Flight control of honeybee in the Y-maze

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Abstract

Honeybee's visual environment is rich with numerous cues that can be exploited for a number of purposes, including the identification of food sources, navigation. Y-maze apparatus is widely using for behavioral test of insects, in order to examine their recognition ability of visual pattern. Behavioral changes during the flight in the Y-maze were measured by counting number of bees which cross the decision line. However, in order to reveal the neuronal mechanisms of flight control, it is needed to analyze their behaviors as a dynamical system, because visual information is dynamically changed by the position and direction. The present study measured honeybee's flight trajectories before and after conditioning, and flight behaviors in Y-maze were reconstructed by a mathematical model in consideration both of visual information and intrinsic factor.

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

1 Introduction

An important aspect of neuronal modeling is to explore how animal behavior emerge from the interactions between animal and its environment. It is well known that honeybee has high accuracy for vision and uses for many purposes, including the identification of food sources, navigation and mating. Furthermore, she can memorize characteristics of visual target by association

[1] This study was partially supported by the project on Neuroinformatics Research in Vision (PI: Shiro Usui) under the Target Oriented Research and Development for Brain Science by the Special Coordination Funds for Promoting Science and Technology (SCF), SCIENCE AND TECHNOLOGY AGENCY, JAPAN.
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with food source and recall them at re-visitation. It has been well investigated behavioral changes during acquisition and recall related with neuronal mechanisms about olfactory learning with association of odor and food.

However, in the case of visual conditioning, it has not been revealed yet how behavioral control signals emerge from visual information. A Y-maze apparatus which is choicing between the two chambers, is using as a standard protocol for honeybee's behavioral experiment[3]. In this experiment, animal behaviors are usually evaluated by counting a number of individuals which is crossing the certain point. However, it is sure that her flight is affected by visual signal depended on her position, direction and velocity. In order to understand flight behavior as output of neuronal processing, it is demanded visual information signals acquired by visual system during her flight. Then, it would be important regenerating behavioral control signals from these signals.

In this study, flight behaviors before and after visual conditioning were measured by the upper-located CCD camera. Time series of acceleration and directional change were calculated from the flight trajectory. As the results of analysis, it was shown that sensitive control for speed and yawing is needed for generating flight behavior. Behavioral control signals and trajectories in Y-maze were regenerated by composition of three signals, which are intrinsic, target-oriented and optic flow.

2 Experiments

Behavioral experiments for visual conditioning were done by the Y-maze apparatus shown in Fig.1. High speed CCD camera was settled 3m above this arena. During the training sessions, a visual target (5cm diameter, blue or yellow painted circle) are displayed with food (30water) at the center of Y-maze. After three or four training sessions, the center target was removed and blue and yellow targets were displayed on the back of each chamber. Images of flying honeybee were recorded at intervals of 30msec, then honeybee position was measured frame by frame for tracing flight trajectory.

As shown in Fig.2, significant difference in the flight trajectory was observed before and after training. During the training sessions, honeybee flight like searching everywhere in the arena, but she was keeping about 10cm space from the target. But, after conditioning, it was clearly shown that she flew toward the left target associated with food source. In this case, no food was presented on the left target, so she tried to approach the target numerous times. She also made attention and approached to another target for another possibility of food source.

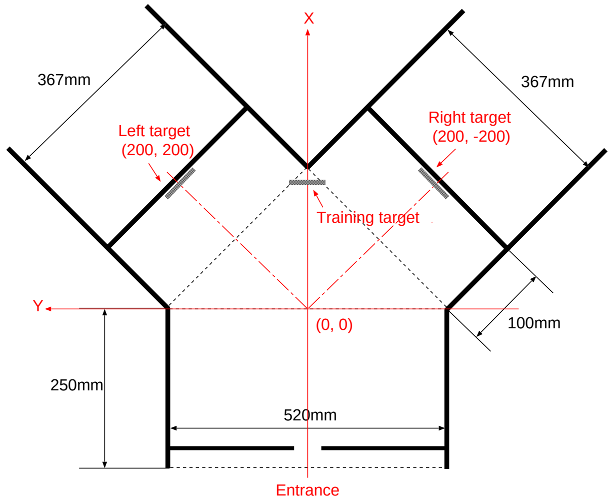

Fig. 1. Y-maze apparatus for behavioral experiment shown from above

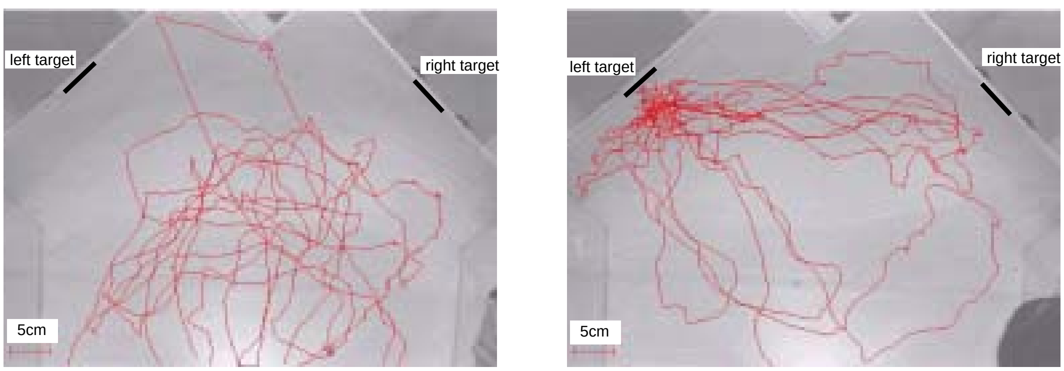

Fig. 2. Change of flight trajectory by visual conditioning, (a) before conditioning, (b) after conditioning (left target was associated with food)

During flight, acceleration and directional changes would be caused by muscle forces of wings. Temporal characteristics of these two sequences are results of behavioral control process in honeybee nervous system. In the case of insect, flight course is controlled by visio-motor mechanisms, such like optomotor response. However several intrinsic factors, for examples, motivation for searching and memory recall could reflect to the behavior. From behavioral experiments, it was shown that flight behavior was not only dependent on the individual innate endowment and also her experience in the Y-maze. So, in order to reveal the neural mechanism of behavior control, it is needed to trace the flight course and analyze the relation between visual information and behavioral changes including intrinsic factors.

Flight trajectory shown in Fig.3(a) is an example trace after conditioning measured from image data. As shown in Fig.3(b), X- and Y- coordinates changed smoothly. These coordinate sequences were smoothed to remove digitization errors using a 11th-order FIR filter with cut-off frequency set at 10Hz. These were interpolated by cubic spline function, then up-sampled by higher frequency (210Hz) for calculation of velocity, acceleration and directional change. Even in such simple flight trajectory, acceleration and yawing were controlled sensitively. It is no wander these values are sensitive, because these are obtained by 1st or 2nd oder derivative of trajectory. But it was still remained in doubt that these signals are possible to generate from information through visual signal.

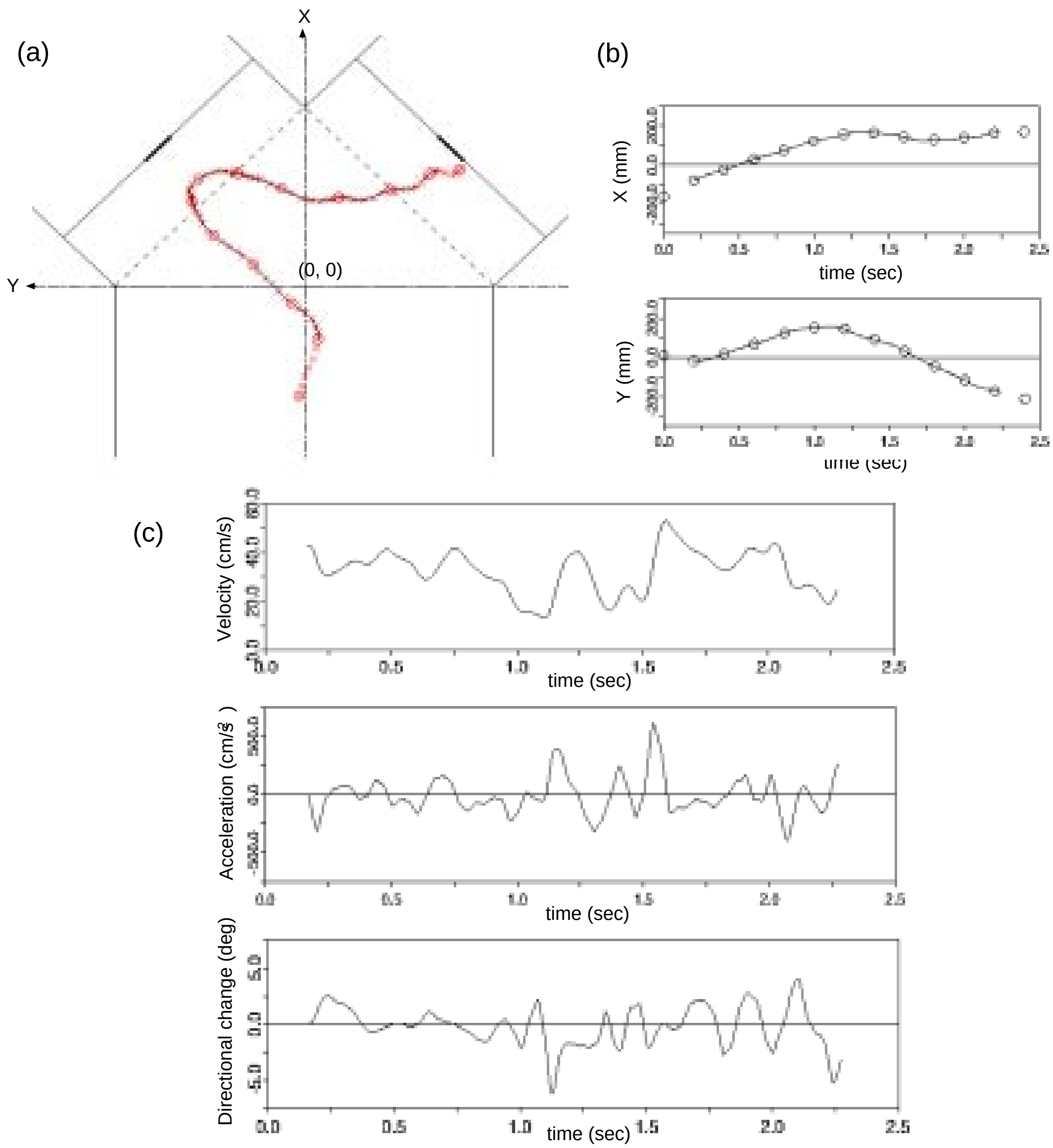

Fig. 3. Flight trajectory, velocity, acceleration and directional change after conditioning, (a) flight trajectory (right target was associated with food, open circles show experimental results sampled by 300msec interval), (b) X and Y coordinates, (c) velocity, acceleration and directional change

3 Model analysis

Recently, it was proposed several methods for calculation of projected image on compound eyes[4], [5]. Visual world of honeybee is formed based on the photoreceptor responses generated in ommatidia. Photoreceptor responses in ommatidia are accommodated with brightness on the surface of compound eye. In order to reveal visual information processing in the optic lobe, lightness of each ommatidia would be important input signal for it. My proposed method is suitable for calculating input signals for insect visual model, because it is calculated projected image based on the illuminance change of a single ommatidium surface. Projected image on the compound eye during flight in the Y-maze was calculated assuming (i))that the flight altitude was nearly constant, (ii) that the bee's body and head were yaw-stabilized with respect to its flight trajectory, and (iii) that the horizontal plane of the head was aligned parallel to the ground. Then it was applied for input signal in a model for image processing.

A three layer model for image processing with capability of target detection and optic flow calculation was proposed here (Fig. 4). Cells in the first layer (retina layer) generate the photoresponses which are used illuminance of each ommatidium surface. 2nd layer cell (filtering layer) has a broad range of circular receptive field, 5–20 degrees and integrates 1st layer's cell reposes inside of its receptive field. In the third layer (feature detecting layer), optic flow are calculated from 2nd layer cell responses. That is, there are three type of cells are allocated in the layer, first type of cell which has circular receptive field shows non-directional sensitivity. Second and third one form Hassenstein-Reichardt motion detector have directional sensitivity for vertical and horizontal image movement[6]. At the last, there are three cells for summation of 3rd layer cell responses independently, then behavioral control signals were calculated from by these results[1], [2].

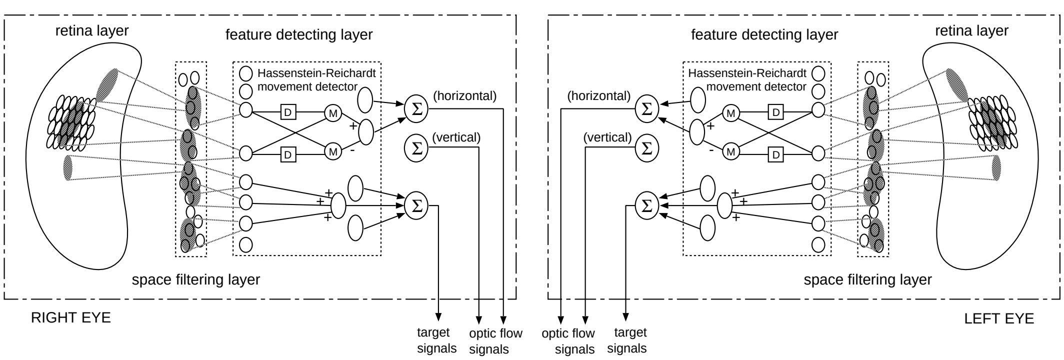

Fig. 4. Model of image processing for flight control.

When bee was approaching to the target, response of first type of cell in the 3rd layer was increased. However, type 2 and 3 cell responses are significantly increased before and after changing flight direction. In the real flight, several factors, such as air flow, fluctuation of body and intrinsic factor, were affected. This uncertainty factor was regarded into model by adding a low-pass filtered Gaussian noise component. As the results of simulation flight in Y-maze, it was shown that similar acceleration and directional sequences were generated by this model. Under the condition of strong effect of contingent factor, unconditioned like flight behavior was generated. On the other hand, increasing of effect of target detecting type 1 cell response, flight courses became to be straight toward target. Optic flow detector, type 2 and 3 cell responses were effective for stabilization of flight course.

4 Remarks

In this study, honeybee flight trajectory was measured by CCD camera. Sequences of acceleration and directional change were calculated from the experimental data. Then, it was presented that a layer model detecting information of target and optic flow from signals of ommatidia. As the result of simulation, it was shown that flight in Y-maze would be controlled by space and time dependent features in the image sequence. It is possible to analyze three dimensional trajectory with two images, further measurements with two cameras are carrying out for modeling of flight control.

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