Flight control of honeybee in the Y-maze

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Abstract

The visual environment of the honeybee is rich with numerous cues that can be exploited for a number of purposes, including the identification of food sources and navigation. The Y-maze apparatus is widely used for behavioral test of insects, in order to examine their ability to recognize visual patterns. Behavioral changes during flight in the Y-maze are measured by counting the number of bees which crossed a decision line. However, in order to reveal the neuronal mechanisms that control flight, it is necessary to analyze the dynamical properties of flight trajectories, because visual information is changed by the honeybee's position, direction and velocity. This article presents a mathematical model for yaw control based on the optical flow and target signals.

Key words: flight control, compound eye, honeybee, mathematical model, vision

1 Introduction

An important aspect of neuronal modeling is to explore how animal behavior emerges from the interactions between an animal and its environment. It is well known that honeybees have high visual acuity and use vision for many purposes, including identification of food sources, navigation and mating. Furthermore, honeybees can learn characteristics of a visual target by associating it with food source. In the case of olfactory learning (associating food with an odor), the relation between behavioral changes during acquisition and recall and neuronal mechanisms have been investigated.

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However, in the case of visual conditioning, it has not been revealed yet how behavioral control signals emerge from visual information. The Y-maze apparatus is used as a standard protocol for performing honeybee behavioral experiments to study visual perception[3]. In this experiment, animal behavior is usually evaluated by counting the number of individuals who fly in a particular chamber by crossing a certain line. However, visual signals controlling honeybee flight depend on her position, direction and velocity. In order to understand flight behavior as the output of neuronal processing, it is necessary to determine the visual information signals acquired by the visual system during the flight. It is also important to confirm that these signals are sufficient for regenerating flight control signals through model simulation.

In this study, flight behaviors before and after visual conditioning were measured using a CCD camera located above the maze. A time series of acceleration and directional changes was calculated from the flight trajectory. Based on these properties, a flight control mechanism for yawing in the Y-maze was derived.

2 Experiments

Behavioral experiments for visual conditioning were performed in the Y-maze apparatus shown in Fig.1. A monochrome CCD camera was placed 3m above this arena. During the training sessions, a visual target (5cm diameter, either a blue or yellow painted circle) was displayed with food (30% sucrose water) at the center of Y-maze. After three or four training sessions, the center target was removed, then both blue and yellow targets were displayed, one on the back of each chamber. Images of flying honeybees were recorded at intervals of 30msec, and then honeybee position was measured frame by frame to trace the flight trajectory.

A significant difference in the flight trajectory was observed before (Fig.2(a)) and after training (Fig.2(b)). It was observed that unconditioned honeybees were not attracted to either target. They stayed about 10cm away from the targets and walls, and made circular trajectories during flight. The flight course tended to be curved near the target due to the optomotor response and collision avoidance, because only targets have high contrast with the background. On the other hand, conditioned bees flew directly toward the right target which was associated with the food source in three cases. In the case of solid line trajectory, honeybee flight toward the left target, then corrected her direction to the right.

During flight, acceleration and directional changes are caused by muscle forces acting on the wings. The temporal characteristics of these two sequences are

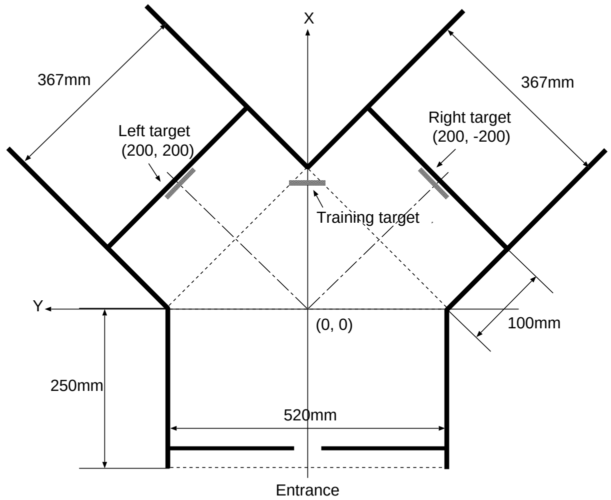

Fig. 1. Y-maze apparatus for behavioral experiment shown from above

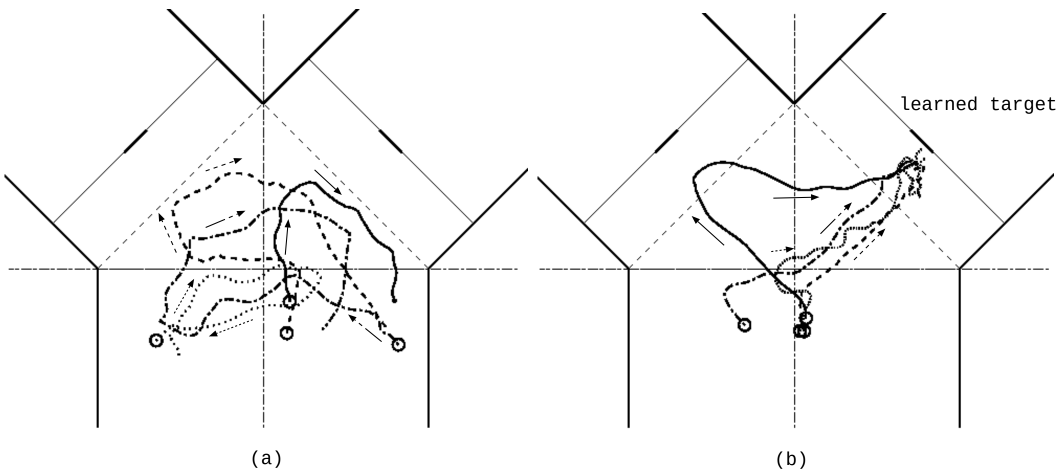

Fig. 2. Change of flight trajectory caused by visual conditioning (○: start point for recording), (a) before conditioning, (b) after conditioning (right target was associated with food)

a result of the behavioral control process in the honeybee nervous system. In insects, the flight course is controlled by visio-motor mechanisms, such as collision avoidance and the optomotor response. However, several intrinsic factors, fsuch as motivation for searching and memory recall, also influence honeybee behavior. Thus, the behavioral experiments show that flight behavior also depends on experience in the Y-maze.

3 Model analysis

Several methods have been proposed for calculation of the projected image on compound eyes[4], [5]. The visual world of a honeybee is formed from the photoreceptor responses generated in ommatidia, which depend on the brightness on the surface of the compound eye. Ommatidia outputs are inportant inputs to the optic lobe for visual information processing. Therefore, projected images on the compound eye during flight in the Y-maze were calculated assuming that, (i) the flight altitude was nearly constant, (ii) the bee's body and head were yaw-stabilized with respect to its flight trajectory, and (iii) the horizontal plane of the head was aligned parallel to the ground.

A three layer feed forward model for image processing is proposed with capabilies for target signal detection and optic flow calculation (Fig. 3). Cells in the first layer (retina layer) generate the photoresponses from brightness on each ommatidium surface[4]. The 2nd layer of cells (space filtering layer) has circular receptive fields, ranging from 5 to 20 degrees diameter, and integrates the response of first layer cells within each receptive field. In the third layer (feature detecting layer), optic flow is calculated from the 2nd layer cell responses. Specifically, there are three type of cells in this layer. The first type of cell has a circular receptive field and non-directional sensitivity. The second and third types form elementary motion detectors (EMD) of the Hassenstein-Reichardt correlation type. They have directional sensitivity for local vertical and horizontal image movement[7].

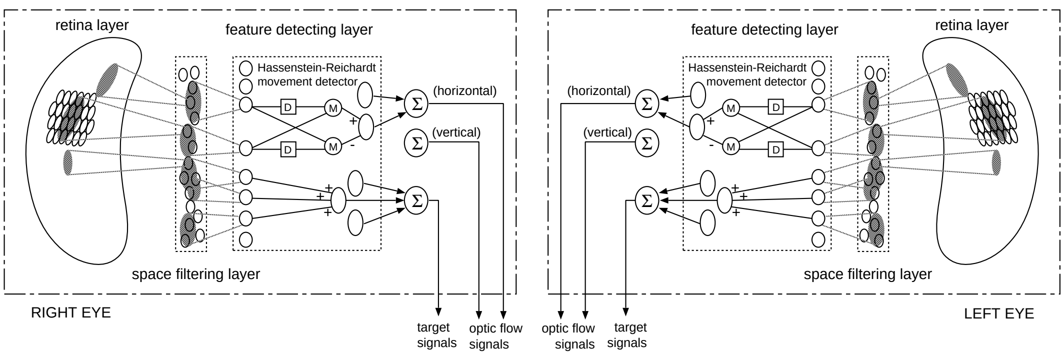

Fig. 3. Model of image processing for flight control.

As shown in Fig.4, four kinds of signals were used to calculate yaw directional changes from space filtering and EMD outputs[1], [2].

(1) s_{target}: attention to target signal
(2) s_{omr}: optomotor response signal (optic flow)
(3) s_{col}: collision avoidance signal (looming)
(4) $N(\mu, \sigma)$: uncertainty factors

s_{omr} was calculated by summation of EMD outputs, and s_{col} was summation of posterior optic flow components. Last signal N mentions uncertainly factors, such as air flow, fluctuation of body and intrinsic factors, described by a Gaussian noise component.

Before conditioning, flight simulations were done without the attention signal

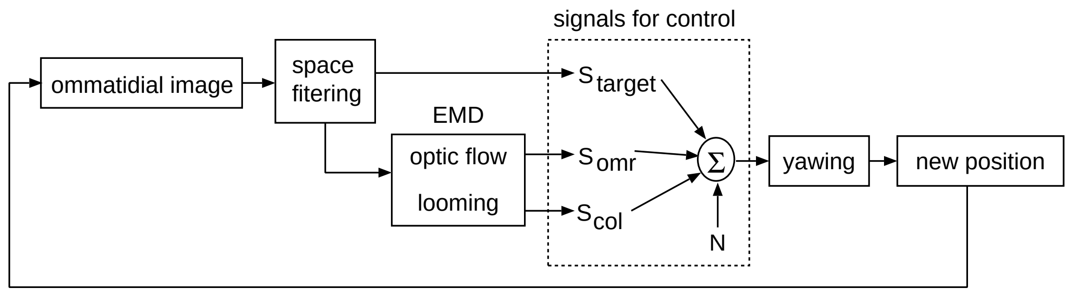

Fig. 4. Scheme of yaw control model simulation

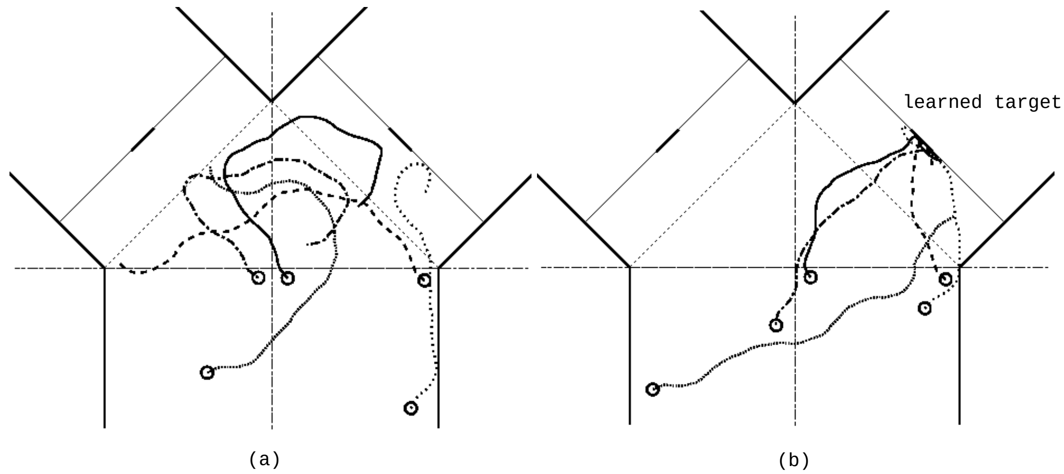

Fig. 5. Simulation results of bee-model flight (○: start point for recording), (a) before conditioning, (b) after conditioning (right target was associated with food)

s_{target}, because neither target had meaning for the food source. In this case, the bee model hovered around and made the circular trajectory shown in Fig. 54(a). Fig. 5(b) is a result of incorporating s_{target} and excluding s_{col} signals due to conditioning. In this case, when bee was approaching the target, s_{target} increased due to enlargement of the target image on the compound eye. By addition of s_{target} and elimination of s_{col}, flight direction headed toward the learned target and the honeybee was lead to the food source target. The optic flow signal s_{omr} was confirmed effective for stabilization of the flight course and compensation of passing in front of the food source.

4 Remarks

In this study, the honeybee flight trajectory was measured using a CCD camera to compare with the simulated flight. A three layer feed-forward model for flight control based on target and optic flow information was presented. Inputs to the model are ommatidia responses calculated from the simulated bee's position. Simulation of flight trajectories before and after conditioning showed that flight in the Y-maze could be controlled by space and time dependent signals (attraction of target, optic flow and collision avoidance). To build a 3D-flight directional and speed control model requires precise measurements of flight trajectory and posture in three dimensional space.

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