition

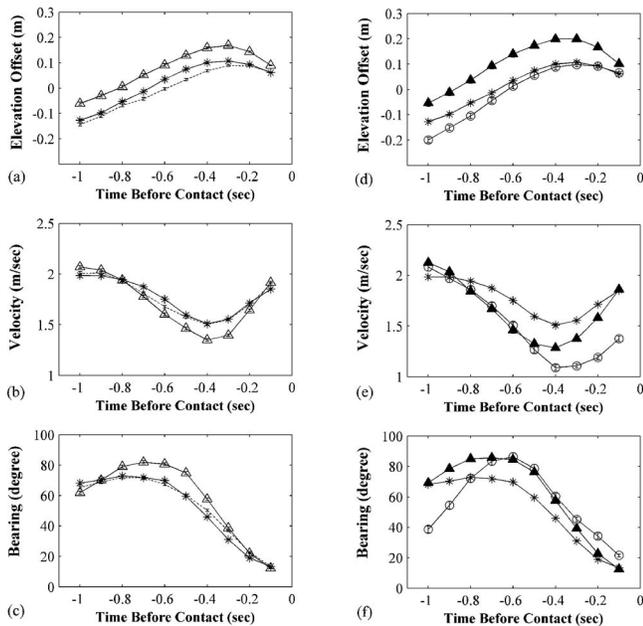


FIG. 8. The bat's adaptive motor behavior. (a) The elevation offset between the bat and the prey; (b) the velocity of the bat from the side view; and (c) the bearing from the side view in direct hit trials across the three conditions: baseline (asterisk), tragus-deflection (open triangle), and recovery (dot). The bat's adaptive motor behavior: (d) the elevation offset between the bat and the prey; (e) the velocity of the bat from the side view; and (f) the bearing from the side view, in the three conditions, baseline condition direct target hit (B-DH) trials (asterisk), the first day tragus condition direct target hit (1st T-DH) trials (closed triangle), and the first day condition target contact (1st T-C) trials (open circle). Error bars represent the standard error of the mean.

target contact (1st T-C) trials. Comparing these three different data sets provides information about how the bat modified its motor behaviors to enable insect capture. We hypothesize that the bat adapted its motor behaviors in response to changed acoustic input as a result of the tragus manipulation.

Following the tragus manipulation, the bat maintains almost the same elevation offset in 1st T-C trials, compared with B-DH trials in the last 0.7 s before prey capture [Fig. 8(d)]. On the other hand, 1st T-DH trials show significantly larger elevation offset between the bat and the prey than the other two conditions ($p < 0.005$). This result is consistent with our hypothesis stated above. The bat shows significantly lower side tangential velocity in 1st T-C and 1st T-DH trials compared with B-DH trials in the last 0.7 s before capturing the prey [$p < 0.005$, Fig. 8(e)]. The 1st T-C trials have the lowest side velocity across three data sets ($p < 0.005$). In the last 0.1 s before prey capture, the bat shows the same side velocity in both 1st T-DH trials and B-DH trials. The tragus-deflected bat only made contact with the tethered mealworm when the side velocity at the last moment did not reach the baseline level. The 1st T-DH trials show significantly larger bearing from the side view than B-DH trials in the final second before prey capture ($p < 0.005$), except for the beginning and end of this period [Fig. 8(f)]. The 1st T-C trials show smaller bearing in the beginning of the last 1 s before contact (1 and 0.9 s before contact) and the bearing increases significantly over B-DH trials ($p < 0.005$), but is similar to 1st T-DH trials ($p > 0.005$). The bearing in 1st T-DH trials is closer to B-DH trials than 1st T-C trials in the final 0.1 s

before prey capture. The difference in bearing across conditions in the final 0.1 s of a trial seems critical to the outcome of prey capture, i.e., direct target hit or off-axis contact of the prey item. Although these results on the velocity and bearing do not statistically support our hypothesis, adjustments of motor behaviors in the very last moment have immediate consequences on prey capture success.

IV. DISCUSSION

A. The influence of tragus deflection on prey capture performance and sound localization

Tragus deflection reduced sound localization accuracy and decreased successful prey capture performance of the big brown bat, with the largest effect on the first test day after the experimental manipulation of the external ear. Similar performance in control and baseline conditions demonstrates that the drop in the prey capture performance under the tragus-deflection condition is caused by changes in acoustic cues used for prey localization. Over test days, the bat adapted to the changes in acoustic cues introduced by tragus-deflection and successfully captured tethered prey after some experience with altered external ears. This result suggests that the bat can adapt quickly to altered acoustic cues for prey localization. The recovery and baseline conditions did not show significantly different performance, which suggests that the bat can switch back to using baseline acoustic cues for sound localization. These results are consistent with human studies: Introducing new spectral cues to the human ear via pinna molds increased sound localization error, particularly in the vertical plane (Fisher and Freedman, 1968; Hofman *et al.*, 1998; Oldfield and Parker, 1984; Van Wanrooij and Van Opstal, 2005). However, subjects regained the vertical sound localization ability after a few days of experience, and the newly learned cues did not interfere with the old ones (Hofman *et al.*, 1998; Van Wanrooij and Van Opstal, 2005).

In the present study, the percentage of trials exceeding the range of capture is used as an index of sound localization error. The more trials exceeding the range of capture, the more consistent is the error. In the vertical plane, the most trials exceeding the range of capture occurred in the tragus-deflection condition compared with baseline and recovery conditions. Tragus-deflection produced no effect on interaction distance in the other two planes. This indicates that the tragus-deflection has the largest effect on vertical sound localization. Previous behavioral studies of vertical localization in *E. fuscus* also came to similar conclusions with different experimental designs (Lawrence and Simmons, 1982; Wotton and Simmons, 2000).

The bat's prey capture performance decreased after tragus were glued down. The performance dropped significantly but did not drop below 50%, which suggests that prey capture ability of *E. fuscus* is not heavily dependent on the contribution of the tragus. This result is consistent with HRTF studies on the echolocating bat, which show some spectral changes following tragus deflection, but they are not very dramatic (Aytekin *et al.*, 2004; Firzlafl and Schuller, 2003; Grinnell and Grinnell, 1965; Müller, 2004; Wotton *et al.*, 1995).

Müller *et al.* (2006) demonstrate that the tragus, as well as the lower ledge of the pinna rim, introduces similar contributions to the directivity patterns in *Nyctalus plancyi*. It is suggested that the spectral cues introduced by the tragus can facilitate sound localization in the vertical plane. However, the contribution of the tragus is limited, and the present study demonstrates that the bat can adapt to changes in the filtering characteristics of the external ear. Although the big brown bat does not have a prominent lower ledge of the pinna rim, other parts of the external ear, such as the ridge along the pinna, may also contribute to sound localization. Human and bat studies have shown that auditory cues for horizontal and vertical sound source localization are not independent (human: Butler and Humanski, 1992; Gardner, 1973; bat: Aytekin *et al.*, 2004; Fuzessery, 1996). Therefore, changes in certain spectral cues caused by tragus-deflection may be compensated by other cues. Therefore, the tragus can contribute to the acoustic cues for vertical sound localization, but they are not exclusive.

B. Sensory-motor adaptation

Two highly interrelated systems, sensory and motor, are required for successful prey capture in the echolocating bat. The bat must localize the source of echoes reflected from prey and use this spatial information to guide motor systems to enable appropriate commands for prey capture. The bat relies upon precise sound localization of prey through binaural and monaural acoustic cues. The effect of the tragus on vertical sound localization has already been described above. Successful prey capture also depends on accurate motor control of the body. Distorted acoustic information about object location is expected to elicit errors in motor behaviors.

Since humans rely heavily on vision and bats on audition to perceive their spatial surroundings, there may be some relevant parallels to explore in sensory-motor adaptations. Several human studies have introduced distorted or rotated visual information to subjects who are required to produce movements to accomplish task-specific goals (Abeele and Bock, 2001; Cunningham, 1989; Cunningham and Welch, 1994; Imamizu *et al.*, 1998; Kagerer *et al.*, 1997; Marotta *et al.*, 2005; Martin *et al.*, 2002; Stratton, 1896, 1897a, b; Van Beers *et al.*, 2002; Yoshimura, 2002). Redding *et al.* (2005) indicate that prism exposure involved three adaptive processes, which are postural adjustments, strategic control, and spatial realignment. All these studies demonstrate that humans show plasticity in visual-motor control and are capable of selecting suitable locomotion to adapt to distorted visual cues. A related study on rhesus monkeys reported that nonhuman primates acquire and generalize visual-motor transformations as do humans (Paz *et al.*, 2005).

In the present study of altered sensory input, the big brown bat attacked from higher elevation in the tragus-deflection condition than the baseline condition. In addition, the trials in which the bat contacted the target show similar flight path characteristics to the baseline condition, suggesting that modifying the flight path can increase the prey capture performance of the bat. The bearing from the side view

also shows a larger bearing in the tragus-deflection condition than the tragus-intact condition, including baseline and recovery. These flight path modifications are the most robust and consistently significant changes in the bat's motor behavior in response to altered acoustic cues for vertical sound localization in the bat. Similar trajectory modification has also been reported in human visual-motor adaptation studies (Abeele and Bock, 2001; Contreras-Vidal *et al.*, 2005; Cunningham, 1989; Seidler, 2005; Wolpert *et al.*, 1995a).

Altered acoustic cues for sound localization in this study bear the same relation to altered visual spatial cues in human studies. Human subjects wearing prisms that shift or rotate visual input showed hand trajectories that deviate from the original when asked to point to a target, but they also corrected the hand trajectory after some practice with feedback. Visual feedback is important for motor behavior adaptation (Redding and Wallace, 1994). A forward model predicts the outcome of the motor behavior and an inverse model records the signals, which are derived from the error between predicted and actual outcomes, used to select a motor command to reduce performance error. The trajectory change is the result of a motor learning process. The forward and inverse models are tightly coupled together and capable of explaining motor learning in humans (Kawato, 1999; Kawato and Wolpert, 1998; Wolpert and Kawato, 1998; Wolpert *et al.*, 1995b).

The same internal model can be applied to explain the bat's motor behavior adaptation in this study. The forward model in the bat predicts the target position and drives suitable motor commands for the animal to successfully intercept the mealworm. The bat typically captures the prey by positioning itself just above the prey item to scoop it up with the tail membrane. When a localization error occurs, the bat may still be able to make contact with the target, but with the wing or the mouth instead of the tail membrane. Through contact with the prey, the bat acquires information about the actual target position. The discordance between the estimated and actual target positions generates a motor error. The motor error signal is conveyed to the inverse model and permits further correction in the next motor command, by adjusting the flight path approach (the elevation offset between the bat and the prey) and angle (the bearing from the side view). Therefore, even when the bat makes an error in localizing the tethered mealworm position in the tragus-deflection condition, it can still use dynamic auditory feedback to correct its motor behavior and initiate a proper motor command to successfully intercept the target.

Other human visual-motor research shows that decreasing the reaction time increases the performance error. There is a trade-off between reaction time and accuracy of pointing to the target location (Fitts, 1966). Although the trial time of the bat in this study did not show any significant difference across baseline, tragus-deflection, and recovery conditions, the approaching side velocity did show significant differences across these three experimental conditions. The result of lowering the side velocity suggests a trade-off between speed and accuracy. A slower velocity may provide the bat with the additional time needed to compensate the alteration of information from the experimental manipulation. The

slower side velocity in the first day contact trials suggests that the bat slowed down to correct its approach for attempted insect capture.

Redding and Wallace (2002) proposed two adaptation processes in human visual prism experiments: strategic calibration and spatial alignment. Prism goggles disrupt the relationship between extrinsic and intrinsic space, and a new visual-motor transformation is needed for visually guided reaching or pointing. The strategic calibration is a faster motor modification to adjust to a change in visual-motor mapping. The spatial alignment is a slower process and requires remapping the visual and motor relation. Similar adaptation processes have been reported by Shinn-Cunningham (2001) for the auditory system. Short-term training changes the perceived sound source location and long-term training may activate a new neural pathway to extract spatial information from altered acoustic cues. The motor adaptation in the tragus-deflection condition of this study suggests that the bat applies a strategic calibration to adapt to new spectral cues introduced by the external ear manipulation. The spatial alignment between the auditory and motor mapping may take place after long-term training.

V. CONCLUSIONS

In conclusion, our results suggest that the tragus plays a role in vertical sound localization for prey capture in the free-flying big brown bat, but the bat can quickly adapt to altered acoustic cues for sound localization. Tragus-deflection does not completely disrupt prey capture ability of the echolocating bat, which suggests that other cues can be used to compensate the effect of changing acoustic cues for target localization in the vertical plane. This is consistent with the report by Aytekin *et al.* (2004) that binaural cues are available to the bat for estimates of vertical sound localization. Moreover, in this study we provide evidence that the bat adapts its flight path in response to altered acoustic cues for target localization. A big brown bat with defective external ears is occasionally found in the wild. Whether the defect is congenital or acquired, this study demonstrates that the animal could successfully compensate for altered acoustic cues for prey localization by modifying its motor behavior.

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