

Chapter 13

Fighting Behavior: Understanding the Mechanisms of Group-Size-Dependent Aggression

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Abstract Aggressive behavior is a common behavior in animals. In most cases, an animal's behavior toward an opponent is a violent attack. Male crickets (*Gryllus bimaculatus*) exhibit intensively aggressive behavior toward other males, most often culminating in fighting. The detection of conspecific male cuticular substances initiates aggressive behavior in male crickets. After a fight, a loser no longer exhibits aggressiveness in a second bout or in separate encounters with another male; rather the defeated male exhibits avoidance behavior.

Aggressive behavior in crickets provides an excellent model system to understand neuronal mechanisms underlying real-time control of sophisticated behavior and social adaptability of animals. Animals alter their behavior in order to respond to the demands of changing social environments. Society and crowding conditions are dynamic environments. In this chapter, we focus on how crickets determine their behavior depending on their social interactions, focusing on behavioral and physiological aspects. Whether the nitric oxide (NO) system and octopaminergic (OAergic) system in the central nervous system of crickets could mediate aggressive behavior of the crickets is discussed. Based on these results, a neurophysiological model is designed to elucidate the mechanisms of social adaptability. This model demonstrates that a multiple feedback structure, composed of a feedback loop in the nervous systems and individual interactions with other crickets, may be a key to aggression influenced by group size (group-size-dependent aggressive behavior).

Keywords Aggressive behavior • Loser's effect • Internal state • Neuromodulator • Brain • Nitric oxide • Biogenic amine

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13.1 Aggressive Behavior of Male Crickets

It is common in animals that a dominant–subordinate hierarchy is established after agonistic aggressive behavior. Agonistic behavior is the result of complex interactions among physiological, motivational, and behavioral systems. Since social and physical environments are two of the most important factors that release aggressive behavior in animals, it is difficult to fully understand aggressive behavior. The cricket provides us one of the greatest model systems to investigate neuronal mechanisms underlying aggressive behavior. In particular, the subordinate cricket (loser of a fight) helps us to understand how aggressive motivation changes depending on social status.

Male crickets exhibit intensive aggressive behavior when they encounter another male, whereas they show courtship behavior to a conspecific female (Alexander 1961). A battle starts out slowly and escalates into a fierce struggle (Fig. 13.1). In crickets, sex discrimination by male individuals is based on cuticular chemical substances on the body surface. In *Gryllus bimaculatus*, studies have shown that the components of the cuticular hydrocarbons are clearly different between males and females (Tregenza and Wedell 1997; Nagamoto et al. 2005). The fact that an isolated female antenna elicits courtship behavior in conspecific males while isolated male antenna elicits aggressive behavior suggests that males detect distinct chemical signals from other crickets. However, both the identity of the signals and

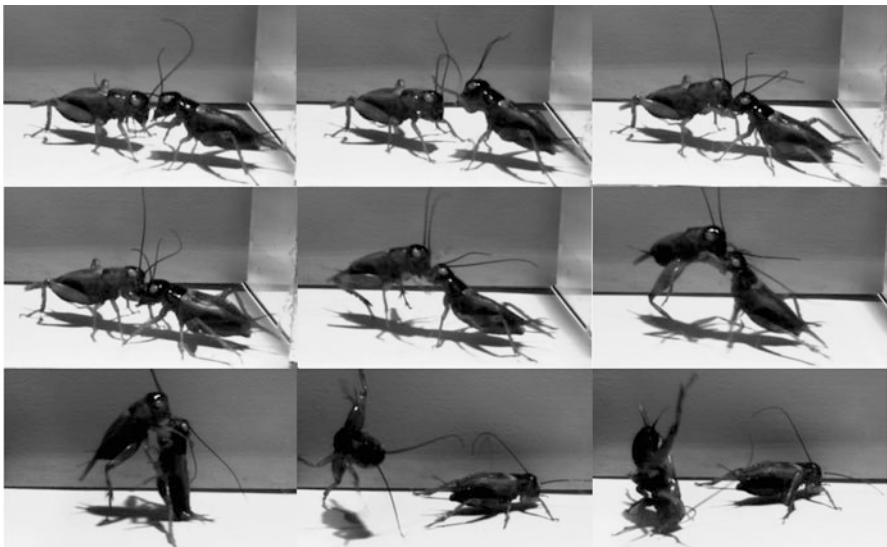


Fig. 13.1 Cricket fights. Fighting between male crickets escalates until an opponent gives up attacking and escapes by moving away. Male crickets start antennal fencing when they perceive cuticular substances through antennal contact. Mandible spreading follows

sensory pathways by which chemical signals alter aggressive and reproductive behaviors have not yet been completely elucidated.

Aggressive behavior of male crickets toward conspecific males has been extensively studied (Alexander 1961; Adamo and Hoy 1995; Hofmann and Stevenson 2000; Stevenson et al. 2005). Males battle with each other over the acquisition of living spaces and mating partners (Simmons 1986). A fight consists of a sequentially escalating series of behaviors beginning with antennal fencing, which leads to the spreading and finally the engaging of the mandibles. The fight continues until one of the crickets gives up attacking his opponent. Then pairs establish a dominant–subordinate hierarchy, with the winner initiating aggressive song and chasing after the loser. The loser, in subsequent encounters with the winner, exhibits avoidance behavior to avoid additional fights (Adamo and Hoy 1995; Hofmann and Stevenson 2000; Funato et al. 2011). This suggests that cuticular substances may be a kind of pheromone that triggers a particular behavior in the cricket. Most pheromone-induced behaviors in insects have been thought to be hardwired: a behavior that could be turned on and off but that lacks plasticity. However, fighting behavior in the cricket is modified by their previous experiences. For example, while cuticular pheromones induce dominant crickets to be aggressive, subordinate crickets respond to cuticular pheromones with avoidance instead of aggression (Sakura and Aonuma 2013). The period in which the subordinate cricket is unwilling to fight continues for more than several hours (Hofmann and Stevenson 2000). Recent experiences such as copulation, flight, the opponent's size and behavior, and population density can also alter aggressive behavior of males (Alexander 1961; Hofmann and Stevenson 2000; Rillich et al. 2007; Funato et al. 2011). Thus, whether males decide to engage in aggressive behaviors with each other may depend on their ability to compare their own motivation to fight with their perception of a potential opponent's fighting performance (Hack 1997; Rillich et al. 2007).

13.2 Antennal Inputs Initiating Aggressive Behavior

13.2.1 *Defensive Aggression*

Chemical and tactile information from antennae are important for male crickets to express proper aggressive behavior, identifying conspecific males and initiating an attack. However, antennal information is not always necessary to elicit defensive aggression (Sakura and Aonuma 2013). Antennal sensory information that consists of chemical and tactile sensory information is important for crickets when seeking food and mating partners, as well as when detecting threats. Males recognize a conspecific's sex using sensory information from antennae. Both chemical and tactile cues from antennae are integrated in the brain to decide

whether to act either in an aggressive or courtship manner. Antennectomized males, for example, express less aggression toward antennectomized opponents, whereas they continue to exhibit typical fighting to an intact opponent. In addition, antennectomized losers showed significantly higher aggressiveness toward the opponent than intact losers do in a second bout. These suggest to us that defensive aggression could be elicited without antennal information. Antennectomized crickets need not use visual or palpal sensory input to elicit defensive aggression. In contrast, intact males showed aspects of aggressive behavior to male cuticular substances before and after winning a fight; however, if these males lost a fight, they showed avoidance behavior. Visual inputs play an important role, since blinded males exhibit more intense fighting than sighted males. Visual information concerning body size, weight, and mandible display behavior of the opponent can suppress aggressiveness (Rillich et al. 2007). Male crickets make decisions whether to fight or flee from a potential opponent based on information from multiple sensory modalities.

13.2.2 Neuronal Pathways Processing Antennal Information

Antennae convey both tactile and chemical sensory inputs to the central nervous system, and components of male aggressive behavior can be elicited by chemical signals released from body parts of another male, such as the forewing and antennae (Nagamoto et al. 2005). On the other hand, male crickets exhibit only weak aggressive behavior toward anesthetized males (Adamo and Hoy 1995), suggesting that chemical signals alone are not sufficient for males to initiate proper aggressive behavior. Thus, multiple sensory cues (i.e., visual, olfactory, and tactile) from a conspecific should be required to elicit intensive aggressive behavior.

Chemical sensory afferents terminate in the antennal lobe, whereas most of exteroceptive mechanosensory afferents terminate in the dorsal lobe of the brain (Homberg et al. 1989). In crickets, seven antennal sensory tracts (assigned as T1-7) were identified (Yoritsune and Aonuma 2012). Tracts T1-T4 project into the antennal lobe, while tracts T5 and T6 course into the dorsal region of the deutocerebrum or the subesophageal ganglion, and finally tract T7 terminates in the ventral area of flagellar afferents. The antennal lobe of the cricket is composed of 49 sexually isomorphic glomeruli (Fig. 13.2). In the protocerebrum ten tracts originate in the antennal lobe, and at least eight tracts arise from the ventral area where flagellar afferents terminate. Projection neurons originating from the antennal lobe terminate in the anterior calyx of the mushroom body and/or the lateral horn, which are secondary centers of chemical processing. The projection neurons originating from the antennal lobe projecting through the inner antenno-cerebral tract terminate in the anterior calyx of the mushroom body. In contrast, the projection neurons originating from the antennal lobe that project through

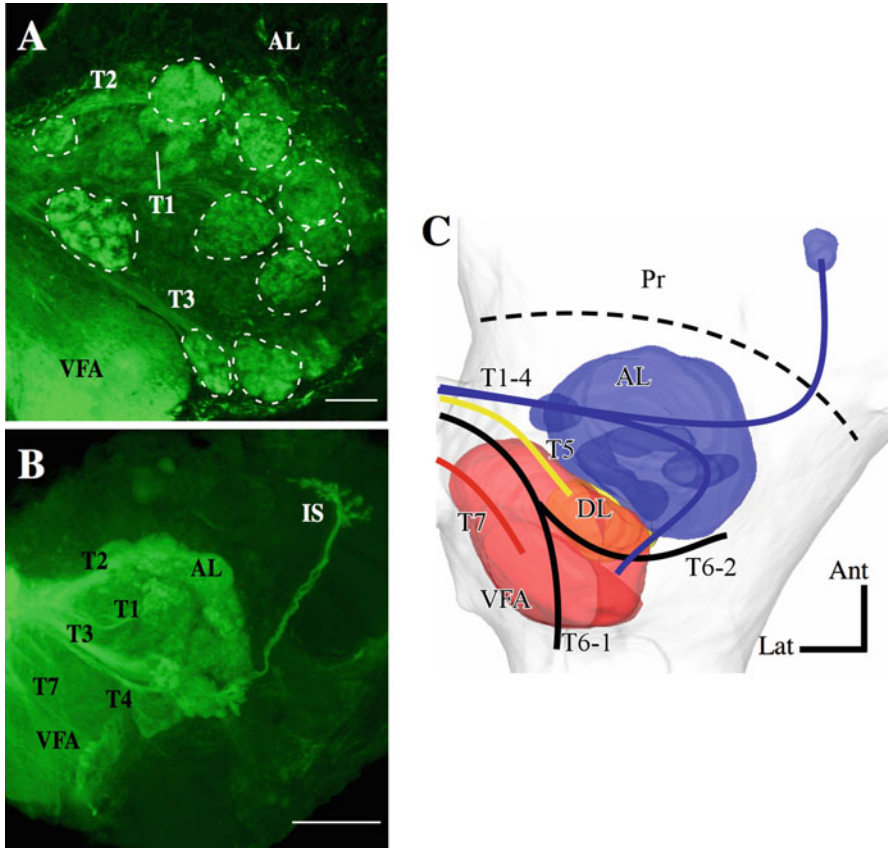


Fig. 13.2 Projection of antennal nerve terminations in the brain. (a) Stacked images of the antennal lobe obtained from optical sections made with a confocal scanning laser microscope. Areas surrounded by *dashed lines* indicate glomeruli where antennal sensory afferents terminate. Scale bar = 40 μm . (b) A ventral view of the antennal lobe. Scale bar = 100 μm . (c) Summary of the projection of antennal sensory afferents. *Dashed lines* indicate the boundary between the deutocerebrum and protocerebrum (Pr). AL antennal lobe, Ant anterior, IS isthmus, Lat lateral, Pr protocerebrum, T1–T7 tact 1–7, VFA ventral area of flagellar afferents

other antenno-cerebral tracts or accessory antenno-cerebral tracts do not terminate in the anterior calyx of the mushroom body. The neurons projecting through the inner antenno-cerebral tract make direct inputs onto Kenyon cells in the anterior calyx of the mushroom body. Therefore, both in the primary centers of the deutocerebrum and in higher centers of the protocerebrum, chemical and mechanical information should be represented in spatially segregated neuropils. It is not yet clear which center of information processing elicits aggression. Further investigation of the molecular and physiological basis of aggressive behavior is needed.

13.3 Group-Size-Dependent Aggressiveness in Male Crickets

Population density strongly influences cricket behavior including aggressive behavior (Funato et al. 2011). In order to investigate how local population density regulates male aggressiveness in a group, the size of a group can be varied (Fig. 13.3). In a group, pairs of male crickets fight locally to establish a dominant–subordinate relationship. Once this relationship is established, victorious males (dominant) retain their aggressiveness, but defeated males (subordinate) exhibit reduced aggressiveness. If victorious males encounter other victorious males, they fight again to establish dominant–subordinate relationships. However, when defeated males encounter the same victorious males within a short period, they exhibit avoidance behavior and retreat from their opponents. Defeated males also show avoidance if they encounter males victorious in other fights, naive males, or even males defeated in other fights. After repeated fights, a repeatedly defeated male loses his aggressiveness. In due course, one or more males are established as the dominant individual(s) in the group. Depending on the number of individuals in a group, the loss of individual aggressiveness limits the number of fighting crickets at any given time. Thus, overall aggressive behavior in a group is changed as a consequence of group size, but is ultimately determined by individual fights. Higher population density increases the probability that individuals might encounter others and start fighting. Subordinates mainly exhibit avoidance behavior when they encounter other males in a high population group. On the other hand, the highest-ranked males could maintain the motivation to be aggressive more than other males,

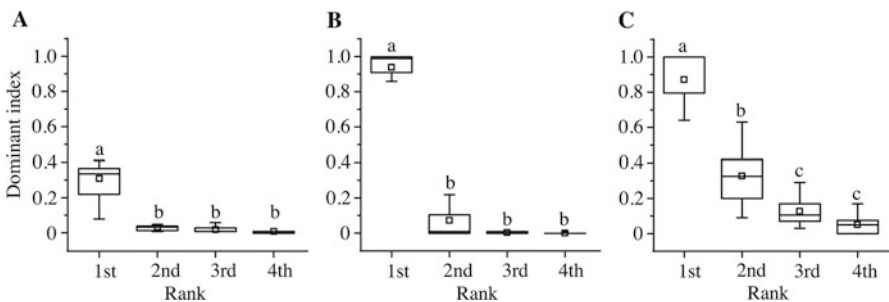


Fig. 13.3 Population density-dependent aggressiveness in cricket. The aggressiveness is evaluated by using a dominance index. The dominance index, X_i , is defined as $X_i = \frac{D_i}{D_i + S_i + N_i}$ ($i = 1, 2, 3, \dots, \text{num}$), where i is the social rank of the cricket. The total number of crickets is Num , and D_i indicates the total number of dominance behaviors performed by cricket i . S_i indicates the total number of subordinate behaviors performed by cricket i , and N_i indicates the number of nonresponsive behaviors when cricket i encounters another male. (a) Four male crickets are placed in a 75 cm² arena ($N = 12$). (b) Four male crickets are placed in a 300 cm² arena ($N = 12$). (c) Four male crickets are placed in a 1200 cm² arena. (Different letters denote significant differences between treatments, $*P < 0.05$, two-tailed Kruskal-Wallis ANOVA with Bonferroni-type multiple nonparametric comparison) (Modified from Funato et al. 2011)

but they suppress aggressiveness in high population density conditions. Therefore, all crickets in high population density group behave with lower aggression.

A decrease in local population density decreases the chance of individuals interacting. The dominant cricket always shows aggressive behavior if it encounters other crickets in a lower population density environment. In contrast, all subordinate crickets show avoidance behavior when they encounter other males, even if that male is also a subordinate. Dominant males establish a despotic hierarchy within a group. This relationship likely depends on local population density. As the local population density decreases, an increasing number of dominant crickets that show aggression will appear in the group.

13.4 Brain Neuromodulators Regulating Cricket Aggression

The male cuticular substances function as releaser pheromones in male crickets. However, the chemicals do not always initiate aggressive behavior. The aggressive motivation is regulated by the previous aggressive interaction. How do subordinate crickets switch to avoidance behavior toward cuticular substances? One of the likeliest possibilities is neuromodulation within the brain.

13.4.1 Role of Nitric Oxide in Aggressive Behavior

NO is thought to function as a neuromodulator in insect nervous systems. Endogenous nitric oxide (NO) is a free radical signaling molecule that diffuses across cell membranes in the nervous system of a wide variety of animals, both vertebrate and invertebrate. It is generated from L-arginine by NO synthase (NOS) (Moncada et al. 1991) and activates the heme-containing enzyme soluble guanylate cyclase (SGC) to generate the second messenger cyclic guanosine monophosphate (cGMP) in target cells (Bredt and Snyder 1989). This results in activation of cGMP-activated protein kinase (PKG) that phosphorylates downstream target proteins and evokes a cellular response (Bicker 2001). Cyclic nucleotide-gated channels (Kaupp and Seifert 2002) and cyclic nucleotide phosphodiesterase (Bender and Beavo 2006) are also major targets of cGMP. Furthermore, evidence for cGMP-independent NO signaling has also been found. NO can act directly, without producing cGMP, on ion channels through S-nitrosylation, which regulates the electrical activity of the target cells (Ahern et al. 2002; Wilson et al. 2007). S-Nitrosylation is thought to require a higher concentration of NO than does activation of soluble guanylate cyclase and tends to proceed with slower kinetics than cGMP-mediated actions.

NO is continuously released at a basal level in the cricket nervous system, and cholinergic activation accelerates NO generation (Aonuma et al. 2008). Therefore, relative changes in the concentration of NO likely mediate physiological properties

of local circuits in nervous systems. Experimental manipulations of NO signaling and histochemical experiments suggest that NO works as a multifunctional mediator in the nervous systems of invertebrate animals. In mollusks, NO modulates the synaptic efficacy of cholinergic synapses (Mothet et al. 1996) and mediates oscillatory neuronal activities underlying chemical information processing in the central nervous system (Gelperin 1994). In crustaceans, components of the NO/cGMP signaling pathway contribute to neuronal network functions that underlie escape behavior (Aonuma et al. 2000), mechanosensory processing (Aonuma and Newland 2001, 2002; Aonuma et al. 2008), and olfactory processing (Johansson and Mellon 1998). In insects, NO is believed to function as a crucial component in motor control (Qazi and Trimmer 1999), pheromone processing (Seki et al. 2005), olfactory processing (Wilson et al. 2007), and olfaction-related learning behavior (Müller 1997; Matsumoto et al. 2006).

The presence of NO/cGMP signaling has been demonstrated in the cricket brain (Aonuma and Niwa 2004). Pharmacological and behavioral experiments demonstrate that NO signaling mediates the motivation of aggressive behavior in the male cricket (Iwasaki et al. 2007). Inhibition of NO/cGMP signaling pathways using the NOS inhibitor L-NAME and SGC inhibitor ODQ restores the aggressiveness of subordinates. The aggressiveness of a cricket that is head injected with L-NAME or with ODQ shows normal aggression at the first engagement. However, the loser that is head injected with L-NAME or with ODQ shows significantly increased aggressiveness.

Interestingly, the behavior of subordinates whose antennae are removed is similar to the behavior of subordinates whose NO/cGMP signaling is inhibited (Sakura and Aonuma 2013). This suggests that NO/cGMP signaling in the antennal sensory processing pathway could participate in the neuronal mechanism underlying aggressive behavior. Indeed, there are putative NO donor and target neurons in the antennal lobe of the cricket (Aonuma et al. 2004).

13.4.2 Role of Brain Octopamine in Aggressive Behavior

Octopamine (OA) is another chemical that affects aggressive behavior in crickets. It has been demonstrated that the biogenic amine level in hemolymph mediates cricket aggression (Adamo et al. 1995). Brain OA titer of the defeated cricket decreases after fighting (Aonuma et al. 2009). In order to elucidate if OA regulates aggressiveness of male crickets, pharmacological experiments are necessary. Mianserin and epinastine are widely used as antagonists of OA in insects (Roeder 1990; Roeder et al. 1998). The octopaminergic (OAergic) system is involved in the motivation of aggressive behavior in cricket (Rillich et al. 2011). Brain OA has been demonstrated to increase aggressive motivation in ants as well (Aonuma and Watanabe 2012). In crickets, head injection of the OA antagonists mianserin decreases the aggressiveness of male crickets (Aonuma et al. 2009). In a sequential encounter, the mianserin-injected crickets show significantly lower aggressiveness

in the first encounter as compared to controls. In a second encounter, after a few hours, the mianserin-injected cricket still shows significantly lower aggressiveness. Therefore, OA antagonist slows recovery of aggressiveness in male crickets.

The depression of the subordinates' aggressiveness is alleviated by an NOS inhibitor, whereas an OA inhibitor prolongs the reduction of the subordinates' aggressiveness. The results of these pharmacological experiments suggest that the NOergic and OAergic systems have mutually opposite effects on initiating aggressive behavior in the cricket. In order to confirm if the effect of NO is countered by OA and vice versa, we co-injected a mixture of L-NAME and mianserin and found that L-NAME rescues the effects of mianserin (Aonuma et al. 2009). The NOergic and OAergic systems regulate experience-dependent aggressive behavior of male crickets. We thus hypothesize that NO/cGMP system mediates the OAergic system in the cricket brain.

13.4.3 Modeling of NOergic and OAergic Modulation During Aggressive Behavior

In order to understand the dynamic activities of the cricket brain, a neuromodulatory model based on pharmacological experiments has been proposed (Kawabata et al. 2007, 2012). The results of neuroanatomical, pharmacological, and behavioral experiments suggest to us the importance of NOergic and OAergic neuromodulation in the brain during aggressive behavior. However, there are still gaps between physiology and behavior. Modeling is a powerful approach that can bridge the gaps between them (see Chap. 20).

According to pharmacological experiments, changing the levels of NO and OA in the brain is suggested to modulate cricket aggressive behavior. Cuticular pheromones from male crickets trigger aggressive behavior in conspecific males. The NOergic system in the chemical information processing center of the brain (i.e., antennal lobe) must be involved in the initiation of aggressive behavior. Because NO is a gaseous molecule, it diffuses about 100–200 $\mu\text{m/s}$, and its lifetime is several seconds in duration (Philippides et al. 2000). A physiological model based on the dynamics of NO/cGMP signaling and OA can be considered. This model consists of a diffusion equation for NO, differential equations for cGMP and OA levels, and a threshold model for behavioral choice, which is based on OA levels (Fig. 13.4a). These components are connected in series. Given the hypothesis that brain OA levels can shift a cricket's behavior from attacking an opponent to avoiding an opponent, it is assumed that fighting behavior is selected when OA is above a given threshold. Likewise, avoidance behavior is selected when OA levels are below this threshold. Computer simulations of the model demonstrate that increased levels of cGMP, caused by the increase in brain NO level, lead to a decrease in OA levels (Kawabata et al. 2007). Since experiencing a defeat during fighting depresses the initiation of aggressive behavior for some time, it assumes that the OA levels in the winner's brain increases to a certain value. Concurrently, the OA level in the loser is

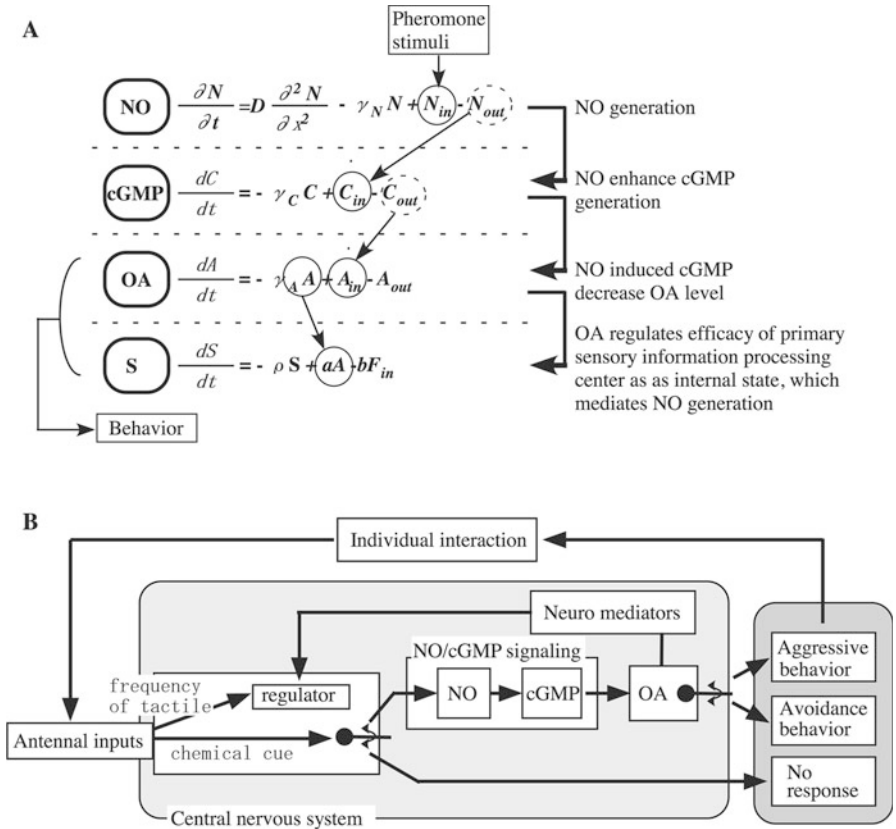


Fig. 13.4 Neuromodulatory model for cricket aggressive behavior. (a) Neuromodulation model consists of a reaction–diffusion equation of the dynamics of the gaseous molecule NO and differential equations for cGMP and OA levels. (b) Multi-feedback structure that regulates behavior changes in aggressive behavior in the cricket

reduced to a lower value and is in proportion to the length of the fighting period. On the other hand, cricket aggression plays out locally in a group, and the aggressiveness of each cricket changes depending on the group size (Funato et al. 2011).

Previous fight experience can influence a cricket’s decision to fight or flee. Furthermore, the brain OA level is modified by the density of the group (Iba et al. 1995). Thus the effect of individual interactions between crickets on the physiological changes in the brain should be considered along with the efficacy of sensory inputs from the antennae. Our hypothesis is that the OAergic system affects the mechanisms for processing sensory information. OA activates the processing of this information and individual interactions suppress this processing. In light of this, the physiological model describes behavior that is determined by two input sources, sensory inputs due to individual interactions between crickets and feedback due to the internal state of the brain (Kawabata et al. 2012). Sensory inputs received from

another individual might be modulated at the primary center for sensory information processing. Thus the model is designed to account for this effect by incorporating a value “S” for the efficacy of antennal inputs. The value “S” expresses the efficiency of processing of antennal sensory information and influences behavior selection. The influence of the internal state is likely due to factors related to the production and output quantity of OA in the cascade model. The efficacy (“S”), which is modulated by the internal state in the brain, as well as individual interactions between crickets could regulate the generation of NO. This would, in turn, influence fight-related decision-making. When the efficacy of sensory inputs is above a particular threshold, aggressive behavior occurs, in keeping with the NO/cGMP-OA model. When efficacy is low, the cricket continues wandering and gives no response to the tactile and chemical cues. The duration is designed to represent the temporary reduction in the efficacy of sensory input, which is caused by individual interactions. Here, the influences are assumed to be proportional to OA levels and stimuli from individual interactions between crickets. The results of computer simulations in multi-individual environments show that this model could be considered appropriate for swarm activities of the cricket. Thus we hypothesize that the main mechanism underlying behavioral adaptability is a multiple feedback structure that is composed of feedback loops in the nervous systems combined with input from the social environment (Fig. 13.4b).

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