The bat's head aim governs its flight, simplifying computation for target interception
(Extended Summary)

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Abstract

We studied the head-directing behavior of echolocating bats as they intercepted insect prey on the wing. We found that the angle between the bat's head and body at a given instant is proportional to its turn rate 80ms into the future. The bat centers its head on its prey during interception. We propose that these strategies simplify the computations required by the bat to guide its flight to the target.

Key words: echolocation, bat, sensori-motor, head-body, orientation

1 Introduction

Echolocating bats forage at night by producing ultrasonic vocalizations and using spatial information carried by reflected echoes[1]. Bats can control many of the parameters in the outgoing sound, which in turn influence the information they receive from the environment[2].

In this study we focus on the spatial pattern of the bat's sonar beam. The sonar beam produced by bats is directional. In the big brown bat, *Eptesicus fuscus*, the half-power width of the sonar beam is around 60^o. The pulse itself is short (.5 - 10 ms during approach and capture phases of insect pursuit) and the duty cycle is low (less than 10%). Therefore, the sonar beam limits what

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part of the environment the bat can probe with a single pulse. The bat locks its head onto a selected target with an accuracy of around 1^o[3]. This accuracy, given the broadness of the beam, is not explained by acoustic considerations alone.

In visual animals changes in head direction lead correlated changes in locomotion[4][5]. There are two main explanations for this behavior. One explanation suggests that in textured environments visual animals use optic flow to extract heading[6] and gaze direction is related to this computation[7]. The other explanation proposes a 'head-first' scheme for locomotion[8], where the head is first stabilized on a locomotor goal or intended direction of motion before the body is reoriented. Below, we present the relationship between head direction and motion in an echolocating bat. We argue that similarities between echolocating and visual animals, in this respect, point to links between head direction and motion planning that go deeper than any modality-specific requirement.

2 Methods

Echolocating bats flew in a large, dark, laboratory flight room. The walls and ceiling of the room were lined with acoustic foam to reduce echoes. The bats were trained to catch meal worms on a fine mono-filament tether. Images from two high-speed infra red video cameras (Kodak MotionCorder, 240 fps) were used to reconstruct the flight path of the bats and the trajectory of the prey. Simultaneously, a linear array of 16 microphones was used to record the sonar beam pattern emitted by the bats. *Eptesicus fuscus* produces brief, frequency modulated (FM) sonar signals with its mouth. The azimuthal axis of the sonar beam is aligned with the head[9]; therefore we infer the azimuthal direction of the bat's head from measurements of the sonar beam axis. Figure 1 shows a graphical representation of the beam pattern from a bat vocalization and the computed head direction $\mathbf{H}$. The bat's body axis is estimated from its velocity vector $\mathbf{V}$. The head-body angle is the angle between these two vectors. Details of the method are provided elsewhere[3].

Two types of experiments were performed in the present study. In one experiment, a single target on a tether was released from a trapdoor into the flight room as the bat flew around, so the bat would have to search for its prey, localize it and then readjust its flight path in order to capture the target. In the other type of experiment, the bat was required to intercept a target moving in a circular path. In this task the bat was forced to make extensive maneuvers in order to capture the prey.

3 Results

We compared the head-body angle of the bat (computed every time the bat vocalizes) with its rate of turn at different time lags with respect to the vocalization. We found that the strength of the correlation between the bat's head-body angle and its rate of turn varied with lag. This is shown in Figure 2. The correlation was maximum at a lag of +80ms. The scatter plot for head-body angle and corresponding turn-rate 80ms into the future is shown in Figure 3. The slope of the regression line is 5.21, with a correlation coefficient of 0.83. The data is taken from 1009 vocalizations recorded from 24 prey capture sessions using 5 different bats .

4 Discussion

The results indicate that the bat's head leads its motion. There is a strong linear relationship between the current head-body angle and the future turn rate of the bat, both when the bat is searching for prey and when it is tracking a selected target. During prey capture, the bat locks onto the target and tracks it accurately with its head. The position of the target with respect to the bat is now specified by one value, the head-body angle. The bat then uses a simple proportional turning rule to maneuver itself into a catching position. We propose that this combination of strategies is a simple and elegant solution to the prey capture problem faced by the bat.

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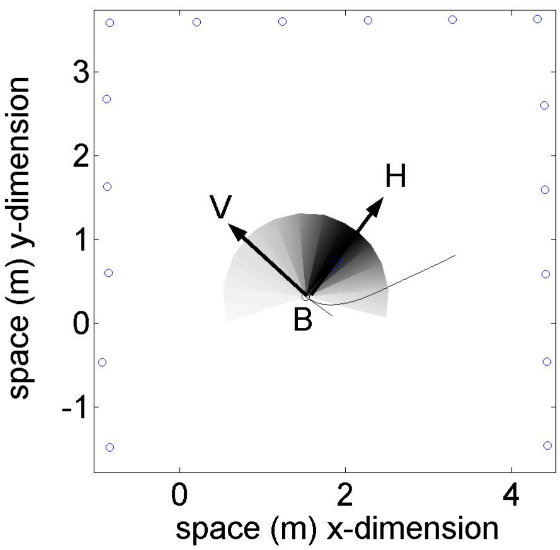

Fig. 1. Sonar beam-pattern, head direction(**H**) and direction of motion(**V**) of the bat

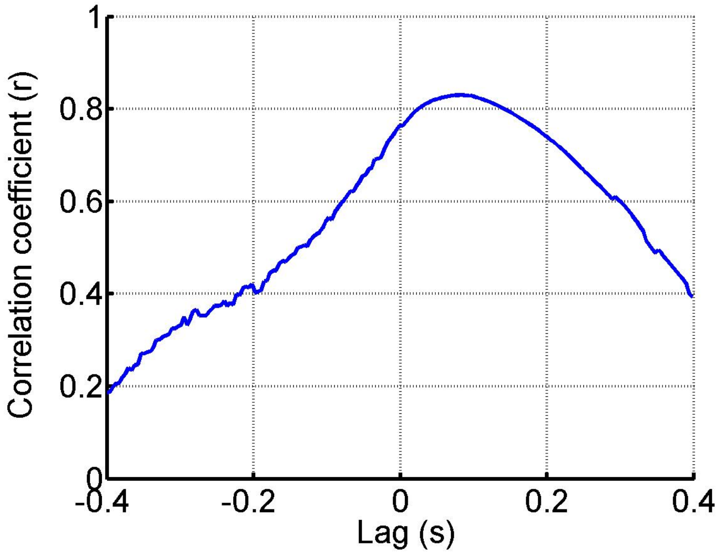

Fig. 2. Strength of the relationship between turning rate and head-body angle at various lags

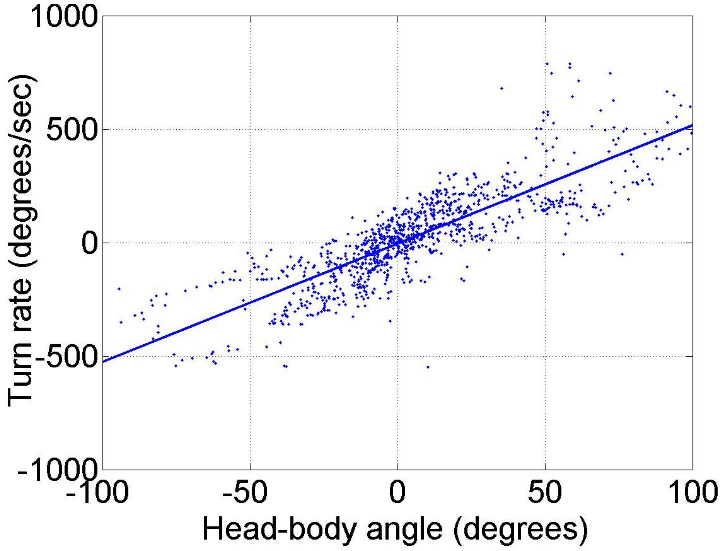

Fig. 3. Relationship between turning rate and head-body angle (80ms lag)