論 文 の 内 容 の 要 旨

論文題目　A study on state-dependent multisensory integration for odor-source localization
（匂い源探索における状態依存的な複数感覚統合に関する研究）

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Biological-inspired algorithms became an attractive topic in the development of odor-plume tracking robot owing to the highly efficient performance and the adaptability to cope with uncertainty in the real-world application despite the simplicity of the algorithm. Some of the interesting algorithms were inspired by insects, such as ants, beetles, flying and walking moths. Several studies have revealed that other than odor cue insects also require visual cue during odor source localization to successfully locate the odor source. Furthermore, studies have also suggested that the response to motion vision is dependent on the ongoing behavioral repertoires (collision avoidance or odor-plume tracking) and locomotion states (resting or walking/flying). In case of the male silkmoth (*Bombyx mori*), it is already known that the detection of the female sex pheromone triggers a programmed walking pattern, starting from a surge (straight-line walking) during which the moth uses bilateral olfactory inputs to determine steering direction (a.k.a. positive chemotaxis), and followed by a programmed zigzag walking when losing contact with pheromone plume. It is believed that the function of surge is to reorient toward the odor source, and the function of zigzagging is to perform a local search for further olfactory cue. Due to the differences in functions and mechanisms, it is highly likely that motion vision plays different roles during these two sequential states of odor-source localization. The primary goal of this study was to investigate the role of optic flow (a motion vision caused by the relative motion between an observer and the surrounding) during the two different sequential states of surge and zigzagging, and then propose a silkmoth-inspired odor-plume tracking algorithm. To achieve our goal, we

carried out a multidisciplinary research consisting a behavioral study, an anatomical study and a computer simulation study, which allowed investigate into the problem in multiple aspects.

Firstly, the behavioral study was conducted on tethered-walking silkmoths to investigate the use of optic flow during surge and zigzagging. It is believed that the function of surge is to reorient toward the odor source, and the function of zigzagging is to perform local search in an endeavor to find further pheromone cue. Due to the difference in behavioral roles and underlying neural mechanisms, we hypothesized that the silkmoth utilizes optic flow information differently during the different behavioral states of surge and zigzagging. In this experiment, the pheromone-triggered behavioral responses of the tethered moths were monitored when presented with pheromone and optic flow stimuli in combination. Two different pheromone stimulus patterns were used to allow monitoring of surge and zigzagging separately, and the experiments were conducted under both open- and closed-loop visual stimuli conditions. As a result, we found that the use of optic flow input was determined by the behavioral state of surge and zigzagging. Precisely, the silkmoth exhibited an optomotor response during surge by turning towards the same direction as optic flow with turning angular velocity correspondent to the strength of the stimulus. However, the similar behavioral response was not observed during zigzagging. Unlike visual modulation of turning angular velocity during surge, the durations of zigzag turns were modulated by accelerated optic flow. The state-dependent use of optic flow observed in this study is a novel finding, and would provide a promising strategy for odor-source localization.

Considering the neural basis of innately programmed behavior in the silkmoth, we speculated based on the results from behavioral study that there exist two neural pathways involving in the state-dependent use of optic flow during odor-source localization. The candidate pathways are: 1) a modulation of turn angular velocity during surge by a direct connection between visual interneurons and descending neurons carrying motor command in the posterior slope, and 2) a modulation of turn duration during zigzagging by visual input to the lateral accessory lobe, a premotor center which generates control signals for zigzag walking. To address this hypothesis, the visual pathways in the silkmoth's brain was investigated by mass-staining the optic lobe, a primary visual processing center. The confocal imaging revealed severals pathways connecting optic lobe to other brain areas including the anterior optic tubercle (AOTu), lateral accessory lobe (LAL), ventrolateral protocerebrum (VLP), posterior slope (PS), mushroom body (MB) and the opposite optic lobe (OL). Both the PS and LAL which were hypothesized to be the sites for multisensory integration were labelled by fluorescent dye, suggesting direct connections to the optic lobe. This study provides a first comprehensive evidence for visual pathways in the silkmoth's brain. Based on the result together with literature review on olfactory pathway in the silkmoth and visual pathways in other arthropods, we speculated the neural circuitries underlying multisensory integration and sensorimotor control during surge and zigzagging. During surge, the visual input from the OL possibly directly modulates the activity of descending neurons carrying motor signals via direct connections sited in the PS. However, for an efficient optomotor control the MB and the central complex (CC) might also play important roles during this behavioral state. On the other hand, it is suggested that the neural circuit in the LAL alone might be sufficient for generation of zigzag walking. Nevertheless, a modulation of programmed zigzag pattern by accelerated optic flow observed in the behavioral study suggested a possible pathway conveying this information to the LAL. Moreover, the CC possibly plays a role in determination of zigzag turn duration due to its vital role in locomotion control and its closed connection to the LAL.

Lastly, a computer simulation study was conducted in order to evaluate the role of visual modulation during surge and zigzagging and to propose a silkmoth-based algorithm for odor-plume tracking. The result from the behavioral study suggested that the appropriate strategy for odor-plume tracking is to perform optomotor response only during surge but not during zigzagging. Although a visual modulation of zigzag walking pattern was also observed, its function was unknown. In this study, the performance of the searcher was tested under abundant and scarce odor cue conditions to allow evaluation of surge and zigzagging algorithm separately. The result confirmed the benefit of optomotor response during surge by providing a course correction strategy to deal with motor perturbation, while suggested no obvious benefit of visual modulation of zigzag pattern. To improve the odor-plume tracking model, a role of positive chemotaxis during surge was validated in this simulation platform. As expected, the use of bilateral olfactory inputs by performing positive chemotaxis improved the performance of the odor-plume tracking model by providing a strategy for accurately orienting toward odor source. The combination use of optomotor response and chemotaxis was then evaluated, and the result showed that a high success rate of locating source under the influence of motor perturbation was obtained without the need of strong sensory gain. This suggests a robustness and efficacy of the multisensory integration surge algorithm which is less dependent to any single sensory input and also susceptible to perturbation and uncertainty. Therefore, we proposed a novel odor-plume tracking model which comprises a multisensory integration surge algorithm for accurately orienting toward odor source and a programmed zigzag walking pattern for zigzagging algorithm which is simple but efficient for exploring the surrounding environment for further odor cue.

In this multidisciplinary research, the role of vision during pheromone-triggered behavior of the male silkmoth was investigated at behavioral and neural network level. The odor-plume tracking model based on the behavioral study's result was then evaluated in a computer simulation platform, which also allowed further development of the silkmoth-inspired odor-plume tracking algorithm proposed in this study. This research provides contribution to the developments in both biological and engineering researches by deepening our understanding of the design principle underlying biological system and also providing a promising model for robotic applications.