Mining of Behavioral Motifs from Individual Ant Trajectory*

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Complex biological systems resemble a “black box,” as it is a priori unclear how interactions among individuals will affect the collective (group) behavioral performance. Network analysis is a suitable method to shed light on these black boxes by studying the collective behavior of highly integrated social organisms such as ants. Individual within the colony have their own personality and task allocation for sustaining the society. Individual-level data are also important for understanding network structure. To obtain individual-level data such as personality and task allocation, individual behavior was assessed using several well-established information processing methods. To detect individual personalities from the position data, trajectory patterns were used. To analyze trajectory patterns, behavioral motif detection was used. The behavioral motif is the minimum unit of the entire trajectory.

1. Introduction

Individual personality is an important factor for determining an ant’s fitness [1] and provides information about the nodes of an interaction network. Individual personality can be identified using experiments involving individual maze performance that assess factors such as boldness or alertness. We were interested in understanding how ants move around and whether there are any quantifiable tendencies in their behavior. This concept can be thought of as the detection of behavioral motifs, which are minimum units of movement comprising an ant’s overall trajectory. An ant’s personality can be expressed using a ratio of components of its behavioral motif. Detecting behavioral motifs of nematodes (Caenorhabditis elegans) and fruit flies (Drosophila melanogaster) [2,3] may have an impact not only on behavioral studies but also on physiological or genetic studies. However, there are no studies of the collective behavior of social insects using behavioral motifs.

In our previous study [4], we analyzed behavioral motifs of social insects using trajectories obtained from individual tracking in squared arenas. The well-established methods of BCPA (Behavioral Change Point Analysis, [5,6]) and DTW (Dynamic Time Warping, [7–9]) were adopted to obtain fragments of the trajectories and perform similarity calculations on them. However, the BCPA and DTW have calculation costs and require time to analyze the fragments of the trajectories. In the present study, although BCPA was employed to fragment the trajectories, DTW was not used to analyze the fragments obtained from the BCPA to reveal their behavioral motifs. Therefore, this workflow was far from practical.

In this study, we improved the workflow for mining behavioral motifs from individual trajectories obtained by the ANTAM (Fig. 1a,b) [10] and utilized information processing methods, such as changepoint detection [11], DTW (Dynamic Time Warping) with random sampling, and cluster analysis to obtain the behavioral motifs. This combination of information processing methods and processing workflow contribute not only by obtaining behavioral motifs but also for

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building a behavioral motif library for various species of ants.

In this paper, we discuss the functionality of this combination of well-established processing methods and resulting workflow and present the preliminary results of its application to the behavioral study of ants.

2. Methods and Materials

2.1 Ants

In March and September of 2017, we obtained samples of *Acanthomyrmex glabfemoralis* (Zhou & Zheng, 1997) from Tay Yen Tu Nature Reserve (Bac Giang Province, Vietnam, March, 2017) and Mt. Mau Son (Lang Son Province, Vietnam, September, 2017). The ants were distributed in Vietnam and southern China. Colonies of this genus are small (with less than 100 workers) and are found in between dead twigs, in cavities in rotten wood, under or between stones, and in litter on the forest floor. They usually contain tiny seeds. The workers exhibit distinct dimorphism (i.e., the existence of both major worker and minor worker). Major worker ants are responsible for defending the colony, milling seeds, and storing food [12–16].

In this study, we used two colonies (Colony ID; 205 and 247) for analysis. Individuals in both colonies were tested (see details below) and their trajectories were obtained by the ANTAM.

2.2 Trajectory Acquisition with ANTAM

Arena arrangements are important for obtaining robust behavioral motif reference library data, as some ants walk beside the wall of the arena, while other individuals remain on the trail after the migration phase. Therefore, it is difficult to obtain all the trajectories using these arena arrangements. This might reflect the ants’ individual personalities or behavioral tendencies. In this study, we found that the ANTAM was the best way to obtain entire trajectories.

The ANTAM can be described as a treadmill device for small insects that allowed us to obtain individual trajectories in an artificial infinite space. Therefore, this device inhibited individuals from walking along the edge of an experimental area such as a petri dish or a square container. In addition, the ANTAM could obtain the walking speed and detailed trajectory pattern of each ant.

For each trial, data for each ant trajectory was collected for 15 min. The first 5 min was designated as acclimatization time, while the final 10 min of trajectory data were used in the following analysis. The surface of the ANTAM was wiped with ethanol before the trial to avoid any effects from previous trials, and the ANTAM was used after the ethanol dried. In total, data from 42 trajectories (42 individuals) were obtained from the two colonies by the ANTAM (the video is available at https://youtu.be/Z8nw-6AE9Dw).

2.3 Trajectory Fragmentation

The next step was to construct behavioral motifs from the ants’ trajectories by dividing the trajectory into sections. The obtained trajectories were fragmented using changepoint analysis according to the persistence velocity, expressed as $V_p = V \cos \theta$ [5,6]. $V$ is the walking speed [pixel/sec] and $\theta$ is heading angle [deg]. The persistence velocity ($V_p$) is one of the most robust variables for dividing the time series data into fragments, the number of which is a priori unknown. Therefore, this method can section the trajectory without any assumptions about the number of motifs. The trajectory was segmented based on the mean and variance of the $V_p$, which differed significantly during the analysis. In this study, 1 s was set as the threshold value to avoid sectioning the trajectory into fragments too short in length. The PELT (pruned exact linier time) method and the BIC (Bayesian information criterion) penalty were used in the `cpt.meanvar` function in R (package for changepoint analysis). In total, 31,458 fragments were obtained from 42 trajectories from 2 colonies. Change point analyses were excused using changepoints [11] in R.

2.4 Fragment Similarity and Cluster Analysis

To measure the similarity among fragmented trajectories for detecting unique classes of motifs, the DTW method was adopted. The DTW method can measure the similarity between 2 temporal sequences of data, such as shapes, genetic and sound analysis data [7,8], and trajectory similarity. The advantage of the DTW method is that it can align two temporal sequences automatically, as each trajectory typically has different time stamps. Typically, it is difficult to decide how to align 2 trajectories appropriately when calculating each similarity.

The DTW method was applied to 1000 randomly chosen, fragmented trajectories per colony. The sim-
Fig. 3 Changepoint analysis on the trajectory to obtain several fragments based on the mean and variance of the $V_p$. The $V_p$ is represented by the black line. The red vertical lines represent significant change points. A trajectory was fragmented on each significant change point. The X-axis represents time (s) and the Y-axis represents the $V_p$ value.

Fig. 4 The DTW (Dynamic Time Warping) method used to analyze similarity among fragments. The DTW process locates the point on each trajectory where it is aligned for the comparison process. The solid line represents the query and the red dashed line represents the reference line. The X-axis represents time [sec] and the Y-axis represents the $V_p$ value.

Fig. 5 Trajectory classification from the similarity value from DTW analysis. Dendrogram of 1000 fragments from colony 205 is shown. The color indicates class and the branches represent the fragments. Examples of trajectories are given below the dendrogram. There are 10 fragments in each row (left to right). Classes with more than 10 fragments extend to the next row. Windows A and B are enlarged views of the classified fragments. The color of a fragment corresponds to its cluster in the dendrogram.

Fig. 6 Characteristics of fragments among clusters. The characteristics represented by the colors (clusters) appearing in Fig. 5. A) The fragment length (in pixels) is compared. B) The total heading angle variation ($\theta$) is compared. C) The median of the velocity (pixel/sec) is compared.

3. Results

An example of an entire trajectory obtained by the ANTAM is shown in Fig. 2. An ant on the ANTAM can walk freely without hitting a wall. Therefore, the shape of the trajectory can be captured.

Changepoint analysis, DTW, and cluster analysis results are shown in Figs. 3 and 4. The entire trajectory has been fragmented based on the $V_p$ (Fig. 3). DTW analysis aligned the 2 trajectories to calculate the similarity between them (Fig. 4). The DTW results on 1000 randomly sampled fragments are shown as a dendrogram and examples of fragments (Colony ID; 205) based on the similarities among the trajectory shapes. DTW analysis classified fragments successfully (Fig. 5). Fragment length [pixels] is significantly different among clusters (Fig.
5A, Kruskal-Wallis chi-squared = 650.29, df = 5, P < 0.001). The total heading angle variation (θ) is significantly different among clusters (Fig. 5B, Kruskal-Wallis chi-squared = 743.26, df = 5, P < 0.001). The median of the velocity (pixel/sec) is significantly different among clusters (Fig. 5C, Kruskal-Wallis chi-squared = 70.42, df = 5, P < 0.001).

Thought plots A–C) The X-axis represents the cluster ID and the Y-axis represents the calculated parameters. Parameters are plotted as box plots. Each box corresponds to an interquartile range. The horizontal lines inside the boxes correspond to the medians of the velocity. The whiskers correspond to values up to 1.5 times the interquartile range. The short horizontal lines correspond to the maximum and minimum values up to 1.5 times the interquartile range. The open circles represent the outliers. The Kruskal-Wallis rank sum test using pairwise comparisons using the Mann-Whitney U test was used throughout the statistical analysis. The small letters beside the boxplot correspond to different combinations of significantly different clusters (e.g., “a” and “b” are significantly different, P < 0.05; however “a” and “c” are not significantly different). Colors correspond to the colors appearing in the dendrogram in Fig. 5.

4. Discussion

Individual behavioral analysis can be used to obtain a summary of individual activity or behavior; however, there is no guarantee that individuals with the same summary value will behave in the same way. These differences in individual movements can be thought of as individual personalities [18] in ants, and these personalities are hidden in the summary analyses. Therefore, a detailed analysis of each of their individual movements will be required. To perform such a detailed analysis, trajectory-based analysis, such as shape analysis, is needed.

In this study, to overcome the disadvantages of the small size of the arena and to obtain information about each trajectory, an infinitely large spacing arena was needed. However, constructing such a space is impossible; in addition, it would be difficult to track each trajectory in such a large area. To solve these problems, artificial, unlimited spacing can be made by using ANTAM, a treadmill device used especially for insects. This device has a ball at the top on which the subject is placed. The ball’s rotation is tracked in real-time using cameras above the ball, and is dependent on the subject’s movement as the ball returns the subject to the center. The subject’s movements are monitored using optical sensors placed under the ball. The ANTAM device is suitable for detecting individual behavioral motifs, and whole trajectories were obtained from each individual. The trajectories obtained provided detailed information about speed, heading angle, walking distance, and the shape of the trajectory.

In this study, the trajectories were analyzed using changepoint analysis [5,6,11]. The trajectories were successfully divided into fragments based on the mean and variance of the V̇p. Changepoint analysis requires less calculation time than BCPA (Behavioral Change Point Analysis), which was used in our previous study [4]. Therefore, changepoint analysis is sufficient for practical use.

The DTW method is one of the methods used for analyzing time series data [1,6–8] and can be adapted for trajectory shape analysis, as was done in this study. This study was successful in demonstrating the effectiveness of using the DTW method for fragment shape analysis. The dendrogram shows fragments were successfully classified into clusters (e.g., Fig. 5AC shows short and fast fragments in cluster 3). In this study, 1000 fragments were randomly sampled, and DTW computed 499,500 combinations per colony. In future studies, increasing the sample size and reducing the calculation time during DTW analysis may be needed.

DTW is the only method used to determine the details of the ants’ movement patterns. It is also the only method that is used to categorize each fragment and detect behavioral parameters such as speed, distance, and heading angle. This category can be thought of as a functional minimum unit of the trajectory shape, i.e., a behavioral motif. The behavioral motif opens the way for analyzing proximate factors in network structure and swarm intelligence.

To detect robust behavioral motifs and construct a motif library, comparing motifs within and among colonies is needed in future studies. The fundamental mechanism of how motifs are regulated by their response to their surroundings or other nest mates is also an interesting and fruitful area for future research.

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