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Model of a sensory–behavioral relation mechanism for aggressive behavior in crickets

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ABSTRACT

In order to gain better understandings how animals establish an internal mechanism, we have focused on the aggressive behavior in the male crickets, in which some different modalities of sensory inputs modify the behavioral motivation. In this research, we examined how aggressiveness changes if crickets cannot perceive normal visual inputs or antennal inputs. First, behavior of the crickets is segmented based on behavioral observation. Second, sensory input–behavior output models are selected by utilizing Minimal Description Length (MDL) criterion. Third, multi-modality sensory–behavioral experiments are realized with handicapped crickets. Last, relations between multi-modality and behavior are discussed based on the obtained parameters in the model derived with experimental results.

1. Introduction

Animals do not always respond in the same way to the same external stimuli. This indicates the internal states of animals regulate the behavioral motivation. The state of the central nervous system must be dependent on their experiences as well as their internal and/or external conditions. Thus, sensory inputs from external environments are one of the important factors to establish and to modify the motivation of behaviors. In this study, we investigate how aggressive motivation in crickets is affected if they lose ordinary sensory inputs. In insects as well as other animals, offensive and defensive aggressions are observed. However it has not been well investigated how animals regulate aggressive motivation. In many cases, sensory information is most important to maintain aggressive motivation.

Insects are one of the useful materials to investigate the neuronal mechanisms underlying aggressive behavior. The simplicity of neuronal organization and identifiable neurons in their central nervous systems are great advantages to contribute our understandings the neuronal mechanisms to maintain behavior motivations. Cricket is one of the popular insects in neuroethological studies. Many kinds of cricket behaviors have been well observed and the neuronal mechanisms underlying these behaviors have been investigated. Fighting between male crickets has been well investigated since Alexander's work [1]. When two male crickets encounter each other, they suddenly start fighting to establish dominant–subordinate relationship. Crickets perceive cuticular pheromones on the body surface of other individuals. The main components of the pheromones are hydrocarbons [2]. The male cuticular pheromones introduce aggressive behavior and the female pheromones introduce courtship behavior in male crickets [3]. Once the battle starts, it escalates into a fierce struggle [1]. Cricket shows stereotyped sequence behavior, when one cricket encounters another male; they show aggressive posture and start antennal fencing. If both males do not retreat from the opponents, the fighting escalates harder. They open the mandible; attack the opponents with the head and bit each other. This tactile combat continues until one of them gives up attacking and retreats from the opponent. After the fighting is settled, the dominant one starts making sound called aggressive song and drives away the subordinate one. The subordinate, on the other hand, actively avoids from the dominant for a certain period of time [4,5]. The aggressiveness of the cricket is known to be modified not only by defeated experiences but also the density of the cricket group (social environment). The aggressiveness of the cricket decreases as the group density increases [5]. On the other hand, aggressiveness of the cricket is known to increase if it is kept isolated, or certain sensory information is blocked. Phillips and Konishi demonstrated that the field crickets increase aggressiveness if their auditory sensors are blocked [6]. Rillich et al. demonstrated that the handicaps (disabled mandibles, blackened eyes, size) affect motivation of aggressive behavior in the cricket [7]. Flight is also known to increase

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aggressiveness of the cricket [8]. Aggressive behavior in the cricket can be one of the greatest model systems to investigate how animals regulate internal state to produce adaptive behaviors. The internal state that regulates behavioral motivation must be modified by the external sensory information.

Constructing a model that explains animal behaviors sometimes help our understandings of neuronal mechanisms underlying behaviors [9]. In this study, we propose a sensory-input–behavior-output model to explain how aggressive motivation is regulated in the cricket. We performed behavioral experiments using handicapped crickets, in which the visual or antennal sensory inputs are inhibited, to investigate how this sensory information affects their aggressiveness. Then using the results of the behavioral experiments, we construct a network model that explains relationships between sensory input and behavioral output.

2. Approach

The following steps were taken in order to determine how the sensory modalities and the results of the previous fight affect aggressiveness of the male cricket.

- *Step* 1: Segmentation of behavior based on behavioral observation
  The aggressive behavior of a cricket intensifies in some typical stages. Because the aim of the present study was to identify the influences of the sensory modalities and the results of the previous fight on each stages of aggressive behavior, the stages were first defined.
- *Step* 2: Construction of a model
  A weighted neural network model, the sensory-input–behavior-output model, was constructed with the sensory inputs, the result of the previous fight, and output as aggressiveness. The structure of the model is based on the observation of cricket behavior and the Minimal Description Length (MDL) criterion. The aggressiveness defined in Step 1 is applied as the output. Thus, by estimating the weight of each part of this neural network based on the results of the behavioral observation, we can examine how the sensory information and the previous fighting experience affect motivation of aggressiveness.
- *Step* 3: Behavioral experiment with handicapped crickets
  We here focused on the effects of antennal sensory inputs and visual inputs on aggressiveness. The antennal inputs in a male cricket were blocked by removing both antennae. The visual inputs were inhibited by performing the behavioral experiments under red light condition.
- *Step* 4: Relation between multi-modality senses and behaviors
  Results of the behavioral experiment were substituted into the sensory-input–behavior-output model to estimate the parameters in the model.

3. Construction of the model

3.1. Classification of the aggressive behavior levels

The aggressive behavior levels in crickets were classified based on [1]. The smallest clear divisions available for the behavioral analysis during video filming fell into three stages, which are used here for modeling. When the male encounters another individual, it selectively displays an aggressive or avoidance behavior, or other behaviors such as no response or courtship behavior. As shown in Fig. 1, aggressive behavior was labeled *Res*+; other behaviors, *Res*−. *P* is the probability of *Res*−. Next to *Res*+, the male cricket engages in antennal fencing and mandible opening with bending forward to threaten the opponent, or it shows

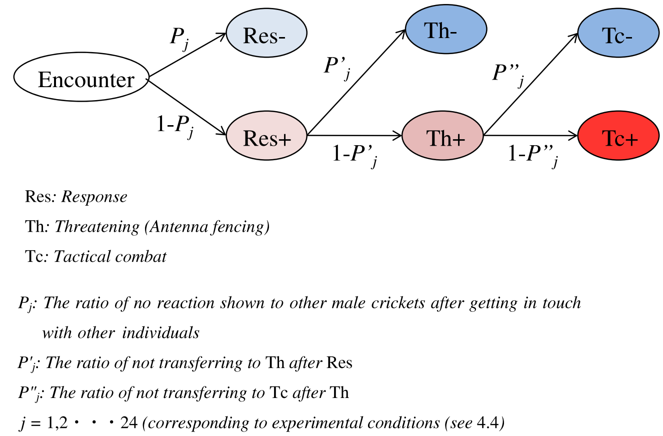

Fig. 1. The substages of aggressive behavior.

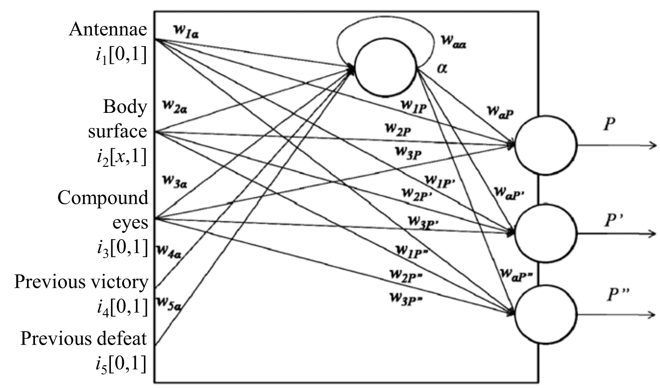

Fig. 2. The sensory-input–behavior-output model of crickets (the model with "two victory and defeat inputs", "one internal state variable," and "integrated type of the sensory input").

avoidance behavior. The threatening behavior was labeled *Th*+; the avoidance behavior, *Th*−. P' is the probability of *Th*−. Next to *Th*+, the male cricket initiates tactical combat by head-butting or biting opponents, which was labeled *Tc*+. Lack of such behaviors is labeled *Tc*−. P'' is the probability of *Tc*−.

3.2. Sensory-input–behavior-output model

We constructed an adequate weighted neural network model (sensory-input–behavior-output model) in which the sensory modalities are related to behavioral selection. In the model, the sensory information and the previous fighting experience (victory or defeat) were considered as inputs, and the behavioral pattern (P, P', or P'') was expressed as output. In order to distinguish between the ratios obtained from the model (P, P', and P'') and those obtained from the behavioral experiment, the latter were defined as P_E, P'_E, and P''_E, respectively. Although the previous fighting experience should be judged in relation to sensory input, it is handled here as one of the inputs for simplification.

We can consider several sensory–behavioral model structures that satisfy existing measurement data. Fig. 2 shows one of the examples of the models. In general, the more parameters and levels, the higher the conformity to measured data with regard to neural network models [6]. However, there is possibility for the models to be forced to conform to changes, such as noises, not related to the structure of the measurement target. On the other hand, they become unfit for data of the same type [10,11]. Though the number of parameters needs to be as small as possible to avoid this problem, the ideal number is difficult to determine. MDL, the statistical measurement level proposed by Rissanen to evaluate