Neural Modeling of Social Adaptive Behaviors of Insects

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***Abstract*— All the life forms such as humans, animals and insects, can behave adaptively even in diverse and complex environment in various types of behaviors. Such adaptive behaviors are considered to emerge from the interaction of the body, brain, and environment, which is induced by the active mobility of the cognitive subject. Base on the consideration, we call the intelligence for generating adaptive motor function mobiligence. The Mobiligence project started from 2005 as s five-years project to understand the mechanisms for the generation of intelligent adaptive behaviors. In the group C of the mobiligence project, we focus on mechanism whereby a cognitive subject adapt to other cognitive subjects or its society. In this paper, some neural models of the social adaptive behaviors of insects are introduced, such as on proportion control in caste differentiation of termites, and on behavior selection in fighting behaviors of male crickets.**

I. INTRODUCTION

Living organisms adaptively select behavior through the interactions with their society in real time. Their behaviors generate sociality and the behaviors are determined by sociality. We call the behaviors selections related in society "social adaptive behaviors" in the group C of the Mobiligence project.

The plasticity plays important and fundamentally roles in adaptation behaviors. This is attributable to various mediators such as neuromodulators in brain, hormones in the body, and pheromones in group as superorganism like colony. If we can know the principle of social adaptations, it can be applied to design methodology for autonomous robotic systems. Just how fragmented information obtained from analytical results operates in an actual system remains unclear, and we believe it is important to alternately repeat synthetic and analytical approaches in which a dynamic hypothetical model is simulated based on information from static physiological experiments and to verify the results obtained in further physiological experiments[1]. Even now, we have a lot of things to learn from efficient insect behaviors because insects are well-researched compared with vertebrate animals. It is wise to determine the equations of evolution of systems with generality from the mutual integration chains. Especially, we treat the termite caste differentiation and cricket fighting behaviors as example of social adaptive behaviors.

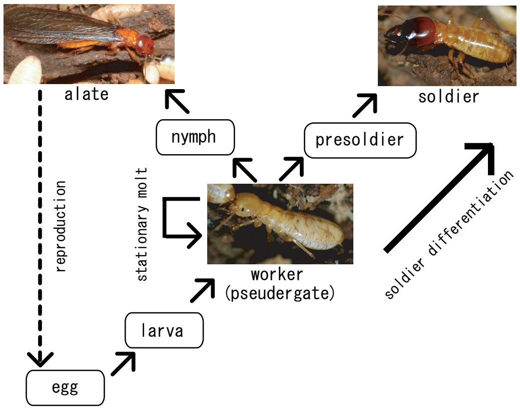


Fig. 1. Termite caste differentiations in termite *Hodotermopsis sjostedti*

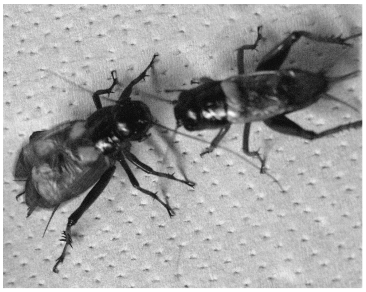


Fig. 2. Male crickets fighting

In termite example, self-organized proportion control is treated as functional differentiations of individuals in a system according to environment conditions and given tasks(Fig. 1). The function differentiation process is seemingly regarded as transition from a homogeneous state to a heterogeneous one in multibody system against the second law of thermodynamics. Although the behaviors of particle in equilibrium systems have been discussed enough, nonequilibrium open systems have not been systematized from the perspective of thermodynamics yet. One reason seems to be that the principle must be modeled by enforced approximation of phenomenon and the experiment data because potentials are not expressly given such as mechanical energy and free energy.

In cricket example, we focus the time evolution of some neuromodulator titers in the brain for behavior selection on the specific behaviors ,cricket fighting(Fig. 2). In behavior selection, nitric oxide (NO) is thought to function as a neuromodulator (NM) for extracting a specific behavior program from polymorphic circuits in the brain and that the NO/cyclic guanosine monophosphate (cGMP) cascade plays an important role[2].

In this paper, we introduce the study examples of termite caste differentiation modeling in section Ⅱ-Ⅳ and cricket behavior selection modeling in section V-Ⅷ. Finally, we conclude in section Ⅷ.

II. TERMITE CASTE DIFFERENTIATION

The termite (Order Isoptera, Class Insecta) is categorized into a eusocial insect that lives in a group based on kinship and forms a colony with a certain size. In a termite colony, there are several castes called worker, soldier, nymph, king and queen in addition to immature larvae. The developmental pathways to caste differentiation are diverse from species to species [3][4][5][6][7][8]. Even though each individual has the similar genetic background, they present different phenotypes through anatomical specialization according to the castes [9][10][11].

Among the various castes, soldier castes is a peculiar one because soldiers are completely sterile and perform altruistically to attack against predators or intruders. The control of soldier ratio in a colony is an important regulatory system in the termite societies[12][13]. In addition, there is a special stage called "presoldier" in the course of soldier differentiation. Soldiers are normally induced from workers via presoldier stage through two molting events. Presoldiers can be regarded as the system buffer for the early adaptations of social systems as shown in figure 1. It is mainly thought that such altruistic behaviors have been evolved by kin selection[14].

The caste differentiation had been acquired as the adaptation for the extremely precise social behaviors and self-organization. The multiple phenotypes of individuals and the caste ratio controls can be respectively regarded as the adaptations in micro and macro level. Both of the adaptations must work out under coherent relations between them. It is important for exploring the strategy of eusocial insects to consider information cycle between macro and micro layers. As Lüscher reported the following working thesis obtained by several biological experiments, the caste differentiation seems to be accomplished under the pheromonal control which is not transferred by diffusion in air of chemical substances, but through trophallaxis behaviors in which colony members exchange food matrials from mouth to mouth[15]. However, there is the hypothesis that caste ratio is also controlled by exocrine volatiles[16][17]. For example, in Nasutitermitinae, defense substances function as the chemical pheromones that inhibit the soldier production[18]. However, the effective pheromonal substances are not identified yet.

In order to realize the caste differentiation processes, it is necessary to approach from both physiological mechanisms in an individual and system methodology in the colony level. In an individual level, several researches succeeded to find the methods of induction from workers to soldiers by the application of juvenile hormone and its analogues [12][19][20]. In a colony level, it is reported that Reticulitermes flavipes adaptively changes the caste ratio according to season[13]. In addition, there are important reports in other eusocial insects, in which colonies increase the soldier proportion when they confront competitors, predators or intruders[21][22][23]. Termite colony generally seems to control the caste ratio precisely, depending on the environment conditions without global controls that means controls determined by congenitally genetic informations[24][25].

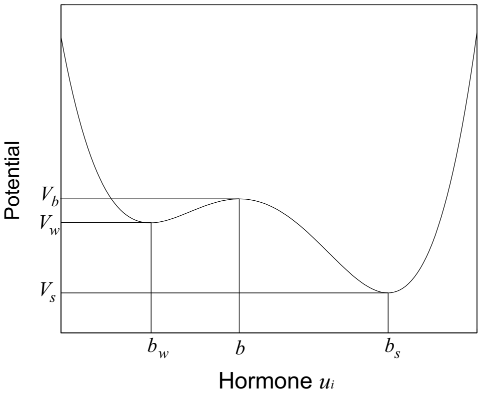


Fig. 3. Landscape by potential V_i.

III. MODELING DIFFERENTIATION PROCESS

The mathematical principle model is constructed based on biological reports and the assumption in section Ⅱ. In order to discuss the basic caste differentiation control mechanism through one kind of pheromone, bare essentials of mathematical model is expressed. In fact, the states of the system consist of group of u_i that is amount of hormone in individual i and the genotype are expressed by one dimensional potential function. The genotype is described as extremal values of the potential function. In this model, therefore, the dynamics of internal hormone are on bistable potential because differentiations between two kinds of caste are focused. The equations of evolution of u_i are as follows:

$$\frac{\partial u_i}{\partial t} = -\frac{\partial V_i}{\partial u_i} - D_i \sum_{j=1, j\neq i}^{N} (w_{ij}u_j - d) \tag{1}$$

$$\frac{\partial V_i}{\partial u_i} = (u_i - b_w)(u_i - b)(u_i - b_s), \tag{2}$$

where $\partial V_i/\partial u_i$ is given as show in figure 3 that describe the shape of genotype potential. N means the constant number of individuals in the colony. V_w, V_s and V_b are the constant number of potential when $u_i = b_w$, $u_i = b_s$ and $u_i = b$, respectively. b_w, b_s and b are constant, those are evolutionarily-conserved, so that they determine optimal caste ratio. D_i is the stochastic variable that mean the number of contacts among individuals over time. w_{ij} is a stochastic variable and satisfies $\sum_{j=1,j\neq i}^{N} w_{ij} = 1$ at any time, meaning the frequency of contact between individuals i and j. d is also the constant number determining the optimum caste ratio which is evolutionarily-conserved. The equations of evolution (1) include stochastic variables depending on both a average number of contacts and which the individual has contacts with other one. The potential of activation for state transition from worker to soldier depend on $V_b - V_w$. The fluctuations are needed for transitions to climb the potential of activation.

In order to separate stochastic factor from average amount, D_i and w_{ij} are replaced in the following equations:

$$D_i = D_i^c + R_i(t) \quad (3)$$

$$w_{ij} = w_{ij}^c + r_{ij}(t) \quad (4)$$

$$\langle R_i(t_1)R_i(t_2)\rangle = 2M_D\delta(t_1 - t_2) \quad (5)$$

$$\langle r_{ij}(t_1)r_{ij}(t_2)\rangle = 2M_w\delta(t_1 - t_2), \quad (6)$$

where $\cdot^c$ is the average concerning time in variable D_i^c and w_{ij}^c. $R_i(t)$ and $r_{ij}(t)$ are stochastic variables assumed to be Gaussian distribution without a time correlation. M_D and M_w are constant numbers that mean amplitude of fluctuation of $R_i(t)$ and $r_i(t)$ respectively. Therefore, equation(1) is replaced in the following equations using equations(3-4):

$$\frac{\partial u_i}{\partial t} = -\frac{\partial V_i}{\partial u_i} - D_i^c G - R_i(t)G - R_i'(t), \quad (7)$$

where

$$G = \sum_{j=1, j\neq i}^{N} (w_{ij}^c u_j - d) \quad (8)$$

$$R_i'(t) = (D_i^c + R_i(t)) \sum_{j=1, j\neq i}^{N} r_{ij}(t) u_j. \quad (9)$$

Equation (7) is a Langevin equation depending on global feedback by parameter G. The set of individuals, that carry out interactions i.e. exchange a pheromon, and its number of individuals are defined as h and N_h, respectively. Under the condition that the number of individual is large, that is $w_{ij}^c = 1/(N_h - 1) \approx 1/N_h$,$i \in h$, the following equation is satisfied:

$$\sum_{j=1, j\neq i, i\in h}^{N} w_{ij}^c u_j = \langle u\rangle, \quad (10)$$

where $\langle u\rangle$ is the average of u_i for $i \in h$. If the number of soldiers that is included in set h decreases (increases), $\langle u\rangle$ decreases (increases) to activate (inhibit) transitions from worker to soldier. However the transition from perfectly transformed soldier to worker is unacknowledged in termite. $R_i(t)$ includes fluctuations depending on G. $R'(t)_i$ is stochastic variables give steady fluctuations to the system and depending on b_w, b_s, b and d. $R'(t)_i$ is time average 0 and Gaussian distribution without time correlation as well as $R(t)$ and $r(t)$. When the caste ratio converges to the optimum value expressed in equation(10), as G approaches a certain value determined by balances between the potential V_i and interaction terms in equation (1), the effect of fluctuation promoting to the system approaches a certain value. As show in equation (7), the amplitude of fluctuation for transition are amplified or attenuated by G.

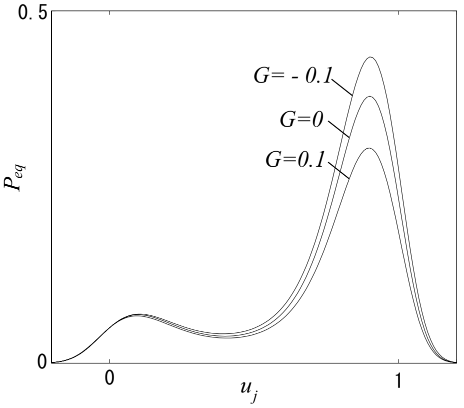


Fig. 4. Transition of probability distributions P_{eq} at $b_w = 0.1$, $b_s = 0.9$, $b = 0.4$, $M = 0.005$, $M_D = 0.01$ and $D_i^c = 0.01$. Global parameter G transits to $G = 0$, $G = 0.1$ and $G = -0.1$.

Changes in G are assumed to be slower than the time evolution of u_i. This is the adiabatic approximation for analysis. When P_i is the probability distribution of u_i, Fokker-Planck of equation (7) and its equilibrium solution are explained as follows using normalization constant A:

$$\frac{\partial P_i}{\partial t} = \frac{\partial}{\partial u_i}\left(\frac{\partial\left(V_i + D_i^c G u_i\right)}{\partial u_i} + \sqrt{(M_D G)^2 + M^2}\frac{\partial}{\partial u_i}\right)P_i$$

$$P_{eq} = A\exp\left(\frac{-\left(V_i + D_i^c G u_i\right)}{\sqrt{(M_D G)^2 + M^2}}\right) \quad (11)$$

Figure 4 shows the transition of P_{eq} according to the changes of global parameter G. If G increases or decreases, the balance of potential curve between b_w and b_s changes based on the effect of $D_i^c G$ as show in equation (11). The gradient also becomes loose by the effect of $\sqrt{(M_D G)^2 + M^2}$. Therefore the changes in parameter G gives the force for state transitions and the mechanism of fluctuation adjustment.

IV. SIMULATIONS OF DIFFERANTIATION

A. Simulation Setup

Computer simulation in this research is carried out at the behavior level of individuals. The overviews of the simulation is shown in figure 5. The number of individuals is fixed at $N = 100$ at any time. The spatial size of the colony and the individual are given as a square, 2 on a side, and a circle of 0.05 in diameter. The initial states of all individuals are set to $u_i = 0.1$, that means all individuals in the colony are set as workers. The caste of individuals is determined as worker and soldier when $u_i < 0.5$ and $u_i \geq 0.5$, respectively. Termite actually seems to fuss around. However what group of termite are doing is unknown for caste differentiation. In this research, therefore, the individual migration is assumed as consistently uniform linear motion. When an individual collide with other one or colony edges, the contacts are assumed as perfectly elastic collision. By these assumptions, each individual behave as molecular motion in closed space. At $t = 200$, predators that has no relationship with termite individuals are put into the colony. It means that an incursion

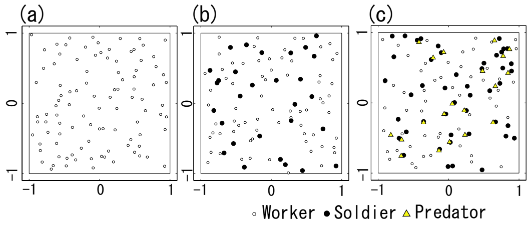


Fig. 5. Simulation view at $N = 100$, $b_w = 0.1$, $b_s = 0.9$, $b = 0.4$ and $d = 0.3$. White circles and black circles indicate the position of workers and soldiers, respectively. Triangles indicate predators put in at $t = 200$. (a) at $t = 0$. (b) at $t = 199$. (c) at $t = 205$.

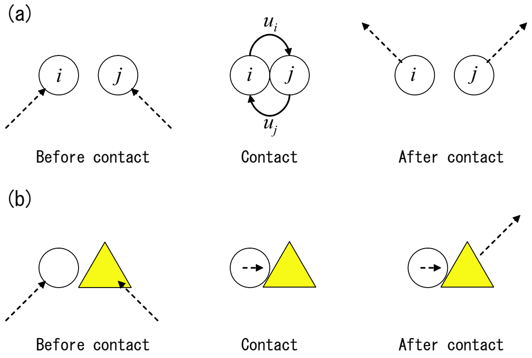


Fig. 6. Interactions between individuals. Circles indicate worker and soldier individual. Dotted arrowed lines indicate a velocity of individuals. (a) Each individual give u at one interaction. (b)Interactions between individuals and predators.

of predators is treated as one of the environmental variation. The predators also behaviors at random as well as termite individuals.

Figure 6 explains interaction rules among individuals in the colony. When individuals contact each other, the they mutually transfer the hormone through pheromone interaction as shown in figure 6 (a). In this simulation, the amount of hormone u_i is subsequently updated by using equation(1) and (2) every iteration. At the same time, u_i is updated with $D_i = 0$ in case that the individual is contacting with an predators.

When individuals contact with an predators, there are no transfer of hormone as shown in figure 6 (b). In this case, u_i is constantly updated using equation(1) and (2) with $D_i = 0$. This assumption means that soldiers interacting with predators lose the effort for pheromone release, so that G decreases and this effect brings results of state transition as above a mathematical analysis in section Ⅲ.

The worker individuals neglect the existence of predators and the soldier individuals follow predators that means soldier attack them. The soldiers continue to follow predators until it turns from predators by reactive force from other individuals. These behaviors are advisedly imitated from observations of real termite behaviors.

Based on above these conditions, the time evolution of u_i and $\langle u \rangle$ are evaluated by computer simulations.

B. Results simulations of differentiation

The simulation results are shown in figure 15. As show in figure 15 (a), the average $\langle u \rangle$ is adaptively changed on the boundary of $t = 200$. The number of soldier individuals are $N_s = 33$ and $N_s = 49$ at $t = 150$ and $t = 400$, respectively. Although actual amount of hormone can not be negative, some u_j are negative in the results. In oder to realize that all values of u_j are located in positive area at any time, the parameter set needs to be changed, however, this problem seems to be nonessential in this paper. The mathematical analysis advanced in section Ⅲ do not need any changes since there are no condition of positive and negative for u_j. As shown in figure 15(b-d), the distributions of u_i dynamically change adapting to an incursion of predators. At $t = 205$, the variance of the distribution increase. The distribution eventually converge to the state of figure 15(d).

In addition, in order to estimate the effects of fluctuations, transitions of G and variances of u_i included N_w are shown in figure 8(a) and (b), respectively. The G temporarily decreases around the interval $200 < t < 220$ and the variance also increases . It means that the inherent fluctuations are increased and decreased according to incursion predators to converge to evolutionarily-conserved optimal caste ratio. In figure 8 (a), G demonstrate rapid fluctuation after $t = 200$, although the its average value are recovered to previous value. It is thought that the rapid fluctuation depends on a spatial constraint after predators putting into a colony. D_i^c, R_i' and R_i in equation (2) must change and the fluctuation characteristic seems to change from radical one. In oder to clarification these reason, the more developmental analysis are needed.

V. CRICKET FIGHTING BEHAVIOR AND NEUROMODULATORS

A. Cricket Fighting Behavior

While pheromone behaviors of insects was once considered ”hard-wired” and specific pheromones thought to cause specific behavior, it is becoming clear that the insect pheromone behavior involves plasticity by modification, as in cricket fighting behavior. Figure 9 diagrams the information pathway in the cricket brain.

A cricket’s body is covered with cuticular substances considered a so-called pheromone, probably for individual identification [26]. A male cricket encountering another cricket first touches it with its antennae to determine its gender, then attempts courtship behavior if the other cricket is female or fighting behavior if it is male (Fig. 10).

Such fighting behavior usually continues 15 to 30 minutes [27]. If the loser later encounters the winner or senses the same pheromone, it shows avoidance behavior *i.e.*, experiencing defeat causes the cricket to select different behavior for the same stimulus adaptively based on the circumstances. Understanding the mechanism behind the switching of a program behavior could lead to clarify neural adaptation.

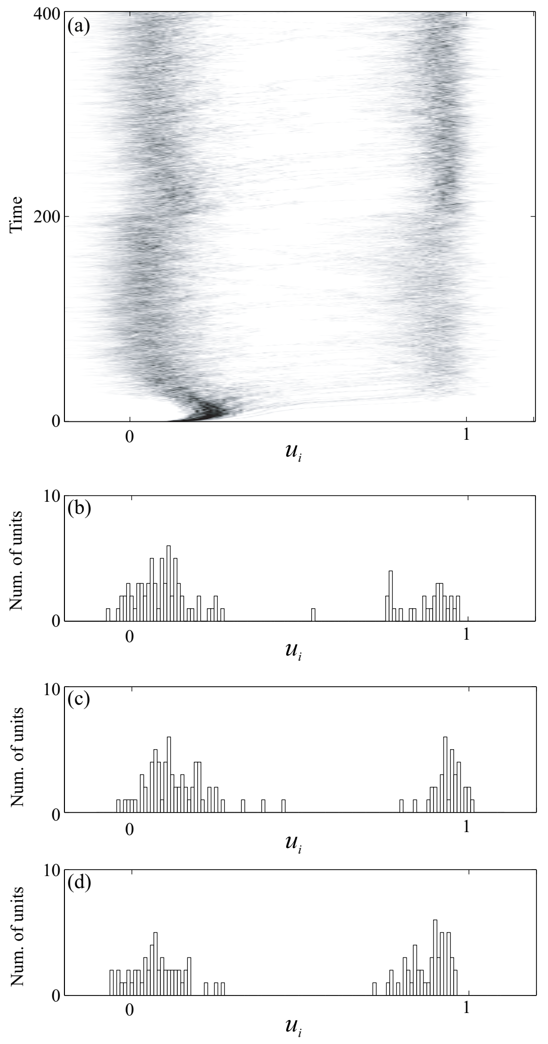


Fig. 7. Simulation results at $N = 100$, $b_w = 0.1$, $b_s = 0.9$, $b = 0.4$ and iteration size, $\Delta t = 0.05$. The number of predators, $Ne = 0$ at $0 \leq t < 200$), $Ne = 20$ at $200 \leq t \leq 400$. (a)Time evolution of u_i and $\langle u \rangle$. The distribution of u_i are shown by the gray scale map. (b)Distribution of u at t=150. (c)Distribution of u at t=205. (d)Distribution of u at t=400.

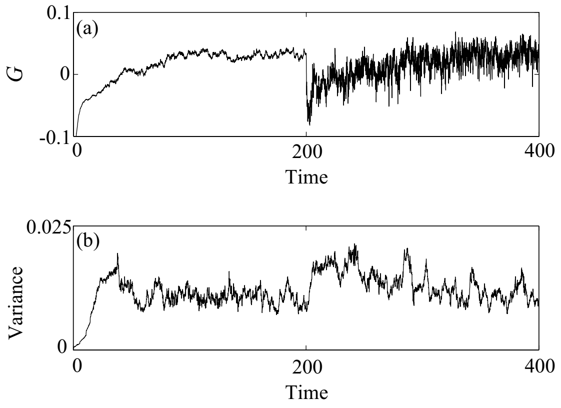


Fig. 8. (a)Transition of G given by equation (9). (b)Variance of u_i $(i \in w)$. The variance is given by $\sigma_w^2 = \Sigma_{i=1}^{N_w}(u_i - \langle u_w \rangle)^2$.

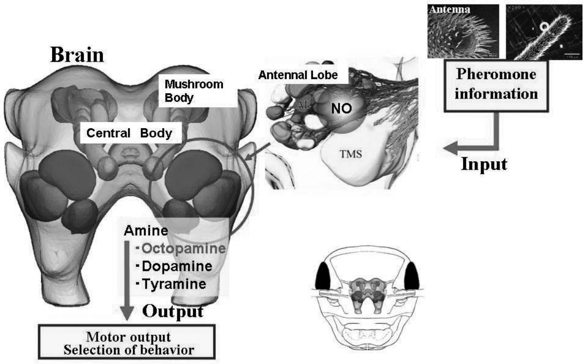


Fig. 9. Information pathway in the cricket brain

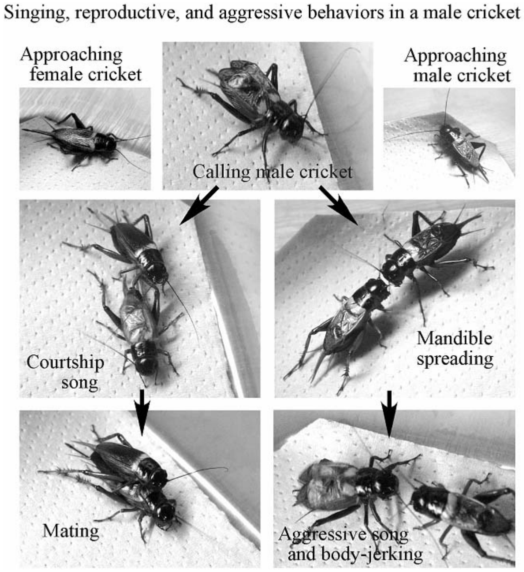


Fig. 10. Cricket behavior selection

B. Neuromodulators and NO/cGMP cascade

Organic neural systems involve a variety of neurotransmitters and NMs. NO, for one, is thought to play an important role in selecting program behavior from polymorphic circuits. NO diffuses in the brain at about 100 [µ m/s] in three dimensions to control neurotransmitter emission [28]. Due to diffusion and reverse propagation, NO is generally considered to be involved in neural plasticity as the basis of learning and memory [29].

The NO/cGMP cascade is considered particularly closely related to fighting behavior selection by crickets. Fighting behavior is observed when an NO synthesis inhibitor is injected into the head of a crickets. When two males encounter one another, fighting starts as usual and soon ends. If these crickets again encounter each another after a 15-minute interval, even the defeated cricket may exhibit fighting behavior instead of avoidance, indicating appropriate behavior is not selected if the NO/cGMP cascade functions normally in the brain. Even under these circumstances, the pheromone is identified and NO is closely related to pheromone behavior

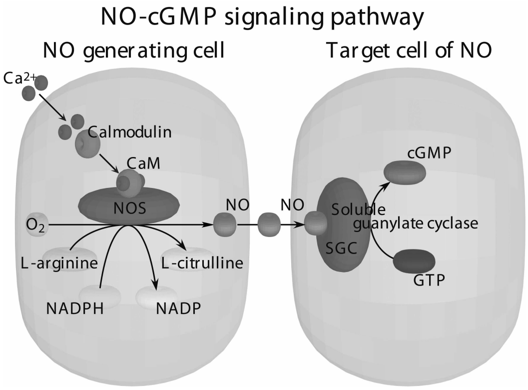


Fig. 11. NO/cGMP signaling pathway

modified by experience [30].

In the NO/cGMP signaling pathway (Fig. 11), the NO/cGMP cascade mediates the efficacy of different neural pathways, or circuits, which in turn affect the cricket's physiological condition. One change octopamine (OA) levels in the brain, for example [31],[32]. As recent research indicates (*Aonuma, unpublished data*), the amount of OA differs significantly before and after fighting and in winner's and loser's OA levels. The NO/cGMP cascade is thus considered deeply related to behavior selection through OA.

Given this background, we constructed a dynamic hypothetical model, discussed below.

VI. MODELING CRICKET BEHAVIOR SELECTION

In attempting to model NO/cGMP cascade function in cricket fighting behavior taking account with the relationship between OA concentration and behavior selection. Many neurons are complexly related in behavior generation and these relationships are difficult to reproduce accurately. In adaptive behavior selection from insect's programmed behavior however, describing relationships between substances is sufficient, so we express each substance as a module.

A. *Internal State Modeling of NO/cGMP Cascade*

Noting a cricket's internal state based on amounts of NO, cGMP, and OA, we modeled behavior selection in fighting behavior (Fig. 12).

Simply put our model takes two states which are aggression and avoidance. Basing the internal state on the amount of OA, aggression causes the cricket to select fighting behavior and avoidance causes it to stay away from a previous winning cricket.

Based on sensory information from its antennae, a cricket first generates NO, and pheromones from another individual increase the NO concentration in the antennal lobe (AL). When NO is generated in the AL, the target range is considered the membrane surrounding the AL. If neural circuits are considered to consist of modules, no information is needed about neuronal regarding the linkage in the AL and only distance information is important. The AL is thus considered as a dimension of $n[\mu\mathrm{m}]$. The amount of NO in the AL is expressed as vector $\mathscr{N}$ of $(n+1)$ dimensions and that at position x $(0 \leq x \leq n, x \in \mathbb{Z})$ as $\mathscr{N}^x$.

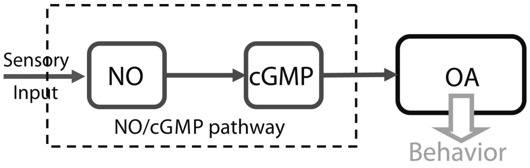


Fig. 12. Model of action selection from NO/cGMP cascade

$$\mathscr{N} = [\mathscr{N}^0 \;\; \mathscr{N}^1 \;\; \cdots \;\; \mathscr{N}^n] \tag{12}$$

NO is a radical that reacts with metal ions immediately after diffusion throughout the brain, after which it disappears, presumably present for about 10 seconds. To express this effect, the equation of NO diffusion with constant γ_N and diffusion constant D is expressed as follows:

$$\frac{\partial \mathscr{N}}{\partial t} = D\frac{\partial^2 \mathscr{N}}{\partial x^2} - \gamma_N \mathscr{N} + \mathscr{N}_{in} - \mathscr{N}_{out} \tag{13}$$

where, $\mathscr{N}_{in}$ and $\mathscr{N}_{out}$ represent the amount of NO generation and consumption. Because NO mainly remains inside the membrane enveloping the AL, the following reflecting boundary is given as a boundary condition:

$$\mathscr{N}^0 = \mathscr{N}^1, \quad \mathscr{N}^n = \mathscr{N}^{n-1} \tag{14}$$

The NO diffusion property in the cricket brain is then modeled based on equations (13) and (14).

cGMP in the NO target cell is generated when soluble guanylate cyclase (SGC) and guanosine triphosphate (GTP) mutually react, and SGC is driven by diffused NO from NO-generating cells (Fig. 11). cGMP affects the amount of OA for behavior selection function. The amount of cGMP in NO target cell C is expressed as a scalar value using the constant γ_C based on the idea that excessive amounts of cGMP are decomposed in the body:

$$\frac{\partial C}{\partial t} = -\gamma_C C + C_{in} - C_{out} \tag{15}$$

where C_{in} and C_{out} represent amounts of cGMP generation and consumption in the NO target cell.

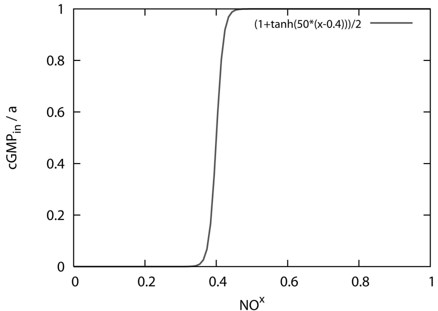
The cricket selects behavior based on the amount of OA, A and OA is generated by cGMP and used to generate behavior. Likewise, the amount of OA is expressed by using constant γ_A:

$$\frac{\partial A}{\partial t} = -\gamma_A A + A_{in} - A_{out} \tag{16}$$

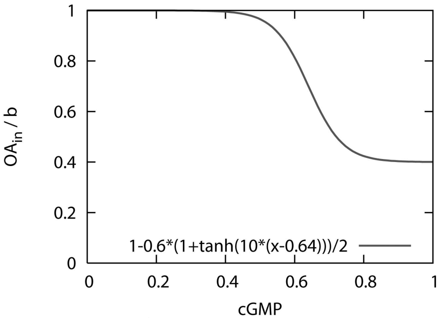
where A_{in} and A_{out} represent the amount of OA generation and consumption

The dynamics of each substances are modeled Based on equations (13),(15) and (16).

In physiological experiments, technical constraints limit the ability to measure NO concentration in the AL, so we measure the NO concentration leaking from AL. The



(a) NO to cGMP



(b) cGMP to OA

Fig. 13. Functions in our model

increased NO concentration in the AL is certain, but the degree of increase is unclear, 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:

$$\mathcal{N}_{in}^{x} = \begin{cases} 0.0 & \text{if } x \notin \mathbb{I}, \\ 1.5 & \text{if } (x \in \mathbb{I} \wedge \mathit{fighting}), \\ 1.0 & \text{otherwise.} \end{cases} \tag{17}$$

This means that the amount of NO generated when the cricket fights becomes 1.5 times that of the normal amount without fighting.

Given that NO is completely consumed in cGMP production, NO consumption depends only on the NO concentration, so, the amount of NO consumption $\mathcal{N}_{out}^{x}$ at position x is determined for position set $\mathbb{O}$ at the source. According to [29], when the amount of NO in the brain is increased by a NO donor, the amount of cGMP in the NO target cell is multiplied by NO consumption. Modeling property $\mathcal{N}_{out}^{x}$ as a smooth function such as equation (18),

$$\mathcal{N}_{out}^{x} = \begin{cases} a \times (1 + \tanh(50 \times (\mathcal{N}^{x} - 0.4)))/2 & \text{if } x \in \mathbb{O}, \\ 0 & \text{otherwise.} \end{cases} \tag{18}$$

where a is a constant and the amount of $\mathcal{N}_{out}^{x}$ is expressed as [0:a]. Fig. 13-(a) shows an example of the mapping function.

As stated, the amount of NO consumption in the NO target cells is related to cGMP generation. Expressing the amount of cGMP in the NO target cell as scalar value C_{in} , C_{in} equals the total amount of NO consumption. Equation (19) indicates that total NO consumption is used to generate cGMP.

$$C_{in} = \sum_{x} \mathcal{N}_{out}^{x} \tag{19}$$

Based on physiological experiments, OA is divided into that which is NO-independent and that which is NO-dependent. cGMP suppresses OA production, so cGMP consumption is modeled as a smooth function.

$$C_{out} = b \times (1 + \tanh(10 \times (C - 0.64)))/2 \tag{20}$$

If the amount of OA, A, is normalized to [0:b], the amount of NO-dependent is about 0.4b (*Aonuma, unpublished data*).

$$A_{in} = b - 0.6 \times C_{out} \tag{21}$$

Fig. 13-(b) shows an example of the mapping function using equations (20) and (21).

OA is used in the cricket, to obtain energy from fat. Using the constant c, A_{out} is:

$$A_{out} = \begin{cases} c & \text{if } \mathit{fighting}, \\ 0 & \text{otherwise.} \end{cases} \tag{22}$$

This indicates that fighting behavior consumes large amounts of energy.

B. Fighting Behavior and Behavior Selection

Bonabeau *et al.* reported the need of probability factors for ranking in a group [33] and Ashikaga *et al.* modeled the effects of breeding density and fighting behavior by introducing probability factors into behavior selection [34],[35]. A deterministic method appears suitable for analyzing the internal state of a single cricket.

As stated, the NO/cGMP cascade in the cricket brain affects its physiological condition changing OA levels. OA is a biogenic amine used to extract energy from fat.

The simplest model assumes behavior selection based only on the amount of OA. When modeling behavior selection, however, fighting behavior itself must be modeled. Assuming that a cricket selects behavior at each step (Δt[sec]) during fighting, probability P of fighting in the next step is expressed as follows:

$$P = \mathrm{sgn}(A - \Theta) \tag{23}$$

where fighting behavior is selected when A is over threshold Θ and avoidance behavior is selected in other cases.

We also assume that penalty $-c$ is given to a defeated cricket after fighting. So, the post-fighting state is obtained deterministically if the pre-fighting state is given.

VII. SIMULATIONS OF BEHAVIOR SELECTION

The behavior of the proposed model was verified in computer simulation in which the internal states of crickets were compared for changes between victory and defeat.

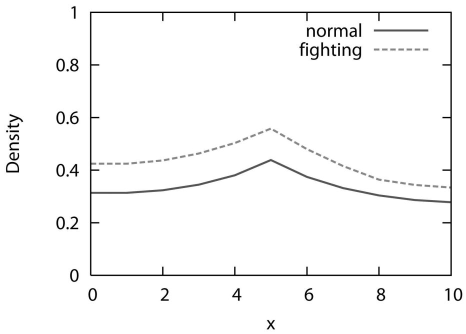


Fig. 14. Density of NO in antennal lobe

A. *Simulation Setup*

As stated, one position was determined for NO generation and consumption, and $\mathbb{I} = \{50\}$ and $\mathbb{O} = \{60\}$ were set. With diffusion coefficient $D = 1000$, $\gamma_N = 1.0 \times 10^{-1}$, $\gamma_C = \gamma_A = 5.0 \times 10^{-4}$ was set as the effect where NO is diffused and disappears in about 10 seconds by reacting with metal ions.

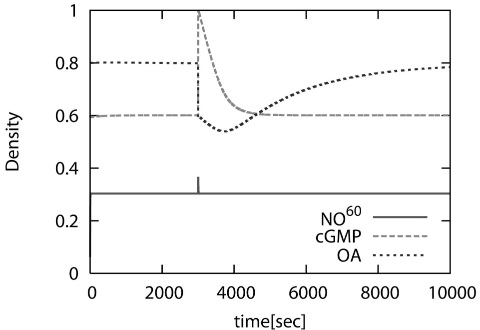
Based on physiological experiments, the stationary state of cGMP was $C = 0.6$ and that of OA $A = 0.8$. To satisfy these values, $a = 1.82 \times 10^{-2}$ and $b = 4.91 \times 10^{-4}$ were set. Hypothesis that NO operates as a type of switch, stationary states were ignored. The values were set $n = 100$, $\Delta t = 0.001$, $\Theta = 0.5$ and $c = 0.1$. Figure 14 gives NO states when the cricket is in an ordinary non-fighting state and at 30 seconds after the start of fighting (ordinary state during fighting). With these settings, fighting behavior clearly increases NO levels in the brain and affects cGMP and OA values.

B. *Results of Behavior Selection*

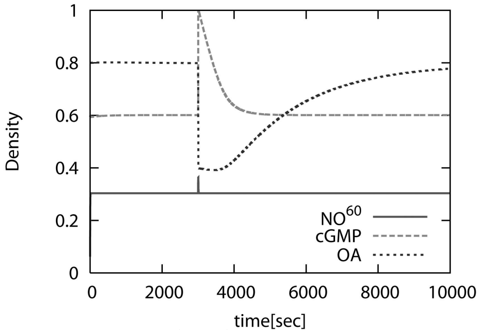
In simulated of a single fight between two crickets and the internal state transition in the simulated winner and loser (Fig. 15). Fighting behavior starts at $time = 3000$ and continues for 15 seconds in (a) and 30 seconds in (b).

The proposed model takes either or state of aggression or one of avoidance, determined by the amount of OA (threshold $\Theta = 0.5$). With aggression state leading to the selection of fighting behavior or avoidance behavior leading to non-fighting.

This model accurately represent behavior in which the cricket exhibits avoidance behavior after a loss and fighting behavior after sufficient time has passed. The effective time effect lasts just over 30 minutes, similar to actual observations, required for a defeated cricket to exhibit fighting behavior or for recovery of $A = 0.5$. This shows that time effects can be matched with actual data by varying γ_C and γ_A.



(a) The winner



(b) The loser

Fig. 15. Simulation result of internal state after fighting ($\Theta = 0.5$)

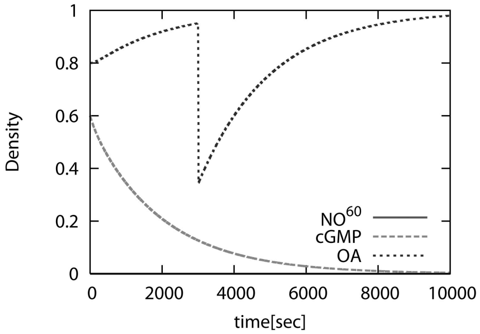


Fig. 16. Simulation result of internal state of loser after fighting (NO generation inhibited)

Results confirms whether another response can be expressed. When NO inhibitor is injected into the cricket's brain, fighting behavior selection increases even though the cricket has been defeated [27] so NO inhibition weakens that the memory of past experience. In simulation utilizing same model, if NO synthesis is inhibited ($\mathcal{N}_{in}^{x} = 0$), C becomes 0, and $A = 1$ indicating that recovery will become shorter (Fig. 16) and that memory based on experience is weakened by blocking the NO/cGMP cascade. Our proposed model thus appears sufficient to explain adaptive behavior selection in crickets.

VIII. CONCLUSIONS

We have modeled the termite caste differentiation and cricket's neural system to understand principles of social adaptive behavior selection. In projected work, the biological experiments in order to justify this conclusion are included in future work. We plan to establish a more accurate model of the colony system and neural system for adaptive behavior selection by continuing discussions with biologists on maintaining consistency between developed model behavior and physiological experimental results for the target insects.

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