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Forgetting curve of cricket, *Gryllus bimaculatus*, derived by using serotonin hypothesis☆

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ABSTRACT

It is thought that the adjustment of intraspecific aggression is an essential factor in the development of a social structure. To understand the natural laws for organizing the social structure, we focus on the fighting behavior of crickets, *Gryllus bimaculatus*, and investigate the neuronal mechanisms to adjust aggressiveness associated with a neuromodulatory biological amine: serotonin (5-HT).

In this paper, we present a working theory of a neurophysiological mechanism based on the past biological studies on the 5-HT hypothesis, and a mathematical model of the mechanism. We analyzed this model and concluded that this neurophysiological mechanism makes the forgetting process slower. Next, we fitted our theoretical forgetting curve to an experimental curve and estimated the parameters of our model. These estimated values were in agreement with common belief in biological science.

1. Introduction

An ethologist has pointed out that the adjustment of intraspecific aggression is an essential factor in the development of a social structure [1]. Animals mediate their aggressiveness depending on social factors such as population density and external threats. The question arises, what kind of internal mechanism do animals possess to mediate their aggressiveness. In this study, we investigate the neuronal mechanisms in insects to mediate their aggressiveness and especially focus on the fighting behavior of crickets, *Gryllus bimaculatus* (Fig. 1). There are two reasons for selecting cricket. First, the different levels of a cricket's fight can be clearly differentiated to observe behaviors [2]. Second, the body size of a cricket is large enough to carry out the neuropharmacological experiments. Thus, crickets are suitable for studying the mechanism of behavior neuromodulation.

The behavior of almost all insects is innate; this implies that there is a limit to the number of behavioral patterns, and therefore, insects can be said to have a behavior-based system. Therefore, insects must have the mechanism to modulate their behavior; they need to show a huge variety of behaviors against a huge variety of social structures for their survival. It has revealed that biochemical substances called neuromodulators, such as neuropeptide and biogenic amine, modulate behavior selection. It is known that crickets change their aggressiveness depending on the amount of biogenic amine: octopamine (OA) and serotonin (5-HT). OA and 5-HT are the neuromodulators that modulate aggressive behavior. It is also known that a fighting experience changes the amount of OA and 5-HT.

Once crickets lose in a fight, they avoid another fight for a prolonged time and recover their aggressiveness gradually [3]. The time evolution of behavior shift is called forgetting curve. Although this forgetting curve should be closely related to OA and 5-HT metabolism, an experimental result shows that the time constant of this forgetting rate is too small to be explained by a simple neurophysiological mechanism.

Kawabata et al. constructed a mathematical model of OA dynamics and succeeded in explaining the specific dynamics of a cricket group with their model [4]. In this paper, we present a working theory of a neurophysiological mechanism and a mathematical model based on past biological studies. For the verification of our model, we also derive another model by removing a specific factor from our model. For each model, we derive the intensity of behavior modulation and compare the time evolution of behavior with the observed time evolution (forgetting curve). We estimate the parameters of our model. Finally, we suggest a biological experiment and predict the result of this experiment.

2. Related works

A cricket shows fighting behavior in resource competition situations. When crickets find their opponent, they start fighting.

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Fig. 1. Cricket fight. Males of *Gryllus bimaculatus* frequently fight each other. When they meet, they start fighting and the result of the fight determines dominance hierarchy.

Their aggression is modulated by the neuromodulators: OA and 5-HT [5–8]. The neuromodulation process can be described as follows.

Crickets sense their opponent's cuticular pheromone with their antennae [9]. The sensing of pheromones could lead to production of nitric oxide (NO) in the brain. NO activates soluble guanylyl cyclase (sGC) to generate cyclic GMP (cGMP) in the target cell, which in turn mediate titer of OA and 5-HT in the brain. Dierick et al. clarified that OA plays a crucial role in deciding individual's behavior between aggression and avoidance [10]. They also found that 5-HT does not determine the behavior, but modulates the intensity of a behavior, which is determined by OA (Fig. 2).

When crickets fight, they consume OA and 5-HT. The dominant agent gets some reward to restore OA and 5-HT. On the other hand, the subordinate agent decreases them [11,12]. After fighting, the amount of neuromodulators is slowly restored to the stationary state.

Although these researches have suggested the involvement of OA and 5-HT in mediating aggressiveness, dynamics of these biogenic amines has not clarified. Kawabata et al. constructed a mathematical model of OA dynamics and been explained the case of phenomena with it. We have constructed the mathematical model of 5-HT dynamics in the case of cricket [13].

5-HT works as the neuromodulator for aggressiveness in a lot of animals [14]. Recent researches have developed a theory of 5-HT neuron's structure and dynamics. This theory is named the 5-HT hypothesis and is the working theory for affective disorder [15,16]. According to Allman, the serotonergic system has been conserved through evolution amazingly, beginning 500 million years ago, and participates in our emotions [17]. We assumed that serotonergic modulation in the case of crickets' aggressiveness is also described by the 5-HT hypothesis.

2.1. Mathematical model of OA dynamics

Kawabata et al. constructed the following mathematical model of OA dynamics [4]:

$$\frac{\mathrm{d}A(t)}{\mathrm{d}t} = -\gamma_{\mathrm{A}} A(t) + A_{\mathrm{in}} - \mathrm{A}_{\mathrm{out}}, \tag{1}$$

$$\mathrm{A}_{\mathrm{out}} = \begin{cases} \text{const.} & \text{if } \textit{fighting}, \\ 0 & \text{otherwise.} \end{cases}$$

Variable A represents the normalized amount of OA in the CNS, variable A_{in} denotes the normalized amount of the OA production, the constant $\mathrm{A}_{\mathrm{out}}$ represents the normalized amount of OA consumption and the constant γ_{A} determines the recovery rate or decomposition rate of OA. They set A_{in} to reproduce an experimental fact: activating the NO–cGMP cascade decreases the amount of OA. They also set the constant $\mathrm{A}_{\mathrm{out}}$ such that OA was consumed during fighting. The time constant of the NO–cGMP cascade is virtually much smaller than that of OA in their model. For this reason, we can assume that A_{in} is approximately constant; we only need to consider the recovery of OA for analyzing the forgetting curve.

Kawabata et al.'s theory of the OA neuron does not contain an autoreceptor that the 5-HT hypothesis contains. Additionally, they assumed that the amount of OA receptor does not change. They succeeded in explaining some phenomena on the basis of this assumption, and therefore, we employ this assumption for describing OA dynamics in this paper.

This theory of OA determines the contribution of OA tor the forgetting curve $F_A(t)$ as:

$$F_A(t) := \mathrm{F}_{\mathrm{A}\infty} + \exp\left(-\gamma_{\mathrm{A}}\left(t - \tau_{\mathrm{A}}\right)\right), \tag{2}$$

where the constant $\mathrm{F}_{\mathrm{A}\infty}$ represents the equilibrium value of the avoidance frequency and the constant τ_{A} determines the initial state of the avoidance frequency after fighting.

2.2. Forgetting curve

We have studied the duration for which a losing cricket refrains from another fight. As we mentioned before, once a cricket loses in a fight, it starts avoiding fights. Subordinate crickets show different levels of avoidance behavior, and we classified two levels as follows [18].

(1) Avoidance which needs to go through antennal contact. It needs only bodily contact with the opponent.
(2) Avoidance which go through antennal contact with the opponent.

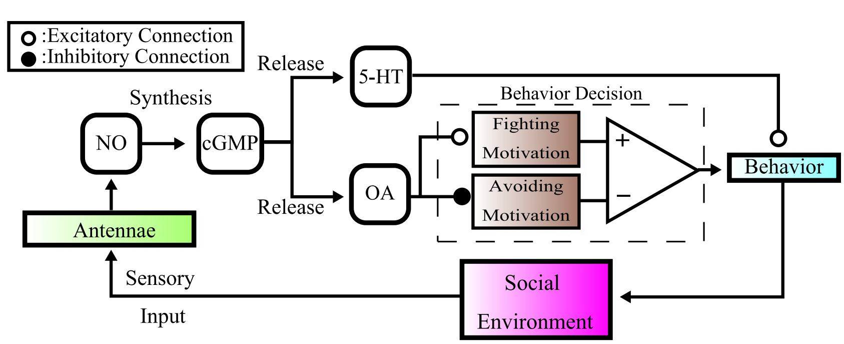

Fig. 2. Behavior selection. Octopamine (OA) determines the behavior, whether the cricket fights or not. Serotonin (5-HT) modulates the aggressive behavior determined by OA.