

Development of Neurotransmitter Modulation on Aggression and Dominance Hierarchy in Cricket, *Gryllus Bimaculatus*

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Abstract: To design distributed autonomous systems, it's effective to mimic animal society. We studied cricket *Gryllus Bimaculatus* as a typically aggressive insect. In this paper, we construct mathematical model of the individual internal mechanisms which modulate aggressiveness and we make agents to fight each other under some density. As a result, it's confirmed to occur critical phenomenon upon each agent's internal states caused by density effect. At last, we discuss the usage of such transition in distributed autonomous system.

Keywords: Aggressive behavior in cricket, Neuromodulator, Dominance hierarchy.

1. Introduction

In recent years, mimicking social system in animal world has been attempted to design distributed autonomous system. Group behavior of fish, birds, crickets and locust swarms have been studied intensively, as their behavior under crowded condition is different from under low-density condition. In animal world, increasing population density causes various effects on individual behavior known as "density effects". Locust, *Schistocerca gregaria*, takes exclusive behavior under solitary state but develops aggregative behavior and stable gregariousness above critically density by neurotransmitter modulation. Cricket also comes to be less aggressive under high density, and extraordinarily aggressive under the condition of solitary growth. In fish and birds, a group evolve from small, isolated, catalyzing clusters rapidly which emerge at the critical point of population density because of their aggregative behavior.

Locust emerges gregarious behavior and cricket comes to be less exclusive under high population density, on the other hand they behave aggressively and exclusively under solitary condition. It indicates that cricket and locust needs to depress or change their exclusive behavior for socialization unlike birds and fish. In many cases, insects make societies with stereotyped behavior and with modulating the intensity of such behavior. Thus there would be confirmed that cricket or locust decreases its aggressivity with increasing density, but there have been very few studies about changing modulation of aggressivity yet.

We studied cricket *Gryllus Bimaculatus* as a typically aggressive insect and to monitor the change of aggressiveness under some populations. Competitive behavior between individuals constructs social hierarchy between superior and inferior which is called "dominance hierarchy". Dominance hierarchy change crickets' behaviors. Winner tends to be a little more aggressive and loser tends to escape easily. This kind of regulation upon be-

haviors is caused by neurotransmitter modulation and developments of its receptors.

In this paper, we construct mathematical model of the individual internal mechanisms which modulate aggressiveness and show decreasing aggressiveness with increasing density. Additionally, it is derived that there occurs the critical phenomenon upon each agent's internal states caused by density effect. At last, we discuss the usage of such transition in distributed autonomous system.

2. Internal model of cricket in fighting behavior

It is known that cricket's fighting is started with opponent finding sensed by antennae. When antennae are stimulated by opponent, there comes up Nitric Oxide (NO) in brain and starts signal cascade which modulates aggressive behavior. Quantity of octopamine(OA) is the threshold of reaction between aggressive behavior and avoiding behavior, and it is excited by NO/cGMP cascades(Fig. 1). While crickets fight, they consume octopamine. If octopamine falls below threshold, agent recognizes its own defeat. Dominant agent has a reward to restore its octopamine and subordinate agent decreases octopamine additionally. Differential equations which explains octopamine dynamics has constructed¹⁾.

Although octopaminergic modulation plays a central role for aggressive behavior, it is indicated that serotonergic modulation upon aggressive behavior also plays a fundamental role. Serotonin(5-HT) enhances the level of aggressiveness in cricket(Fig. 2). Cause of genetic homology, dynamics of serotonin related to aggression in cricket is thought to follow serotonin hypothesis²⁾³⁾(Fig. 3). While crickets fight, serotonin is released and NO/cGMP cascade decreases serotonin. Dominant agent has a reward to restore its serotonin.

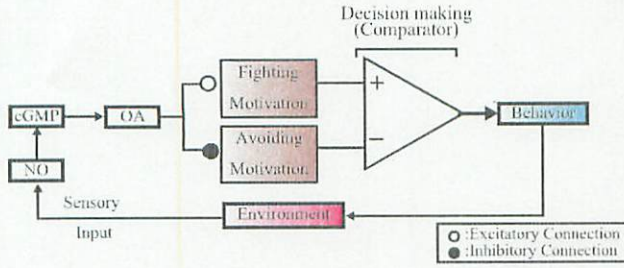


Figure 1: Modulation upon aggressive behavior by OA.

Sensory input increases NO in brain. NO increases cyclic Guanosine MonoPhosphate(cGMP) and cGMP decreases OA.

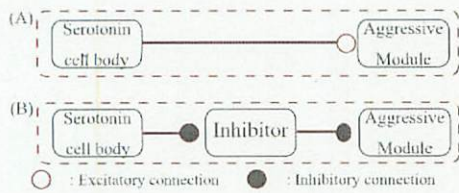


Figure 2: Serotonin enhances aggressive module.

Serotonin works as excitatory role. Details have been unconfirmed yet but it is assumed that 5-HT would cascade like as (A) or (B).

3. Mathematical Model

In cricket, behaviors are modulated by octopamine and serotonin. The model of behaviors modulation by these monoamines is illustrated in Fig. 4. As mentioned before, serotonin plays a considerable role in development of neuromodulation on aggressive behavior. Regulation of neuromodulation on aggressive behavior. Regulation of neurotransmitter-signal constant, has an influence on such development (Fig. 3). There contains two layer of time constants.

1. increase and decrease of neurotransmitters(1 hour)
2. increase and decrease of 5-HT receptors(100 hour)

We constructed mathematical model of serotonin system and improved previous octopamine mode¹⁾.

3.1 Dynamics of serotonin

The dynamics of serotonin is expressed as follows :

$$\frac{\partial S}{\partial t} = -\gamma_S S + S_+ - \gamma_d R_{auto} r_0 r S \quad (1)$$

$$= -(\gamma_S + \gamma_d r r_0 R_{auto}) S + S_+ \quad (2)$$

where $S(t)$ represents amount of serotonin in or out of the cell. $S_+(t)$ represents amount of serotonin production which is inhibited by cGMP, and $R_{auto}(t)$ represents sensitivity of autoreceptors. $r(t)$ represents the

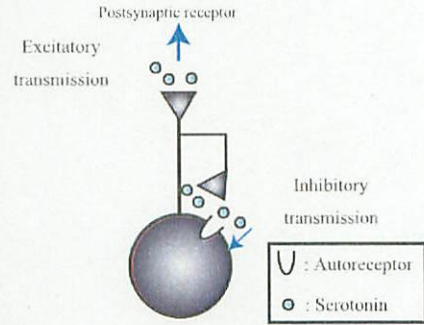


Figure 3: The picture of Serotonin system based upon hypothetical model.

There are two receptors in this system. One, called autoreceptor, controls its own neural activity and the other acts as a neurotransmitter toward postsynaptic cell. Released 5-HT takes negative feedback via autoreceptor and regulates 5-HT release to steady level. Postsynaptic receptor and autoreceptor regulates its receptivity to the value that keeps cell activation constant, which is called physiological homeostasis⁴⁾.

proportion of serotonin out of the cell. Parameter γ_S represents metabolic rate of serotonin and γ_d represents the contribution rate of metabolic rate via autoreceptor. Parameter r_0 represents the contribution rate of serotonin at the outside of cell which affects autoreceptor.

In the right-hand side of eq. (1), first term is the effect of metabolism. Second term is the contribution from production modulated by NO/cGMP cascade and third term is from depression of serotonin production caused via activation of autoreceptors.

Time evolution of r is described as follows :

$$\frac{dr}{dt} = \gamma_r (r_E - r) \quad (3)$$

$$r_E = \begin{cases} r_1 \times g(R_{auto}) & \text{if not releasing,} \\ r_2 \times g(R_{auto}) & \text{if releasing,} \end{cases} \quad (4)$$

$$\gamma_r = \begin{cases} \gamma_{r0} & \text{if not releasing,} \\ 0.05 \times \gamma_{r0} & \text{if releasing,} \end{cases} \quad (5)$$

$$\text{and } \frac{dg(R_{auto})}{dR_{auto}} \leq 0. \quad (6)$$

Thus R_{auto} increases, release rate decreases.

3.2 Dynamics of serotonin receptors

As mentioned before, there are two receptors in serotonin system. In this model, these receptors follow the same dynamics known as Turrigiano-model⁵⁾ eq. (7).

$$\frac{\partial R}{\partial t} = R_+ - \gamma_R R \quad (7)$$

$R(t)$ represents the sensitivity of receptors, sensitivity of autoreceptor is described as R_{auto} and that of

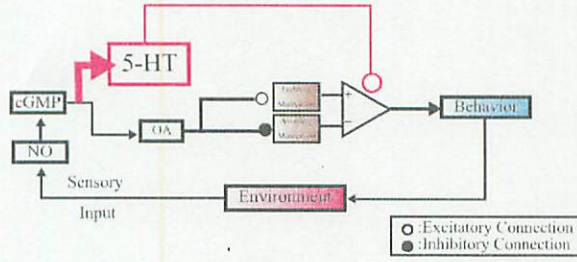


Figure 4: Neuromodulation upon aggressive behavior.

Serotonin(5-HT) doesn't work as threshold of behavior, however, regulate aggressiveness excitatory. Serotonin reaction system is constructed with neuromodulator and receptor.

post-synaptic receptor is described as R_{post} . Parameter γ_R represents metabolic rate of receptors. In the right-hand side of eq. (7), first term means the effect of receptor-insertion from the intracellular region to the cell membrane. Second term means the effect of receptor-removal from the cell membrane to the intracellular region.

It is known that the insertion rate $R_+(t)$ varies to meet the homeostatic signaling condition³⁾: if we use a $ST(t)$ which defines intensity of signal transfer, homeostatic signaling condition requires eq. (8).

$$\lim_{t \rightarrow \infty} (ST(t) \times R_+(t)) = const., \quad (8)$$

and $ST(t)$ expresses the signaling on autoreceptor or on postsynaptic receptor: $r_0 r(t)S(t)$ or $(1 - r_0)r(t)S(t)$. Because $ST(t)$ fluctuates rapidly, regulation of receptor-insertion rate R_+ keeps such homeostatic activity. Receptor-insertion rate is regulated by Protein Kinase A (PKA) or C(PKC) in many situations, and generation of Protein Kinase is triggered by Ca^{2+} influx. We introduce the dynamics of Protein Kinase(eq. 9).

$$\frac{\partial P(t)}{\partial t} = P_+(ST(t)) - \gamma_p P(t). \quad (9)$$

Although serotonin-reuptake from the extracellular region into the intracellular region is completed in a few seconds to a few minutes, second-messengers as like as Protein Kinase $P(t)$ last a few minutes to few dozens of minutes. And changes of receptor sensitivity $R(t)$ keep a few dozens of minutes to a few days. So introduction of above three factors $S(t)$, $P(t)$ and $R(t)$ is necessary for its cascades in terms of time-scale.

3.3 Dynamics of octopamine

Although the growth of serotonin receptor is well mentioned among neuromodulators related to fighting behavior, octopamine receptor is merely mentioned in the topic of growth. Hence octopamine receptor is treated as a constant parameter in this study.

We introduce the previous model¹⁾ to describe the dynamics of octopamine(eq. 10).

$$\frac{\partial A(t)}{\partial t} = -\gamma_A A(t) + A_+(t) - A_-(t), \quad (10)$$

where $A(t)$ represents quantity of octopamine possessed in the brain, $A_+(t)$ represents quantity of octopamine production which is inhibited by cGMP, and $A_-(t)$ represents quantity of octopamine consumption which is in requisition for muscle activity.

Amount of octopamine $A(t)$ plays a role of threshold for behavior decision between fight/flight.

3.4 Dynamics of NO/cGMP

When crickets meet, they start antennae fencing. Pheromone stimuli through the antennae increases Nitric Oxide in the brain, and NO diffuses toward the target cell with its permeableness. Once NO arrive at the target cell, NO approaches soluble Guanylate Cyclase(sGC) to generate cGMP.

We introduce the previous model¹⁾ to describe the dynamics of NO/cGMP(eq. (11,12)).

$$\frac{\partial \mathcal{N}(x,t)}{\partial t} = D \frac{\partial^2 \mathcal{N}(x,t)}{\partial x^2} - \gamma_N \mathcal{N}(x,t) + \mathcal{N}_+(x,t) - \mathcal{N}_-(x,t), \quad (11)$$

$$\frac{\partial C(t)}{\partial t} = -\gamma_C C + C_+ - C_-, \quad (12)$$

where $\mathcal{N}(x,t)$ represents the amount of NO which is function of time and position, and C represents the amount of cGMP. Spatial distribution of $\mathcal{N}(x,t)$ is described with one-dimensional space. $\mathcal{N}_+(t)$ represents quantity of NO production, and $\mathcal{N}_-(x,t)$ represents quantity of NO consumption which is used for generating cGMP. D is the diffusion coefficient. C_+ represents the quantity of cGMP production which is function of $(\mathcal{N}_-(x,t)|_{x=c})$ where c is the position of target substance of NO (i.e. sGC). C_- represents quantity of cGMP consumption which is used for inhibiting octopamine production.

3.5 Relation between substances

$$\mathcal{N}_+(x,t) = \begin{cases} 0 & \text{if } x \neq 0, \\ N_f & \text{if } (x = 0 \wedge \text{fighting}), \\ N_s & \text{otherwise,} \end{cases} \quad (13)$$

where $x = 0$ is the coordinate of NO emission.

$$\mathcal{N}_-(x,t) = \begin{cases} a \times (1 + \tanh(50 \times (\mathcal{N}(x,t) - N_{th}))) / 2 & \text{if } x = c, \\ 0 & \text{otherwise,} \end{cases} \quad (14)$$

where $x = c$ is the coordinate of NO consumption, and $(\mathcal{N}(x,t) - N_{th})$ decides displacement from default position. Production of cGMP is described as

$$C_+(t) = \mathcal{N}_-(c,t), \quad (15)$$

and consumption of cGMP is described as

$$C_- = b \times (1 + \tanh(10 \times (C - 0.64)))/2. \quad (16)$$

Production of octopamine is described as

$$A_+(t) = b - A_p C_-(t), \quad (17)$$

where A_p express octopamine production in natural situation and α_A is normalization constant. Production of serotonin is described as

$$S_+(t) = b - S_p C_-(t), \quad (18)$$

where S_p express serotonin production in natural situation and α_S is normalization constant.

$$R_+ = \frac{2\gamma_R}{1 + \exp(\eta_R P)} \quad (19)$$

$$P_+(ST(t)) = \gamma_P \tanh(\eta_{pk} ST(t)) \quad (20)$$

3.6 Fighting behavior selection and modulation

As mentioned before, fight-or-flight response is determined by the quantity of octopamine in the brain and intensity of behavior is modulated by that of octopamine and serotonin. So we described the intensity of fighting behavior as follows:

$$F = \frac{1 - \tanh(-30(r(1-r_0)SR_{post} - S_{th}))}{2} \times \tanh\left(\frac{\eta_y(A_{end} - A_{th})}{2}\right) \quad (21)$$

In the right-hand side of eq. (21), first term means the effect of serotonin and second term means the effect of octopamine. The condition " $F \geq 0$ " expresses the fighting behavior and " $F \leq 0$ " expresses avoiding behavior. The absolute value of " F " expresses intensity of the behavior.

3.7 Effects of winning or losing

If agent wins, he raises octopamine $+\epsilon_A$ and serotonin $+\epsilon_S R_{auto}$.

If agent loses, he raises cGMP to the constant-value C_L . This effect inhibits the generation of octopamine and serotonin continuously and it makes short-term memory about his losing. He decreases its own motivation toward fighting with this inhibition.

3.8 Frequency of crickets' interaction

To model the frequency of fighting interaction between crickets, there are two significant factor. One factor is the encounter rate, and the other factor is probability which decides whether or not to start fighting.

As mentioned before, loser keep away from fighting with other agent, especially with winner. Of course loser

essentially chooses avoidance over fighting but sometimes chooses fighting, and it is known that loser tends to select other lost agent to start fighting compared with winner or unexperienced agent.

Cricket has poor eyesight and involatile pheromone. It indicates that encounter rate depends on their field of activities. If we posit the premise that loser or winner doesn't change its field of activities, encounter rate is estimated by making an analogy to collision of gas molecule in kinetic theory. So we estimated the encounter rate in proportion to population density ρ .

We constructed the frequency of interaction between agent i and j as eq. (22) (Fig. 5).

$$P_{ij} = \frac{\rho}{N-1} \times F_i F_j \exp(-|F_i - F_j|/P_c) \quad \text{if } F_i > 0, F_j > 0, \quad (22)$$

$$P_{ij} = 0 \quad \text{otherwise.}$$

Parameter N represents number of individuals. As discussed, $\rho/(N-1)$ expresses encounter rate and latter term expresses the probability of fighting together. F_i expresses agent i 's motivation for fighting defined by eq. (21). $\sum_{j=1, j \neq i}^N P_{ij}$ expresses the probability that agent i encounters somebody and starts fighting, on the other hand $(1 - \sum_{j=1, j \neq i}^N P_{ij})$ expresses the probability that agent i encounters but doesn't start fighting.

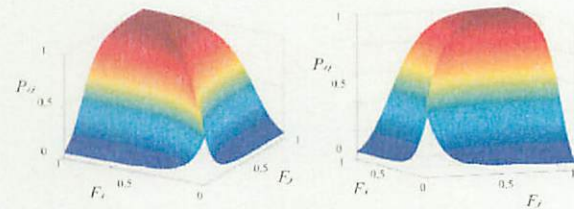


Figure 5: Coupling strength between cricket i and j .

x -axis is motivation of cricket i , and y -axis is that of cricket j . z -axis is coupling strength P_{ij}/ρ . $P_c = 0.125$. Recent study shows that loser starts fighting with other loser by about 60%. If loser encounters winner or unexperienced cricket, loser starts fighting by about 30%. If winner encounters other winner or unexperienced cricket, winner starts fighting by about 90%.

In computer simulation, we calculate with following algorithms per each step time.

1. Generating random number and arranging crickets i according to random number.
2. Calculating P_{ij} and choosing opponent j for crickets i . If two crickets choose the same opponent, cricket is preferentially selected by arranged order.
3. When some crickets start fighting, encounter rate is not affected but the probability to start fighting with them is fixed to zero in next step time.

4. Simulation

Crickets develop to be more aggressive under solitary condition than crowded condition. This feature is important for the gregarious system. So we construct computer simulation in order to observe this process.

Four crickets are living in the same cage over 14 days. The floor space of the cage is fixed and set to some initial value. Crickets interact each other with eq. eq:freq). 5-HT autoreceptors are observed at the 14th day, because fighting intensity is estimated by 5-HT autoreceptors.

Other conditions are as follows. In the eq. (5), we use eq. (23) as monotone decreasing function $g(R_{auto})$.

$$g(R_{auto}) = \left(1 - \frac{0.5}{1 + \exp(-5(R_{auto} - 0.5))}\right) \quad (23)$$

With one step time $\Delta t = 1.0 \times 10^{-3} [sec]$.

Table 1: Parameter conditions.

$\gamma_S = \gamma_A = \gamma_C = 5.0 \times 10^{-3}$	$\gamma_N = 3.0 \times 10^{-1}$
$\gamma_d = 7.2 \times 10^{-3}$	$r_0 = 0.7$
$\gamma_P = 5.0 \times 10^{-2}$	$r_1 = 0.04$
$\gamma_{r_0} = 1.0 \times 10^{-2}$	$N_j = 1.5\Delta t$
$\gamma_R = 2.8 \times 10^{-6}$	$N_o = 1.0\Delta t$

$r_2 = 0.75$	$N_{th} = 0.4$	$S_{th} = 0.01$
$D = 10$	$S_p = 0.2$	$A_{th} = 0.5$
$c = 5$	$\eta_R = 108.6$	$\eta_g = 50$
$a = 7.4 \times 10^{-3}$	$\eta_{pk} = 3$	$P_c = 0.125$
$b = 5.0 \times 10^{-7}$	$\epsilon_A = 4.0 \times 10^{-7}$	$\epsilon_S = 5.0 \times 10^{-3}$

$A_{-,i}$ represents cricket i 's octopamine consumption

$$A_{-,i} = d \times \left(\frac{1}{2} + F_j\right) \quad (24)$$

where, $d = 4.0 \times 10^{-5}$. In the right-side hand of eq. (24), second term F_j expresses the effects of intensity of opponent's attack.

Maximum intensity of aggressive behavior is proportional to the term $h(R_{auto})$ in eq. (25).

$$\begin{aligned} h(R_{auto}) &= \frac{(1 - r_0)r_2g(R_{auto})S_+}{(\gamma_S + \gamma_d r_2 g(R_{auto})r_0 R_{auto})} \times R_{post} \\ &= \frac{(1 - r_0)r_2g(R_{auto})S_+ - r_0 R_{auto}}{(\gamma_S + \gamma_d r_2 g(R_{auto})r_0 R_{auto})} \frac{1}{1 - r_0} \\ &= \kappa \frac{C_0 R_{auto} g(R_{auto})}{1 + C_0 R_{auto} g(R_{auto})} \end{aligned} \quad (25)$$

Equation (25) expresses maximum excitatory modulation of aggressiveness derived from eq. (1). Using eq. (23), aggressive intensity is described as Fig. 6.

5. Results

Decreasing the floor space of the cage is proper for increasing population density. Figure 7 shows time

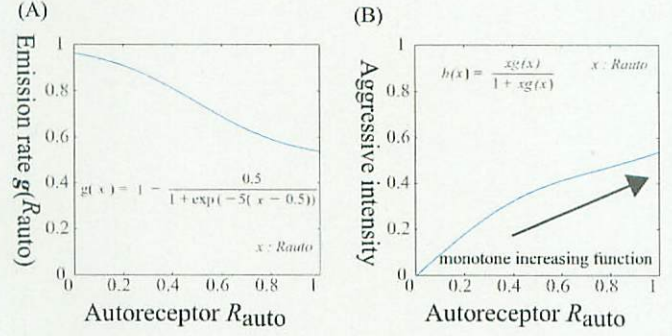


Figure 6: Emission rate and aggressive intensity.

(A) Emission rate decreases when autoreceptor increases. (B) Aggressive intensity monotonously decreases when autoreceptor decreases.

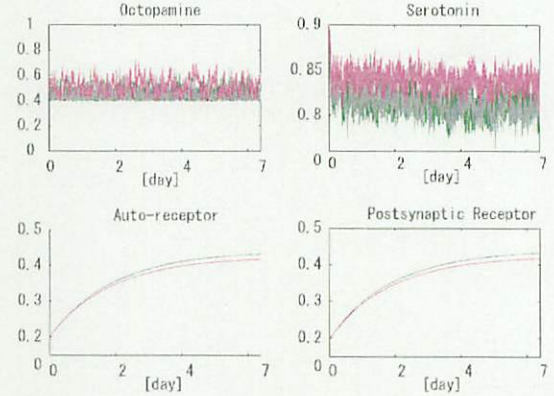


Figure 7: Time evolution of each substances under the condition of $\rho = 5 \times 10^{-4}$.

4 crickets develops under the condition of $\rho = 5 \times 10^{-4}$. Making difference between crickets which is greater than forgetting effect per unit of time causes bifurcation.

evolution of four crickets under the condition of $\rho = 5.0 \times 10^{-4}$. Parameters develops differential each other.

And figure8 shows the sensitivity of 5-HT autoreceptor at the 14th day under some density conditions. There shows 4 lines which corresponds to each crickets' sensitivity. In the simulation result, the multistep bifurcation is observed. Bifurcation of sensitivity reflects existence of dominance hierarchy. In addition, autoreceptor decreases with increasing density. This result represents that cricket decreases its aggressiveness as explained in Fig. 6.

6. Discussion

It is known that cricket has multilevel memory system which is called short-term memory, middle-term memory and long-term memory. Short-term memory

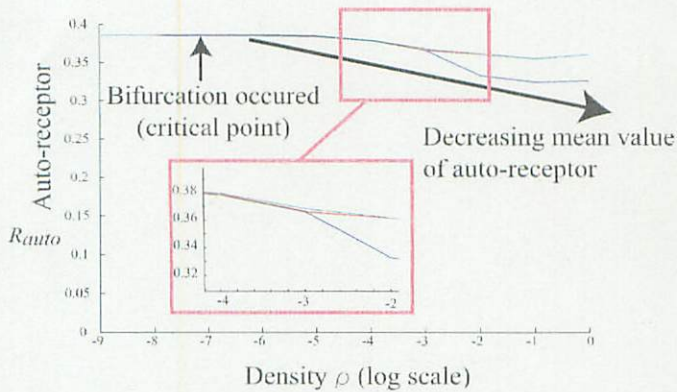


Figure 8: Density effects upon 5-HT receptors.

Bifurcating at the critical density. Internal state bifurcates in several batches, it has root in multiple layer of time constant relating to internal dynamics.

is controlled by neurotransmitter and last few minutes. Middle-term memory is controlled by second messenger or protein phosphorylation and last from a few minutes to several hours. Long-term memory is controlled by protein expression or mRNA transcript and last from several hours to several days. Figure 8 reflects these memories. Around the range that population density is very low and crickets have an opportunity to interact each other once-in-a-week, autoreceptor remains static. On the other hand, autoreceptor starts changing over the critical population density and there comes up gap between four crickets' receptors. At the high population density, gap between crickets' receptor is clearly confirmed. In future experimental verification, these three patterns would be observed in receptor distribution. If any test doesn't coincide this result, it is expected to make new findings.

Observed transition at critical density is one of the way to know global state for local agents. If agents doesn't change its exclusive behavior, group member spreads and returns to solitary phase. It is suggested that crickets, locusts or any other animals change its exclusive behavior to gregarious one under high density, and gregarious behavior maintains society stable. While there exists enough resources, locust behaves exclusively. This exclusiveness would be selfish strategy to maximize foraging efficiency for each agents. When heavy infestations of locusts have occurred, they switch from exclusive behavior to gregarious behavior. This gregariousness would reduce costs of energy consumption by aggressive behavior and maximize group's foraging efficiency.

This behavior switching can be applied to design distributed autonomous system. For example, spatial formation of distributed autonomous agents is expected to be stability controlled by behavior switch with usage of this critical phenomena. Of course, when we apply this

behavior switching upon autonomous system, we must consider the switching from the gregarious state to the solitary state. In this system, gregarious agents don't come back to solitary behavior if population density decrease slightly. So fish let out such gregarious behavior by the special signal that spreads throughout all agents, which is first light of dawn. Using the similar mechanism as fish, distributed autonomous system agents can assemble and fan out freely.

7. Conclusion

At first, we constructed mathematical model of internal cascade which modulates cricket's fighting behavior. Then we analyzed this model and clarified that decreasing sensitivity of autoreceptor causes decreasing fighting intensity. Next, we simulated the group behavior with several field and showed that the mean value of receptor sensitivity decreases with increasing density. Thus we showed fighting-intensity decreasing over the critical point in cricket. At last, importance of this decreasing is discussed in transition from aggressive mass to aggregative mass. Finally we also suggested the way of using this behavior-modulation for the distributed autonomous system.

8. Acknowledgements

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