A neuromodulation model of behavior selection in the fighting behavior of male crickets

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ABSTRACT

The results of neurophysiological research have indicated the important role of neuromodulation in behavior decisions during fighting between male crickets. To understand such a dynamic behavior generation mechanism, we attempt to construct a neuromodulation model of behavior selection for the fighting behavior of a cricket. In this paper, we propose a dynamic system model of neuromodulation with the efficacy based on neurophysiological knowledge, facts, and hypotheses from the viewpoint of synthesis. The efficacy of the sensory processing center is introduced to our previous model and its dynamics is influenced by the frequency of the interactions with the other cricket. Utilizing an extended neuromodulation model, computer simulations related to a multiple-individual environment were carried out, and the results are discussed. In particular, the properties related to the standard deviation of the value of octopamine in several population density cases are discussed.

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1. Introduction

Biologists have often performed neurophysiological and behavioral experiments to elucidate the neuronal mechanisms underlying adaptive behavior in animals. However, usually, such experimental approaches accumulate plenty of spacio-temporally independent pieces of data. In order to understand the mechanisms underlying adaptive behavior, we need to reconstruct our knowledge, and we propose a synthetic approach to bridge the gap between physiological aspects and behavioral aspects by constructing a dynamic system model [1].

Cricket fighting provides us with a good model system to understand the neuronal mechanisms underlying adaptive behavior selection [2]. When a male cricket comes across another male cricket, it first senses the cuticular substances called cuticle pheromone using its antennae and then shows fighting behavior.

Fig. 1 shows an example of the sequence of fighting behavior between male crickets. Usually, when it perceives cuticular pheromones on the body surface of the opponent cricket, the male cricket shows aggressive behavior. However, a cricket does not show aggressive behavior after it becomes a loser in a previous fight. Thus, if the defeated cricket senses the same pheromone within several minutes, it shows avoidance behavior. The experience of defeat thus makes the cricket select a different behavior for the same stimulus. The nitric oxide (NO)/cyclic guanosine monophosphate (cGMP) cascade has been particularly considered to be closely related to fighting behavior selection by crickets [3,4].

The motivation and aim of our current study is to clarify the adaptive behavior selection mechanism by modeling the role of neuromodulation in the central nervous system by focus on fighting behavior between crickets. In our previous work [5], based on several neuroethological issues, we modeled the NO/cGMP cascade function in cricket fighting behavior with regard to the relationship between octopamine (OA) concentration and behavior selection. We also discussed our proposed neuromodulation model as an NO/cGMP-OA system being considered an appropriate one for an individual cricket's response in a fight between crickets.
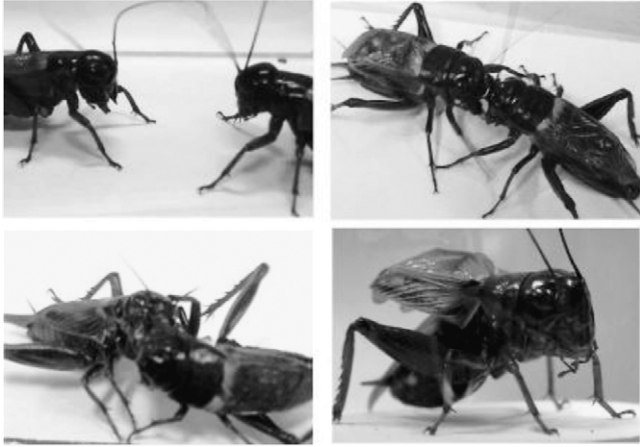
Fig. 1. Snapshots of fighting behavior between male crickets.

Fig. 2. A basic neuromodulation model for behavior selection based on the NO/cGMP-OA system [5].

However, the model could not explain the behavior modification to the size of the environment in the multiple-individual cricket situation [6]. As a certain factor for the differences, we considered it was important to focus on the interaction effect among the crickets [7]. There also have been reports [8–10] that the information processing mechanism of the insect is modulated by the biogenic amine system. Therefore, we put forward a hypothesis that the interactions among the crickets affects the efficacy in the neuronal system for behavior selection.

In this paper, we modify our proposed neuromodulation model based on the NO/cGMP-OA system and also extend the model, introducing the efficacy of the sensory processing center. Multiple-individual simulations are also carried out, and we discuss simulated behaviors depending on the size of the field by using cricket agents depending on the effect of the size of the space. We also discuss what effect the efficacy has on the internal properties and behavior selection.

2. A neuromodulation model for behavior selection of an individual cricket in a fight

As we described above, the NO/cGMP cascade has been considered to be related to fighting behavior of crickets. To demonstrate this, fighting behavior was observed when an NO synthesis inhibitor is injected into the heads of the crickets. In this case, even the defeated cricket may exhibit fighting behavior. This indicates that the appropriate behavior is not selected if the NO/cGMP cascade does not function normally. Even under these circumstances, the pheromone is identified and NO is closely related to the pheromone behavior modified by past experience [11]. The NO/cGMP cascade mediates the efficacy of various neural pathways. One of these is to change OA levels in the brain [12,13]. Therefore, the NO/cGMP cascade is considered to be deeply related to behavior selection through the OA system.

In our previous work, a basic neuromodulation model [5], namely the mimetic NO/cGMP-OA system, was proposed (Fig. 2), and it was confirmed that the model was an adequate one to be an individual cricket's internal dynamics model [5]. Subsequently, we gave some modifications to our previous neuromodulation model. Here, we describe the formulations [5] once more.

By noting the internal state of the cricket based on the amounts of NO, cGMP, and OA, we modeled a basic NO/cGMP-OA model in fighting behavior, according to sensual information from antennae: the pheromones from another individual increase the NO concentration in the antennal lobe (AL). For simplification, the AL is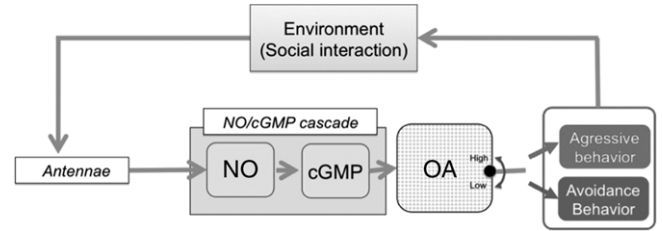 considered as a row of discrete NO generation/consumption points, and its dimension is n (μm). The concentration state of NO in the AL is expressed as a vector $\mathcal{N}$ of $(n+1)$ dimensions and that at discrete position x ($0 \leq x \leq n$, $x \in \mathbb{Z}$) as $\mathcal{N}^x$. NO is a free radical that reacts with metal ions and oxygen immediately after diffusion throughout the brain, after which it disappears, presumably being present for about 10 s. To express this effect, the equation of NO diffusion is given as follows.

$$\frac{\partial \mathcal{N}}{\partial t} = D\frac{\partial^2 \mathcal{N}}{\partial x^2} - \gamma_N \mathcal{N} + \mathcal{N}_{in} - \mathcal{N}_{out}, \tag{1}$$

where $\mathcal{N}_{in}$ and $\mathcal{N}_{out}$ represent the state vector for NO generation and consumption at each position in the AL. The increased NO concentration in the AL is certain, so we assume that the amount of NO generation $\mathcal{N}_{in}^x$ at position x is determined for position set $\mathbb{I}$ at the source:

$$\mathcal{N}_{in}^x = \begin{cases} 0.0 & \text{if } x \notin \mathbb{I}, \\ 1.5 & \text{if } (x \in \mathbb{I} \wedge fighting), \\ 1.0 & \text{otherwise.} \end{cases} \tag{2}$$

Modeling property $\mathcal{N}_{out}^x$ as a smooth function such as Eq. (3), we obtain

$$\mathcal{N}_{out}^x = \begin{cases} a \times (1 + \tanh(50 \times (\mathcal{N}^x - 0.4)))/2 & \text{if } x \in \mathbb{O}, \\ 0 & \text{otherwise.} \end{cases} \tag{3}$$

The amount of cGMP is expressed as a scalar value C. The behavior of cGMP is expressed in Eq. (4) using the constant γ_C based on the idea that excessive amounts of cGMP are decomposed in the body:

$$\frac{dC}{dt} = -\gamma_C C + C_{in} - C_{out}, \tag{4}$$

where $C_{in} = \Sigma_x \mathcal{N}_{out}^x$ and C_{out} represent amounts of cGMP generation and consumption. Based on physiological knowledge, cGMP suppresses OA production, so cGMP consumption is modeled as a smooth function.

$$C_{out} = b \times (1 + \tanh(10 \times (C - 0.64))/2). \tag{5}$$

The cricket selects its behavior based on the amount of OA. The scalar A indicates the OA value, and OA is generated by cGMP and used to select the behavior. Likewise, the amount of OA is expressed in Eq. (6) by using the constant γ_A:

$$\frac{dA}{dt} = -\gamma_A A + A_{in} - A_{out}, \tag{6}$$

where A_{in} and A_{out} represent the amount of OA generation and consumption. OA is used in the cricket to obtain energy from fat. Here, A_{in} is

$$A_{in} = b - 0.6 \times C_{out}. \tag{7}$$

Also, using the constant c, A_{out} is

$$A_{out} = \begin{cases} c & \text{if } fighting, \\ 0 & \text{otherwise.} \end{cases} \tag{8}$$

High density : settled and calm

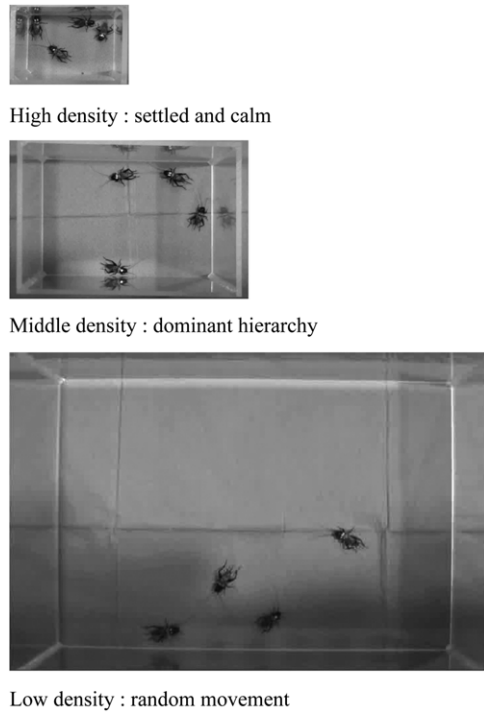Middle density : dominant hierarchy

Low density : random movement

Fig. 3. Typical behavior modification that depends on the population density of the cricket.

Additionally, using knowledge from [12,13], we also assume that the reward ϵ to the octopamine value depending on the experience after the battle is given as Eq. (9).

$$\epsilon = \begin{cases} \epsilon_{win} & \text{if } win, \\ -\epsilon_{lose}T & \text{otherwise.} \end{cases} \quad (9)$$

Here, T (s) indicates the time period for fighting.

The modification points based on some examinations and discussions are as follows.

- The form of differential equations for cGMP and OA was changed from a partial one to an ordinary one because the equations treat the time course evolution of the amount of the chemicals.
- A reward for a winning experience is introduced to give a more significant difference of OA level between the winner and loser after fighting.

This is our basic neuromodulation model based on the NO/cGMP-OA system with modifications, and we confirmed that it still has adequate response related to behavior selection response at an individual level.

3. Behavioral and physiological facts

3.1. Behavior modification of the cricket depending on the density

Generally, the cricket *Gryllus bimaculatus* is classified as a solitary insect. Although individuals of this species do not form groups, but, rather, are solitary in their activities, individuals of this species do show some social adjustment behavior. Such behavior is modified by social and individual experiences. The group size and density of the group also affect animal behavior, and this is called a kind of crowding effect. This indicates that the otherwise solitary cricket selects its behavior on the basis of interactions with other individuals. This forms the basis for other research on crickets. Crickets reared in environments (Fig. 3) with low-density
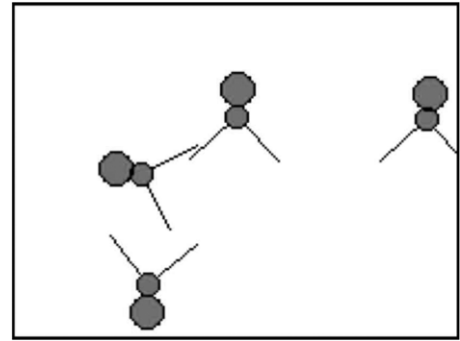

Fig. 4. A snapshot of multiple-individual simulation.

populations often fight, while those raised in environments with high-density populations tend to show much lower incidences of this behavior [14]. Populations in environments with intermediate densities, between high and low (medium), have been observed and reported to contain one cricket that continues to attack other males, while the rest of the males attack less and less often. We can also consider this an adaptive behavior that occurs in response to interactions during changes in population density [15] (see Fig. 3).

3.2. Sensory property modulation by biogenic amine

Iba et al. found that the concentration of OA increased when crickets were under crowded conditions [8]. Here, from the viewpoint of OA concentration, the crickets seemed to be able to exhibit aggressive behavior under these conditions, but did not choose to fight with each other. Gatellier et al. demonstrated that serotonin (5HT) modulates the pheromone behavior in the male silk moth *Bombix mori* by changing the sensory intensity [9]. Pribbenow et al. demonstrated that OA and 5HT affect antennae movements in bees [10]. When given OA, calm bees became excited, and moved their antennae constantly. Excited bees became calm when given 5HT. Moreover, it has been reported that the antennae of the cricket are essential to fighting behavior [16].

Thus, there have been reports that the information processing mechanism in the AL is modulated by the biogenic amine system in many species of insects.

4. Extended neuromodulation model with efficacy value

We conducted multiple-individual computer simulations with our previous proposed neuromodulation model (Fig. 4). Fig. 5 shows the results (experimental conditions: 4 simulated crickets in the same space, one period of time is 4000 s, 50 trials at every space size). In these simulations, 100×75 pixels, 200×150 pixels, and 400×300 pixels were used as high-density, medium-density and low-density populations, respectively. The body length of the cricket was 20 pixels. The number of aggressive crickets in each size of the space is almost exactly one, and different types of behavior occur with real crickets depending on the density.

Here, using the information in Section 3, we consider hypotheses that the biogenic amine system affects the function of the sensory processing center, in that it is activated by OA and suppressed by contact. The hypothesis of sensory inputs from the antennae was formulated based on observations of cricket interactions related to antennae. Therefore we focused on efficacy to sensory inputs from each individual's antennae as an element to compensate for differences between cricket behavior and the behavior of model crickets based on the above-mentioned NO/cGMP-OA model.
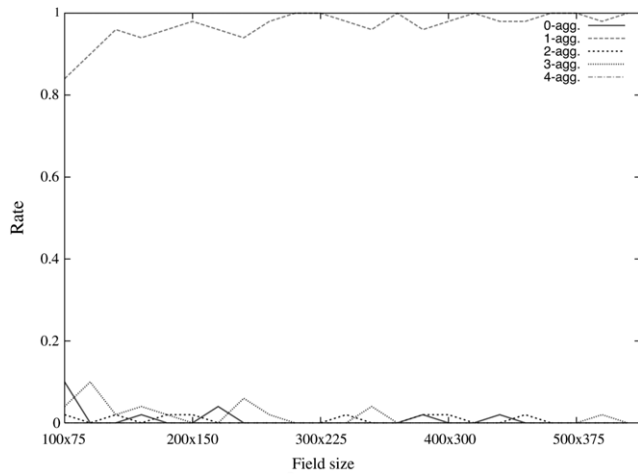
Fig. 5. Computer simulation results in the multiple-individual environment utilizing the neuromodulation model based on only the NO/cGMP-OA system.
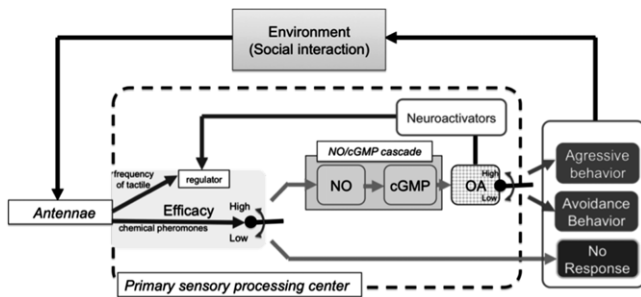

Fig. 6. Extended neuromodulation model based on the NO/cGMP-OA system and efficacy S.

In the extended model (Fig. 6), behavior is determined by two input sources, sensory input due to contact with the other individual's body and feedback due to the internal state. Sensory input from other individuals is modulated in the primary sensory information processing center. We attempted to account for this effect by incorporating a value S for the efficacy to input from the antennae. The value of this efficacy expresses the efficiency of processing sensory information from the antennae, and it affects behavior selection. We believe that the influence of the internal state is due to the relationship of some substance related to the production and output quantity of OA in the existing cascade model. This is based on the efficacy to sensory input from the antennae as noted in silkmoths [9] and the bee [10], among other results, that are reported to be influenced by the biogenic amine system. The changes in the behavior of the crickets due to crowding described in Section 3.1 were interpreted to be changes in behavior due to the frequency of contact with other crickets, and the crickets' efficacy to sensory input could well diminish with an increase in the number of such contacts.

Here, the influences were assumed to increase in simple proportion with OA volume and stimuli from individual interaction. This has been formulated in Eq. (10).

$$\frac{dS}{dt} = -\rho S + f(A) - g(F_{in})$$
$$= -\rho S + hA - kF_{in} \quad (S \geq 1.0), \quad (10)$$

where ρ, h, and k represent the parameters to adjust the efficacy value dynamically. F_{in} was defined in a stepped shape (Fig. 7) to affect the behavior for Δt (s) after each contact.
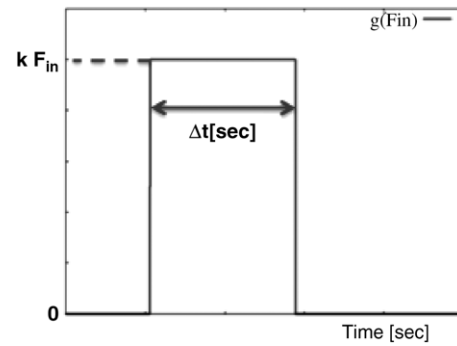

Fig. 7. Step function $g(F_{in})$ for contact stimulation.

Our hypothesis is that efficacy, modulated by the internal state and individual interaction, may in turn modulate the generation of NO, resulting in the behavior selection indicated by these stimuli. When the efficacy to sensory inputs is greater than some threshold, aggressive behavior occurs in keeping with the NO/cGMP-OA model. When the efficacy is low, the cricket continues to wander and gives no response to the stimuli. The term was designed to represent the temporary reduction in efficacy to sensory input when coming into contact with other individuals.

5. Simulation results and discussion

5.1. Computer simulations utilizing the extended neuromodulation model in a multiple-individual environment

Computer simulations were carried out with our extended neuromodulation model utilizing four simulated crickets as described above for 4000 s. The size of the model field cricket was considered while designing the experimental environment for these computer simulations; the environment was created to represent the experimental conditions used for real crickets.

In the computer simulations, the following dimensions were used again: 100×75 pixels, 200×150 pixels and 400×300 pixels as high-density, medium-density, and low-density populations, respectively; and the body length of the cricket was 20 pixels. The condition for selecting fighting behavior was at least 0.5 for the normalized OA level and at least 1.0 for the sensory input sensitivity, which was modulated by the OA level and frequency of contact. The suppression of sensitivity by contact was set to stop 30 s after the last contact.

Here, each internal state of the cricket is indicated in Fig. 8. "OA is high" means $A \geq 0.5$ and "S is high" means $S > 1.0$. Thus, an aggressive individual means one with $A \geq 0.5$ and $S > 1.0$. In each simulation, the number of aggressive individuals was counted.

Fig. 8 shows a snapshot of the simulation for each environment and Fig. 9 shows the results of the simulation experiment. The simulation was carried out 50 times at each density.

Not all of the individuals exhibited aggressive behavior in the crowded environment. One or zero individual became aggressive under the medium-density population condition. The aggressiveness trends of individuals were random in the low-density population environment, but one or two always become aggressive.

This experiment qualitatively reproduced the pattern observed in biological experiments, where individuals show increasingly aggressive behavior as the population density decreases. The efficacy S to sensory input was set to 1.0 on interaction with another individual, so that aggressive behavior was not seen when the individual was in an environment that forced frequent contact with others, but this also allowed the tendency for increasingly
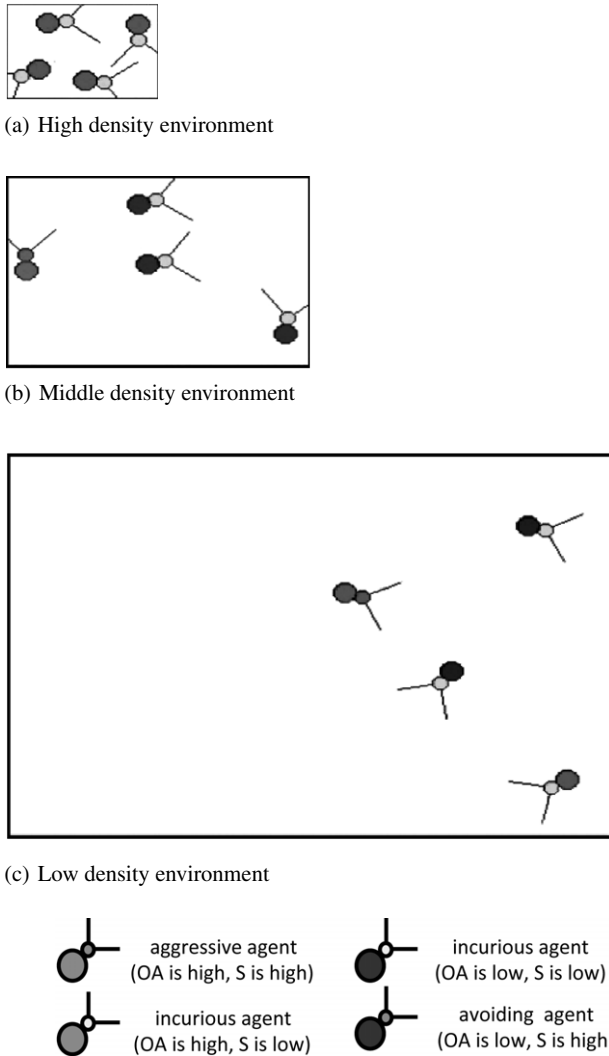
(a) High density environment

(b) Middle density environment

(c) Low density environment

Fig. 8. Snapshots of computer simulations in each size of the environment. The legends indicate the simulated cricket's internal state.

Fig. 9. Results of multiple-individual environment simulation utilizing the extended neuromodulation model.

aggressive behavior when the interactions occurred at lower frequencies.

Thus, the model incorporating the efficacy to sensory input from the antennae is confirmed to express adaptive behavior at both the individual and group levels. This indicates that changes in the efficacy to sensory input are important elements in the formation of groups.

5.2. Properties of internal state of simulated agent

In this section, we discuss the effect of the contact stimulation to the efficacy of sensory processing center. Fig. 10 shows the results of the standard deviation value for four simulated cricket agents in each environment. Here, $\Delta t = 0$ s means there is no influence on the efficacy S from any contacts. In such cases, $\Delta t = 0$ s provides similar performance to the neuromodulation model based on the NO/cGMP-OA system because the efficacy S is not inhibited by the contacts and remains at a high value. Also, the others mean our proposed extended neuromodulation model in Section 4.

From these results, when Δt is small, there is small variation among the standard deviations of the OA value of the simulated cricket agent in each population density environment. When Δt has a larger value, there is a significant difference in the variation of the OA. I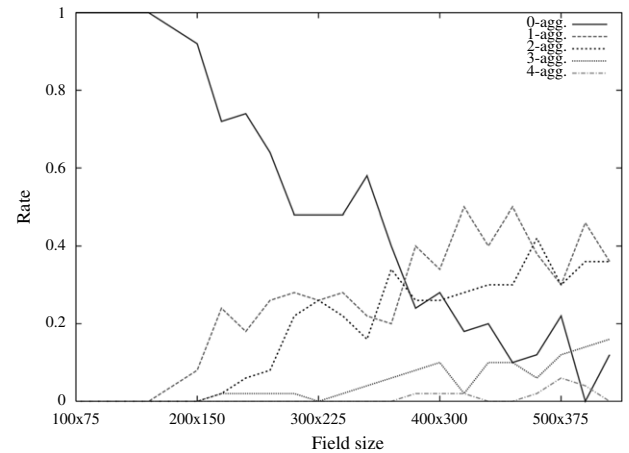n particular, when Δt becomes greater than 20 s, the standard deviation for high density converges to 0.0 and those for middle and low density converge to different values.

Computer simulation results indicate the internal state of the simulated agent when the contact stimulation in our proposed model increases from 20 to 30 s. At this stage, we do not have any idea what this means. However, we expect that it will produce some suggestions to formulate hypotheses for contributing some ideas or conducting new neurophysiological experiments.

6. Conclusion

Our current research is attempting to model the cricket's neural system for systematic understanding of the principle of the adaptive behavior selection mechanism. Therefore, we examined and proposed a neuromodulation model of behavior selection in the fighting behavior of crickets. This paper describes our neuromodulation model of behavior selection in the fighting behavior, introducing the efficacy of the sensory processing center, and presents the results of computer stimulations in multiple-individual environments. The proposed neuromodulation model of cricket's behavior selection shows similar response compared to those of our previous model based on the NO/cGMP-OA system for an individual agent although the efficacy is introduced. By the results of computer simulations in multiple-individual environments which makes its size be changed, it also could be considered as an appropriate one for group activities of real crickets.

We also discussed the properties of the OA level of the simulated cricket agent depending on the effect of contact stimulation in the environment. It is clarified that the standard deviation of OA is affected by the time effect of contact stimulation.

In our future work, we will try to conduct some biological and physiological experiments related to the issues that are discussed in this paper. Also, we will continue to improve the neuromodulation model based on results from synthetic knowledge and physiological knowledge. Finally, this approach will help us to understand the neuronal mechanism of adaptive behavior. Moreover, such understanding will contribute to providing knowledge related to the design principle for the behavior selection mechanism of the artifacts based on the interactions.

(a) $\Delta t = 0$ s.

(b) $\Delta t = 10$ s.

(c) $\Delta t = 20$ s.

(d) $\Delta t = 30$ s.

Fig. 10. Differences in standard deviation of OA against Δt (s).

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