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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]:

$$\frac{dA(t)}{dt} = -\gamma_A A(t) + A_{in} - A_{out}, \tag{1}$$

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

Variable A represents the normalized amount of OA in the CNS, variable A_{in} denotes the normalized amount of the OA production, the constant A_{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 A_{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:

$$F_A(t) := F_{A\infty} + \exp\left(-\gamma_A\left(t - \tau_A\right)\right), \tag{2}$$

where the constant $F_{A\infty}$ 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.

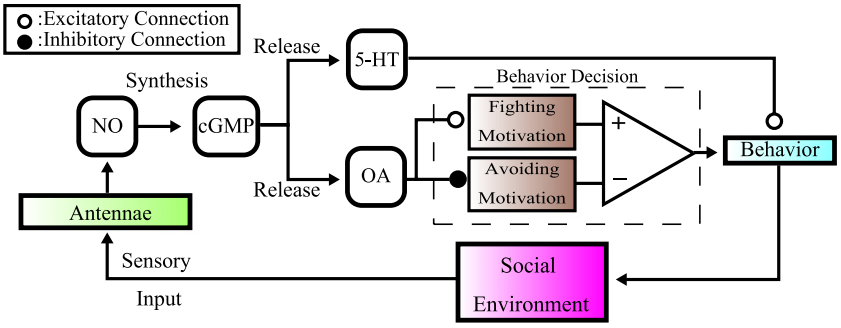

Fig. 2. Behavior selection. Octopamine (OA) determines the behavior, whether the cricket fights or not. Serotonin (5-HT) modulates the aggressive behavior determined by OA.

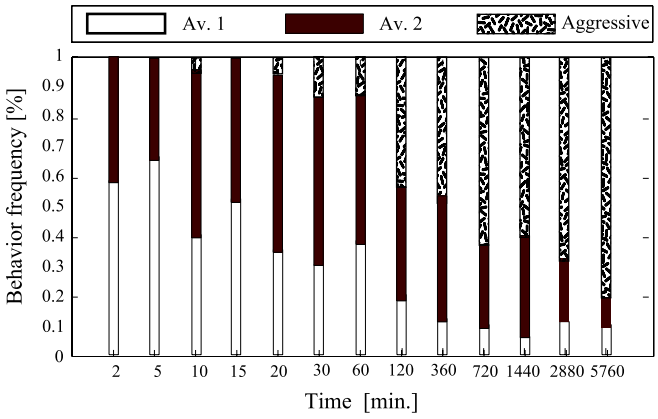

Fig. 3. Time evolution of avoidance behavior frequency. A logarithmic time scale is used to plot the time evolution of avoidance behavior frequency. The Av. 1 behavior returns to a stable condition about 180 min after fighting. The Av. 2 behavior returns to a stable condition about 2 days after fighting. This figure has been obtained from Refs. [18,19].

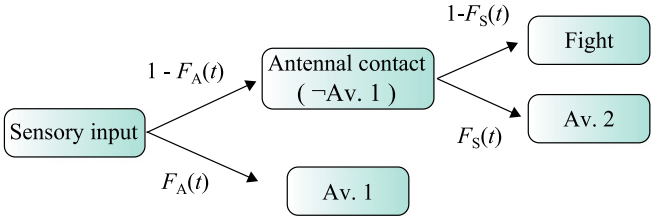

Fig. 4. Behavioral diagram. If a cricket does not have enough OA, it starts avoiding level 1. If a cricket has enough OA but insufficient 5-HT, it starts avoiding level 1.

The avoidance behavior gradually disappears within a few hours to a few days. This time evolution is called forgetting curve.

We used a male cricket 1–2 weeks after the imaginal molt for experiments. They were kept in crowded conditions with females, and before experiments, the adult males were kept in isolation from the other crickets for 3–4 days. After isolation, crickets experience only one losing. Behavior changes in subordinate cricket last for about 1 week (Fig. 3) [19].

3. Mathematical model construction

In this section, we construct a mathematical model on the basis of the 5-HT hypothesis and derive the intensity of behavior modulation from this model. Next, we derive its time evolution, which is equivalent to obtaining the forgetting curve. Third, we derive another forgetting curve by removing specific factors from the 5-HT hypothesis. Thus, we prepare two forgetting curves for comparative verification.

3.1. Serotonergic contribution to forgetting curve

We use $F_S(t)$ and $F_A(t)$ for representing the serotonergic and octopaminergic contribution to the forgetting curve.

As introduced in RELATED WORKS, Av. 2 is the avoidance behavior that is exhibited after antennal contact with the opponent (Fig. 4). Past study assumed that decreased amount of OA represents Av. 1, and succeeded in explaining the specific dynamics of a cricket group [4]. The time evolution of Av. 1 dynamics is much faster than that of Av. 2, so it is difficult to suppose that OA contributes to Av. 2. The time evolution of Av. 1 comes to stable equilibrium very soon (Fig. 3), so we assumed that 5-HT mainly contributes to Av. 2 and not or very few to Av. 1.

We calculate conditional probability of Av. 2, given ¬ Av. 1 (Fig. 5). In the ANALYSIS section, we calculate the time constant of

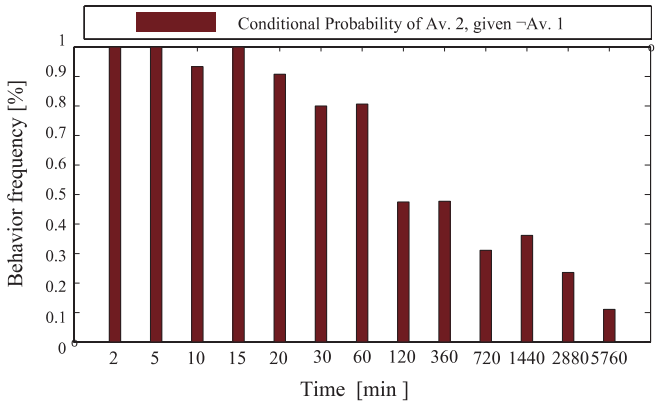

Fig. 5. Time course of avoidance behavior frequency. A logarithmic time scale is used to plot the time course. The figure shows that conditional probability of Av. 2, given ¬ Av. 1. This figure is obtained by using Fig. 3.

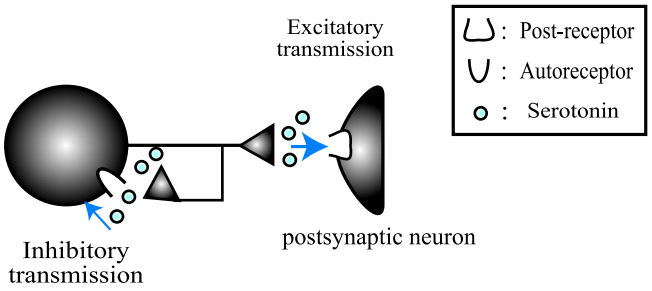

Fig. 6. 5-HT system. The 5-HT system is composed of two receptor types. One is the autoreceptor that controls its own neural activity. Another is the postsynaptic receptor that determines the intensity of excitation.

the serotonergic contribution from this experimental data. In this section, we model a serotonergic system and theoretically derive an expression for the time constant.

3.2. Serotonin hypothesis

We employ 5-HT hypothesis to describe the dynamics of 5-HT system in crickets' brain. The 5-HT hypothesis is the working theory for explaining emotional disorders physiologically. As previously mentioned, serotonergic system has been conserved through evolution and thought to participate in many animal species emotions [17]. Although there would be some 5-HT neurons functionally unrelated to aggressive behavior, it is also possible to assume that 5-HT system which modulates aggressive behavior in cricket's brain is described by 5-HT hypothesis. We assume that serotonergic modulation in the case of crickets' aggressiveness is also described by the 5-HT hypothesis.

The hypothesis has three major features: spontaneous firing, presence of an autoreceptor, and serotonin reuptake (Fig. 6).

Spontaneous firing is a typical characteristic of a 5-HT system. The 5-HT neuron fires spontaneously even if it does not receive any signal from presynaptic neuron.

Negative feedback through the autoreceptor is also a characteristic of the 5-HT system. The amount of extracellular 5-HT cannot be very high or very low because neuronal activity is inhibited by extracellular 5-HT via the autoreceptor: 5-HT release is under homeostatic control. The amount of 5-HT also decreases when the 5-HT autoreceptor is activated [20].

The amount of receptor protein on the cell membrane also changes to maintain homeostatic signaling. If a very large (or too small) signaling is transmitted via the autoreceptor, the autoreceptor on the cell membrane is internalized (or externalized) into the cell. The postsynaptic receptor is also under control; the amount

of postsynaptic neurons changes to maintain homeostatic signaling [16]. It has been reported that the expression level of receptors varies according to dominance hierarchy [21]. This indicates that internalization and externalization occur because of fighting behavior.

After a neuron releases 5-HT to the extracellular region, a 5-HT transporter (5-HTT) returns it to the internal cell; this phase is called 5-HT reuptake. The returned 5-HT is reused for the next activation, but is also partially deconstructed. Therefore, the 5-HT system needs to produce 5-HT and supply the deficit.

This hypothesis involves four time constants associated with the following dynamics:

(1) Dynamics of vesicular release and reuptake.
(2) Dynamics of neurotransmitter metabolism.
(3) Dynamics of receptor internalization and externalization.
(4) Dynamics of receptor degradation, which proceeds with continual stimuli.

In nature, there are many other dynamics that have larger time constants than those of the above dynamics, for example, a changing network of nerves, physical disruption due to an accident, and changing social structure. However in this study, we consider only the three cases (1)–(3); it is natural to not consider receptor degradation when there is only one fight.

3.3. Dynamics of serotonin system

We constructed a mathematical model of 5-HT dynamics by using the 5-HT hypothesis, as follows:

$$\frac{dS(t)}{dt} = -\gamma_S S(t) + S_{in}(t) - S_{out} - \gamma_d I_{auto}(t), \tag{3}$$

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

$S(t)$ represents the amount of 5-HT inside and outside the cell. S_{in} represents the amount of 5-HT production. $I_{auto}(t)$ represents the 5-HT signal received by the autoreceptor. $I_{post}(t)$ represents the 5-HT signal received by the postsynaptic receptor. The constant γ_S and γ_d represent the metabolic rate of 5-HT and proportionality factor.

On the right-hand side of Eq. (3), the first term represents the effect of metabolism. The second term represents the contribution from 5-HT production. The third term represents a decrease in the 5-HT production caused by autoreceptors. Similar to an OA model, the time constant of the NO–cGMP cascade will be virtually much smaller than that of 5-HT [4]. For this reason, we can assume that S_{in} is approximately constant; we only need to consider the 5-HT recovery and receptor recovery for analyzing the forgetting curve.

By considering the receptor theory in pharmacodynamics, we described I_{auto} and I_{post} as follows:

$$I_{auto}(t) \coloneqq r_{auto} \times r(t)S(t) \times R_{auto}(t), \tag{4}$$

$$I_{post}(t) \coloneqq r_{post} \times r(t)S(t) \times R_{post}(t). \tag{5}$$

Variable $r(t)$ represents the proportion of extracellular 5-HT, $r(t)S(t)$ denotes the amount of extracellular 5-HT. Signaling via autoreceptor I_{auto} suppresses $r(t)$. A constant r_{auto} represents the contribution rate of extracellular 5-HT, which affects the autoreceptor. Similarly, constant $r_{post} = (1 - r_{auto})$ represents the contribution rate of extracellular 5-HT, which affects the postreceptor. $R_{auto}(t)$ represents the amount of autoreceptors.

The dynamics of the release rate $r(t)$ can be described as follows:

$$\frac{dr(t)}{dt} = -\gamma_r \{r_{in} \times r_0(I_{auto}) - r(t)\} \tag{6}$$

$$r_0(I_{auto}) = (1 - \eta) + \frac{\eta}{1 + \exp(\lambda (I_{auto} - I_{a0}))}, \tag{7}$$

$$r_{in} = \begin{cases} r_{r-in} & \text{if } \textit{fighting}, \\ r_{s-in} & \text{otherwise.} \end{cases}$$

The release rate monotonously decreases with increasing I_{auto} (Eq. (7)). The constants η, λ, and I_{a0} determine the contribution of I_{auto} to the monotonousness. Variable r_{in} indicates the status, either releasing or spontaneous firing ($r_{spontaneous} < r_{release}$).

3.4. Derivatives of forgetting curve

3.4.1. Forgetting curve under 5-HT hypothesis

The forgetting curve is derived from $I_{post}(t, r_{s-in})$. At first, we estimate $S(t)$ by using an adiabatic approximation. Then, we derive $I_{post}(t, r_{s-in})$ and the forgetting curve.

As the dynamics of $S(t)$ and $r(t)$ are fast enough to use the adiabatic approximation, and Eqs. (3) and (6) are modified as follows:

$$S(t) = \frac{S_{in} - S_{out}}{\gamma_S + \gamma_d r_{auto} r_{in} r_0(I_{auto}) R_{auto}(t)}. \tag{8}$$

The serotonergic system changes the amount of 5-HT and receptors to maintain I_{post} and I_{auto} homeostatic. Hence, we assume $I_{auto} = I_{post}$ and conclude that

$$r_{auto} \times R_{auto} = r_{post} \times R_{post} \tag{9}$$

from Eqs. (4) and (5). Then, we rewrite I_{post} (Eq. (5)) as

$$I_{post}(t, r_{in}) = \frac{S_{in} - S_{out}}{\gamma_d} \left\{ 1 - \frac{1}{1 + \frac{\gamma_d}{\gamma_S} r_{post} r_{in} r_0 R_{post}(t)} \right\} \tag{10}$$

by using Eqs. (8) and (9). Hereinafter, we call $I_{post}(t, r_{r-in})$ as $I_{r-post}(t)$ and $I_{post}(t, r_{s-in})$ as $I_{s-post}(t)$.

As mentioned before, the intensity of aggressiveness is proportional to I_{post}. We represent the intensity of aggressiveness as

$$Agg(t) \coloneqq I_{r-post}(t). \tag{11}$$

This means that

$$Av(t) = 1 - I_{r-post}(t). \tag{12}$$

On the contrary, 5-HT is not released during the interval the cricket refrains from fights. We conclude that the 5-HT contribution to the forgetting curve is

$$\begin{aligned} \frac{dF_S(t)}{dt} &= \frac{d}{dt} Av(t) \\ &= \left(\frac{r_{s-in}}{r_{r-in}} \frac{\gamma_d Agg(t)}{S_{in} - S_{out}} - 1 \right) \left(1 + \lambda I_{s-post}(t) \frac{r_0 - 1}{r_0} \right. \\ &\quad \left. \times \frac{r_0 - (1 - \eta)}{\eta} \right) \frac{Agg(t)}{R_{auto}(t)} \frac{dR_{auto}(t)}{dt}, \end{aligned} \tag{13}$$

and

$$F_S(t)|_{r_{in} = r_{r-in}} = Av(t). \tag{14}$$

3.4.2. Forgetting curve after the removal of autoreceptor

If the serotonin neuron does not have an autoreceptor, it is necessary to modify the equations. The intensity of modulation is

changed to

$$\mathrm{Agg}_{\mathrm{removalRa}} := I_{\mathrm{removalRa}} = \frac{\mathrm{S_{in}} - \mathrm{S_{out}}}{\gamma_S} r_{\mathrm{in}} r_0 R_{\mathrm{post}}. \tag{15}$$

In this case, the forgetting curve is derived as

$$\frac{\mathrm{d}F_{S\mathrm{removal}}(t)}{\mathrm{d}t} = -\frac{\mathrm{dAgg}_{\mathrm{removalRa}}(t)}{\mathrm{d}t} = -\frac{\mathrm{Agg}(t)}{R_{\mathrm{post}}(t)} \frac{\mathrm{d}R_{\mathrm{post}}(t)}{\mathrm{d}t}. \tag{16}$$

4. Analysis

To confirm whether or not the 5-HT system has autoreceptors, we estimate a major parameter by using two types of forgetting curves which are obtained as discussed above. Then, we compare this parameter with those obtained in past studies and make an assumption on the presence of an autoreceptor. Finally, we predict the time constant of 5-HT receptor internalization, which has never been measured for crickets.

4.1. Generalized regression function

When the time evolution of $\mathrm{Agg}(t)$ is expressed as

$$\frac{1}{f(t)} \frac{\mathrm{d}f(t)}{\mathrm{d}t} = \beta \frac{1}{g(t)} \frac{\mathrm{d}g(t)}{\mathrm{d}t}, \tag{17}$$

it is solved formally to give

$$f(t) = g(t)^{\beta}. \tag{18}$$

From Eqs. (13) and (16), we write $g(t) = R_{\mathrm{post}}(t)$. Receptor dynamics are easily expressed by an exponential curve [22]:

$$R_{\mathrm{post}} = \mathrm{a} + \exp(\mathrm{b}t - \mathrm{c}), \quad (\mathrm{b} < 0). \tag{19}$$

We write $f(t)$ as

$$f(t) = \mathrm{a}^{\beta} + \exp\left(\beta\left(\mathrm{b}t - \mathrm{c}\right)\right), \tag{20}$$

because experimental data shows $a \ll 1$, as we will see later.

We use the method of least squares for analyzing experimental data on the forgetting curve. We analyze experimental data by using two regression functions (Fig. 7):

$$F_A(t) := \mathrm{a}_1 + \exp\left(\mathrm{b}_1 \times t - \mathrm{c}_1\right), \tag{21}$$

$$F_S(t) := \mathrm{a}_2 + \exp\left(\mathrm{b}_2 \times t - \mathrm{c}_2\right) + \exp\left(\beta \mathrm{b}_3 \times t - \mathrm{c}_3\right). \tag{22}$$

We estimate β by using Eq. (22) and make an assumption on the presence of an autoreceptor in the 5-HT system.

There are two levels in avoidance behavior. We assume that $F_A(t)$ represents the time evolution of Av. 1 and $F_S(t)$ represents that of the conditional probability of Av. 2, given ¬ Av.1 (Fig. 4). We represent the time evolution of the avoidance probability as $F(t)$, and these two levels adds up to $F(t)$:

$$F(t) = F_A(t) + (1 - F_A(t)) \times F_S(t). \tag{23}$$

4.2. Estimation of β for each model

When the autoreceptor is removed, $\beta = 1$, as expressed in Eq. (16). In this case, the largest time constant of the fitting curve is equal to b_3.

Using the 5-HT hypothesis, we obtain

$$0.55 < \beta = -\left(\frac{\gamma_{\mathrm{d}} \mathrm{Agg}(t)}{(\mathrm{S_{in}} - \mathrm{S_{out}})} - 1\right) \times \left(1 + \lambda \mathrm{Agg}(t) \frac{r_0 - 1}{r_0} \frac{r_0 - (1 - \eta)}{\eta}\right) < 0.7, \tag{24}$$

(see Appendix). In this case, the largest time constant of fitting curve is approximately βb_3.

For the verification of our theory, we compare the theoretical prospect, which we have derived in this section, and experimental data (Fig. 3).

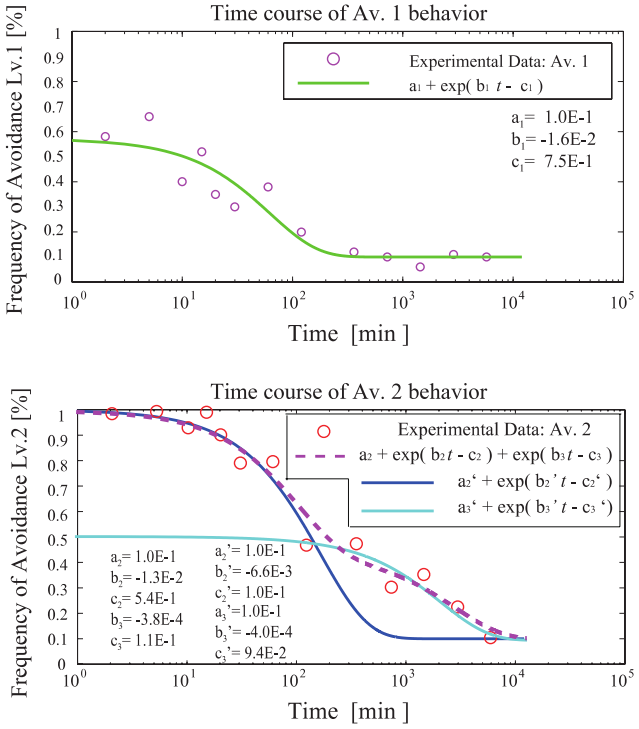

Fig. 7. Fitting curves. Fitting curves for Avoidance level 1 and Avoidance level 2. Time constant of Av. 1 is about 60 min. Av. 2 has two time constants: about 75 min and about 2600 min. Experimental data is from Fig. 3.

5. Results

As shown in Fig. 7, the time constant of avoidance level 1 is about 60 min. Avoidance level 2 has two time constants: about 75 min and 43 h. In Fig. 7, we draw three curves. The broken line represents $F_S(t)$. The other two lines are fitting curves for 0–120 min data and 120–5660 min data.

During the interval 0–120 min, the effect of 5-HT recovery is dominant. We compare the theoretical prospect and fitting curve for 120–5660 min. The comparison shows that the model constructed by using 5-HT hypothesis accounts for the experimental results better than the model without an autoreceptor.

In the absence of the autoreceptor, the largest time constant of the fitting curve is equal to b_3. In this case, $b_3 \approx 3.8\mathrm{E}-4$ and the time constant is about 43 h.

When the 5-HT hypothesis is used, $5.4\mathrm{E}-4 < b_3 < 6.9\mathrm{E}-4$ and the time constant is not below 24 h and not greater than 30 h.

6. Conclusions and discussions

We constructed a 5-HT system on the basis of the 5-HT hypothesis and estimated the time constant of the 5-HT receptor, b_3, in crickets.

The time constant b_3 has never been measured experimentally in crickets; the time constant, if available, can be used as a reference point to obtain the time constants associated with the 5-HT system for other animals. In this study, we use the 5-HT hypothesis that involves four time constants associated with the following dynamics:.

(1) Dynamics of vesicular release and reuptake (∼1 min) [23].
(2) Dynamics of neurotransmitter metabolism (∼1 h) [24].
(3) Dynamics of receptor internalization and externalization (∼10 h) [22].
(4) Dynamics of receptor degradation, which proceeds with continual stimuli (∼1 day).

Time scale of receptor degradation matches well with the that of Av. 2 when the 5-HT hypothesis is used. However, it is known that receptor degradation occurs under continuous stimulation. The crickets had been under isolation for about 1 week, and they had experienced only one fight. For this reason, it is improper to conclude that Av. 2 results from receptor degradation. Thus, if the 5-HT system has no autoreceptor, the time constant of the postsynaptic receptor is found to be 43 h. On the other hand, if the 5-HT system has an autoreceptor, the time constant of the receptors are estimated to be about 24 h. Additionally, although we considered $1 + \frac{R_{\text{post}}}{r_0}\frac{\mathrm{d}r_0(t)}{\mathrm{d}R_{\text{post}}} \approx 1$ in this paper, there is a possibility that the value is smaller, e.g., 0.5. So this study advocates the existence of the 5-HT autoreceptor, which is related to fighting behavior.

Then, we mathematically showed that existence of an autoreceptor that slows the forgetting rate. Our study suggests that continuous injection of a 5-HT autoreceptor antagonist such as WAY 100135 will significantly reduce the time constant of the forgetting curve; the time constant is expected to be about 10 h. It is also expected that continuous injection of a selective serotonin reuptake inhibitor (SSRI) increases the time constant of the forgetting curve. This is a consequence of Eq. (10) because the injection of the SSRI eventually increases r_0.

Next, the following discussions forms a bridge between insect ecology and engineering.

Social animals also control their group size under conditions of resource competition. For their survival, it is important to achieve a suitable group size around the resource. If we consider territorial competition as an example, the area comes to be divided into individuals' territories. After the area is divided, it is hard for new arrivals to enter; they have to leave the place. If individuals do not have the ability to change their behavior, they continues to be stuck in their territories until their death. Thus, changing their behavior to control the group size is important for their survival.

In the field of swarm intelligence, there have been researches on control of group size and aggregation. Melhuish et al. researched a behavior-based multirobot system and revealed the existence of a constrained condition related to the lack of control of group size [25]. They pointed out the possibility of a deadlock in the multirobot system because this system always outputs a fixed behavior against specific inputs. They considered an internal parameter for each robot so that the robots could use a subjective state themselves. Wawerla et al. called this parameter that are frustration level [26]. The internal parameter is increased by intermittent signals that are broadcasted by other robots; hence, a robot comes to have a higher parameter when it is close to a dense group. Once the internal parameter exceeds the threshold, robot changes its behavior and is able to avoid the deadlock. Thus, an internal parameter is necessary for behavior-based robots to decrease the possibility of social deadlock.

Almost all of insects' behavior are referred to as "programmed behavior"; this implies that they have a behavior-based system. They have to use a system to avoid social deadlocks. How do insects avoid a deadlock in nature? Different amounts of the neuromodulator in the central nervous system result in different behaviors [5], and Murakami et al. suggest that social status influences the amount of neuromodulator [11]. Thus neuromodulator in animals is equivalent to the internal parameter in robots. Eq. (10) also predicts that the level of autoreceptor expression also influences the time constant of the forgetting curve. There are many past studies; the growth environment such as population density, dominance hierarchy, etc. change the level of autoreceptor expression [27,21]; the level of autoreceptor expression is affected by the social status. It suggests that animals change the time constant of forgetting by regulating receptor expression in response to social status adaptively.

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Appendix. Estimation of the time constant of the forgetting curve

We defined

$$\begin{aligned}\mathrm{Agg} &:= I_{r-\text{post}}(t)\\ &= \frac{r_{r-\text{in}}}{r_{s-\text{in}}}\frac{S_{\text{in}}-S_{\text{out}}}{\gamma_d}\left(1-\frac{\gamma_S}{\gamma_S+\gamma_d r_{\text{post}} r_{s-\text{in}} r_0 R_{\text{post}}}\right). \end{aligned} \tag{A.1}$$

We introduced a 5-HT contribution for the forgetting curve as

$$\begin{aligned}\frac{\mathrm{d}F_S(t)}{\mathrm{d}t} &= \frac{\mathrm{d}}{\mathrm{d}t}\mathrm{Av}(t)\\ &= \frac{\mathrm{d}}{\mathrm{d}t}\left(1-\mathrm{Agg}(t)\right)\\ &= -\frac{r_{r-\text{in}}}{r_{s-\text{in}}}\frac{S_{\text{in}}-S_{\text{out}}}{\gamma_d}\frac{\gamma_d r_{\text{post}} r_{s-\text{in}} r_0 R_{\text{post}}}{\left(\gamma_S+\gamma_d r_{\text{post}} r_{s-\text{in}} r_0 R_{\text{post}}\right)^2}\\ &\quad\times\frac{\gamma_S}{r_0 R_{\text{post}}}\frac{\mathrm{d}\left(r_0 R_{\text{post}}(t)\right)}{\mathrm{d}t}\\ &= \mathrm{Agg}(t)\left(\frac{r_{s-\text{in}}}{r_{r-\text{in}}}\frac{\gamma_d \mathrm{Agg}(t)}{S_{\text{in}}-S_{\text{out}}}-1\right)\\ &\quad\times\left(1+\frac{R_{\text{post}}}{r_0}\frac{\mathrm{d}r_0(t)}{\mathrm{d}R_{\text{post}}}\right)\frac{1}{R_{\text{post}}}\frac{\mathrm{d}R_{\text{post}}(t)}{\mathrm{d}t}. \end{aligned} \tag{A.2}$$

We estimate the time constant of the forgetting curve from Eq. (A.2) as discussed below. From Eq. (3), it is derived that

$$S(t) = \frac{\gamma_d}{\gamma_S}\left(\frac{S_{\text{in}}-S_{\text{out}}}{\gamma_d}-\frac{r_{s-\text{in}}}{r_{r-\text{in}}}\mathrm{Agg}(t)\right). \tag{A.3}$$

From Eq. (A.3) and [28], we write the equation

$$\frac{S(\infty)}{S(0)} = \frac{r_{r-\text{in}}/r_{s-\text{in}}\times\left(S_{\text{in}}-S_{\text{out}}\right)/\gamma_d-0.9}{r_{r-\text{in}}/r_{s-\text{in}}\times\left(S_{\text{in}}-S_{\text{out}}\right)/\gamma_d-0.6}\approx 0.8, \tag{A.4}$$

where relation $\frac{S(\infty)}{S(0)} = 0.8$ is an analogical assumption [28], i.e.,

$$\frac{r_{r-\text{in}}}{r_{s-\text{in}}}\frac{S_{\text{in}}-S_{\text{out}}}{\gamma_d} = 2.0. \tag{A.5}$$

Thus,

$$-0.7 < \frac{r_{s-\text{in}}}{r_{r-\text{in}}}\frac{\gamma_d \mathrm{Agg}(t)}{S_{\text{in}}-S_{\text{out}}}-1 < -0.55. \tag{A.6}$$

Next, r_0 is a monotone decreasing function of R_{post}, and therefore,

$$1+\frac{R_{\text{post}}}{r_0}\frac{\mathrm{d}r_0(t)}{\mathrm{d}R_{\text{post}}} < 1. \tag{A.7}$$

In conclusion,

$$0.55 < \beta < 0.7. \tag{A.8}$$

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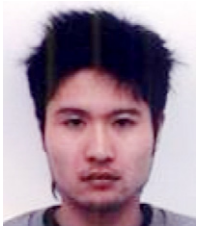

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