

VISUAL-MOTOR FEEDBACK IN THE TRACKING BEHAVIOR OF HOVERING *MANDUCA SEXTA*

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Introduction

Insight into the complex interplay of sensory information, musculoskeletal mechanics, and aerodynamic forces is critical for understanding the dynamics of insect flight performance. While the way each of these systems has been studied extensively, integrative studies that investigate multiple systems working together help us assemble a more complete picture of insect flight. While feeding at flowers in the wind, hovering hawkmoths must track a moving target in a spatially complex environment. Although the visual system can detect motion in different directions, characteristics of the musculoskeletal system could constrain the precision of directional control. Moreover, frequency tuning in the visual system may not account for the frequency response of tracking behavior at the organismal level.

We took advantage of the moths' tracking behavior to investigate the constraints that emerge from sensorimotor integration. We used a digital video camera to record hovering moths as they fed at an oscillating artificial flower. We digitized the positions of the moth and flower in order to quantify the performance of the moth as it tracked the flower in the looming (forward-back), vertical (up-down) and lateral (side-to-side) directions.

Background

In the laboratory, hawkmoths will continue feeding on one artificial flower for as long as a minute.^{1,2,3,4} Farina et al.¹ measured distance regulation for looming motion, simulating forward and back movement of flowers by expanding and contracting an image of a blue disk on a screen while hawkmoths fed at a nectary in the center of the disk. They found that the moth effectively regulates its distance relative to the flower, with the highest gain at flower oscillation frequencies between 1 and 5 Hz. What has not been done is a comparison of tracking responses to other patterns of flower movement. Towards this end, I compared tracking performance for all three linear

dimensions, and in doing so, established an experimental protocol that will allow for further exploration of other patterns of movement, such as in circular or elliptical paths, in order to fully characterize the tracking behavior.

Methods

Adult male and female hawkmoths (*Manduca sexta*) were taken from a colony maintained within our building. A rotating population of moths (30-40 individuals) was housed in an environmental chamber at 25° C under a 16L/8D light cycle with artificial lights. Experiments began fifteen minutes after lights out and ended after approximately one hour.

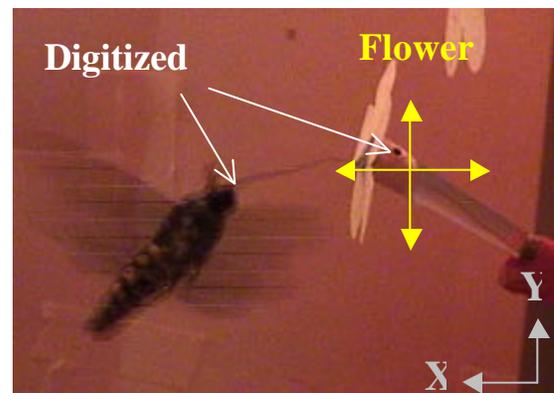


Figure 1. Hawkmoth hovering and feeding from the artificial flower. From this aspect both looming and vertical motion could be videotaped.

Setup: Nine artificial flowers, with diameters from 3 to 6 cm, were attached to a red background, simulating a bush. The artificial flower in the center of the bush was attached to an X-Y plotter allowing periodic, controlled motion of the flower along the X, Y or Z axis. A nectary in the center of the flower provided 1 ml of 20% sucrose solution.^{1,2} We used a digital video camera (30 frames/second) to simultaneously record the positions of the flower and the moth. The points

that we digitized were the base of the proboscis and a black dot on the flower (Fig. 1).

Experimental Procedure: Nine hovering moths were videotaped tracking the oscillating flower. Each sequence consisted of one moth tracking the oscillating flower along one of three axes (looming, vertical, lateral) at one of three amplitudes (10 mm, 20 mm or 30 mm). At a given amplitude the moth faced randomly varying frequencies of 1, 2 and 3 Hz. Each feeding bout lasted long enough to provide nine short video sequences – three of each frequency at each of the three amplitudes.

We used two measures of performance: gain and distance from the flower. Gain is the ratio between the average amplitude maintained by the moth and the average amplitude of the flower. Distance from the flower was obtained by comparing the mean position of the moth with the mean position of the flower, in the direction of interest.

Results

For each direction of flower movement we obtained mean values of gain and distance for moths tracking flowers oscillating with different frequencies and amplitudes. There was a peak in gain at 2 Hz, indicating that at that frequency the moths follow a path with the highest amplitude compared to that of the flower. The gain at 1 and 2 Hz was consistently greater than 1.0, indicating the tendency of the moths to 'overshoot' the flower at those frequencies. The moths maintained a much greater average distance from the flower when tracking it in the looming dimension (~4cm, Fig. 2) than in the vertical or lateral dimensions (~1cm).

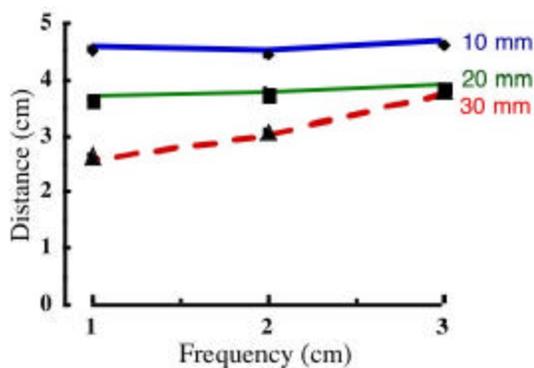


Figure 2. Distance between moth and artificial flower for three amplitudes versus frequency (looming motion).

One view of the camera captured motion in two of the three dimensions. Therefore, we used the terms 'primary' motion and 'secondary' motion to describe

movement of the moth parallel and perpendicular to the movement of the flower, respectively. We found that the amount of secondary motion was between 20 and 60% of the amount of primary motion.

Discussion

At 1 Hz and 2 Hz, moths have a spatial 'overshoot' in their tracking response. However, in looming motion there is less overshoot than in either vertical or lateral motion at the same frequencies. It is possible that inherent to looming flight are a set of controls that differ from those of vertical and lateral flight. This difference would explain why both gain and distance are similar for vertical and lateral motion, and different from looming. Future studies should pair the tracking behavior with flight kinematics and recordings of muscle activity to study whether this characteristic is based in the physiology or in the mechanics of flight control. While there were no clear relationships between secondary motion and amplitude, frequency or direction, it seems important to consider that a large portion of the moth's total movement is in a direction that does not seem to improve its feeding success. We are currently investigating the characteristics of the off-axis motion to determine the extent to which they are an essential component of the flight control system.

References

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