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RESEARCH ARTICLE

A model for group-size-dependent behaviour decisions in insects using an oscillator network

Tetsuro Funato[1], Masahito Nara[2], Daisuke Kurabayashi[2], Masatoshi Ashikaga[3] and Hitoshi Aonuma[4],*

[1]Department of Mechanical Engineering and Science, Kyoto University, Yoshida-honmachi, Sakyo-ku, Kyoto 606-8501, Japan, [2]Department of Control and Mechanical Engineering, Tokyo Institute of Technology, 2-12-1 Ookayama, Meguro-ku, Tokyo 152-8552, Japan, [3]Department of Precision Engineering, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-8656, Japan and [4]Research Institute for Electronic Science, Hokkaido University, Kita 12, Nishi 6, Kita-ku, Sapporo 060-0812, Japan

*Author for correspondence (aon@es.hokudai.ac.jp)

SUMMARY

Aggressive behaviour within pairs of male crickets leads to the establishment of a dominance hierarchy. Defeated males avoid their victorious adversaries for several hours before regaining aggressiveness. However, the defeated male does not regain aggressiveness if repeated fighting occurs. Loss of individual aggressiveness is limited by group size, which constrains the number of crickets fighting at any given time. Thus, group aggressive behaviour is modulated by an environmental factor, group size, which is ultimately determined by individual actions, i.e. fighting between two individuals. We developed a robot model to elucidate the mechanism of group-size-dependent behaviour alternation in crickets. The behaviour of individual robots was evaluated experimentally with mobile robots and the group behaviour of the robots was evaluated by computer simulation. We demonstrated that the group-size-dependent strategy in crickets could be generated by local interactions between robots, where the behaviour was governed by an oscillator and memory of the outcome of previous fights.

Key words: oscillation, cricket, local interaction, social behaviour.

INTRODUCTION

Individuals or groups of individuals typically have to adapt to environmental change in order to survive. Environmentally determined behaviour, and the ability to adapt, is also of crucial importance in the future management of robots in unpredictable animal societies, including human societies. However, previous research into the application of biological functionality to group robotic behaviour has generally been constrained to action algorithms and few studies have considered brain functions as factors in their models. Gaining an understanding of how neuronal functioning controls insect behaviour at an individual level and leads to a change in group behaviour might provide interesting results that could be applied to robotics. This biomimetic approach, developed from the study of animal structures and functions, models the creation of materials or products by reverse engineering. Insect biological systems have provided abundant insights for a large range of biomimetic robots (Quinn and Ritzmann, 1998; Ritzmann et al., 2000). In this study, we focused on insect behaviour and mimicked how brain functions select behaviour. Our underlying assumption was that insects temporally arrange the global structure of neural networks to assist in the selection of the most effective behaviour in a given environment. This multi-scale model correlated environmental and brain effects.

We approached animal behaviour from two levels to elucidate the neuronal mechanisms underlying the environment-dependent behaviour: (1) modelling the neuronal mechanism underlying behaviour selection in the brain, and (2) identification of a functional component in the brain that responds to the global environment at the individual behavioural level. To correlate these two levels, a robot was developed that was controlled by our brain functional model. The robot movement generated an interaction between the social environment and the brain function model, allowing both levels to be studied simultaneously.

We focused on neuronal oscillations in the brain when constructing the brain function model. These oscillations are known to be evoked by sensory stimuli in both vertebrates and invertebrates (Adrian, 1942; Bressler and Freeman, 1980; Galambos et al., 1981; Gray and Singer, 1989; Eeckman and Freeman, 1990; Laurent and Naraghi, 1994; Stopfer et al., 1997; Kashiwadani et al., 1999; Neville and Haberly, 2003; Schadow et al., 2007; Tanaka et al., 2009), but their functional role is still disputed. Insect olfactory systems are a model system used to elucidate the functional role of neuronal oscillations. Neuronal oscillations evoked by odour are detectable as a local field potential in the brains of several insects, including locusts (Laurent and Naraghi, 1994; Stopfer et al., 1997), *Drosophila* (Tanaka et al., 2009) and moths (Ito et al., 2009). The synchrony between coupled oscillators is influenced by the network structure (Barahona and Pecora, 2002; Jadbabaie et al., 2004). This phenomenon can be interpreted as a temporal transformation of the neural network. Imitation of the oscillation as a component of the neuronal function of the brain makes it possible to construct an oscillator network where the output changes depending on the network transformation.

We modelled the fighting behaviour, or aggressiveness, of crickets. After aggressive encounters between two male crickets, one cricket becomes a winner and the other a loser. Conspecific

recognition in crickets is mediated by the perception of a chemical substance on the cuticle surface known as a cuticular pheromone (Tregenza and Wedell, 1997). Male cuticular pheromones elicit aggressive behaviour in male crickets, whereas female cuticular pheromones induce courtship behaviour in male crickets (Nagamoto et al., 2005). When male crickets encounter other males, battles begin slowly and escalate into a fierce contest (Alexander, 1961). When the battle is settled, the winner commences body jerking and produces an aggressive song. In contrast, the loser actively avoids the victorious cricket for a period of time (Adamo and Hoy, 1995; Aonuma et al., 2004). After more than 3h have elapsed, the loser may again engage in an aggressive bout with the victor, if they encounter each other. However, if the winner and loser fight repeatedly, the defeated male fails to regain aggressiveness and avoids all opponents. As a result, the number of crickets in a population engaging in repeated fighting is limited by cricket density. The proportion of aggressive individuals declines and the frequency of aggressive encounters decreases (Aonuma et al., 2007). Thus, the effect of repeated encounters is to alter group behaviour. The speed of the emergence of this group-level behaviour depends on both the density of the group (i.e. environment) and the local result of the fight (i.e. individual). Group-size-dependent aggression is known in many animals, including crayfish (Bovbjerg, 1953; Patullo et al., 2009) and domestic fowl (Pagel and Dawkins, 1997; Estevez et al., 2003). However, few studies have focused on the neuronal mechanisms underlying group-size-dependent behaviour.

This study aimed to elucidate the fundamental neuronal factors that are elicited during group-size-dependent behaviour in crickets. This behaviour should be mediated by an interaction between the brain and the environmental mobility of crickets, so we developed mobile robots with movements governed by a brain function model (an oscillator network). A particular focus of this study was to determine whether the behaviour of an individual cricket in a group is controlled solely by available environmental information, or whether crickets need to maintain a memory of previous social interactions. To better address this question, robots either possessed or did not possess an embedded memory of previous social interaction. This synthetic approach might provide advantages in understanding the brain function of animals.

MATERIALS AND METHODS
Animals
Adult crickets, *Gryllus bimaculatus* De Geer 1773, were reared in plastic cases (80×45×20cm) under a 14h:10h light:dark cycle at 28±1°C. Crickets were provided with a diet of insect food pellets (Oriental Yeast Co., Tokyo, Japan), chopped carrot and water *ad libitum*.

Behavioural experiments
This study used adult male crickets aged between 8 and 21days after the imaginal moult. Socially naive males were prepared for behavioural experiments by isolating individual crickets in 100ml glass beakers for 2days (D'Yakonova et al., 2002; Stevenson et al., 2005; Yano et al., 2009). The test animal masses were matched to ensure that body size differences did not affect the outcome of fights between two males. Population density is one of the major environmental factors that affect animal behaviours. In crickets, the motivation to be aggressive changes depending on the population density. Therefore, we used three different arena sizes to test social rank establishment, i.e. large (300×400mm), medium (150×200mm) and small (75×100mm), each with four socially naive crickets. The aggressive/dominance behaviours and

avoidance/subordinate behaviours were judged according to the criteria set by Alexander (Alexander, 1961). The behaviour of each cricket was observed for 15min before we evaluated the group behaviour using a dominance index. The dominance index, X_i, was defined as:

$$X_i = \frac{D_i}{D_i + S_i + N_i}(i = 1,2,3\ldots,N) , \qquad (1)$$

where i is the social rank of the cricket, N is the total number of crickets, D_i is the total number of dominance behaviours performed by cricket i, S_i is the total number of subordinate behaviours performed by cricket i and N_i is the number of non-responsive behaviours when cricket i encountered other males. Cricket behaviour was recorded using a Panasonic (Osaka, Japan) NV-GS500-S digital camcorder for later analysis. Data were analysed using a two-tailed Kruskal–Wallis test with a Bonferroni-type nonparametric multiple comparison. Differences were considered significant at $P<0.05$ (two-tailed). The mean value of each individual dominance index is expressed ±s.d.

Modelling of the behavioural selection mechanism
This study investigated the brain function required by crickets for the condition-dependent behavioural transition using a constructivist approach (building a robot and performing computer simulation). Because the environmental factor and individual (cricket) factor were involved in the objective cricket behaviour, the model (i.e. robot) could move and interact with the environment, under the control of algorithms characteristic of the cricket brain.

The aggressive behaviour of crickets is elicited by a chemical cue (Nagamoto et al., 2005). Chemical information is processed and integrated in the central nervous system. In some insects, neuronal oscillation is known to be an important neuronal event in chemosensory information processing (Laurent and Naraghi, 1994; Stopfer et al., 1997; Ito et al., 2009; Tanaka et al., 2009). Thus, chemical cues are a major information source used in insect decision-making. Neuronal oscillation might be involved in neuronal mechanisms that lead to the production of motor control signals.

We hypothesised that the following three main characteristics are crucial components of the agonistic behaviour process: (1) agonistic behaviour is linked to diffusive chemicals; (2) diffusive chemicals change the synaptic connection; and (3) the information governing the agonistic behavioural response is coded as an oscillation. Suppose the oscillators comprise an oscillator network; then the information (characteristic 3) can be controlled by changes in synaptic connections (characteristic 2). We previously proposed a strategy for controlling the synchrony of oscillations by the manipulation of the network connection (Funato et al., 2006; Funato and Kurabayashi, 2008). This method allowed the oscillator network to encode alternative states, such as the aggression and avoidance of crickets, by considering synchrony as behavioural states.

Fig. 1 shows the proposed model (model details are described in Appendices 1 and 2), where circles are oscillators and the control signal of the motor unit is determined by the synchrony of oscillations. New links between oscillators, determined by the level of 'capacitor' on the circuit, play a role in the switching of behaviour, which can change after a certain period of fighting. In this study, the new links mimic neuromodulation, which mediates behavioural change.

The robot was constructed and behaviour was validated before testing the conditions (robot mechanisms) that induce interaction-dependent behaviour.
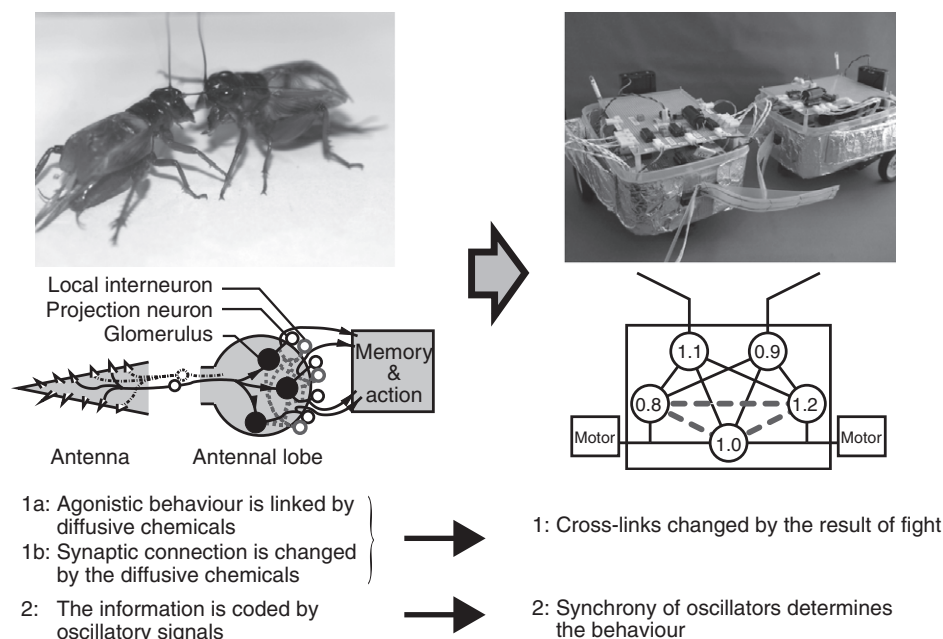
Fig. 1. Modelling cricket behaviour with robots. The robot model is composed of an oscillator network, which transfers the network structure to robot behaviour. Circles represent oscillators and lines represent connections between oscillators. The numbers in the circles represent an example of the eigenfrequencies of the oscillators. The numbers do not have meaning themselves, but the relative values among the neighbouring oscillators determine the synchrony. The robot has two states depending on the existence of cross-links (dashed lines). The activation of motors connected to the oscillators is changed by the synchrony of the oscillators, whilst the synchrony of the oscillators is modified by the cross-links. Thus, the cross-link connections change several minutes after the robot starts fighting, and change the robot behaviour.

Local interneuron
Projection neuron
Glomerulus
Memory & action
Antenna   Antennal lobe

1a: Agonistic behaviour is linked by diffusive chemicals
1b: Synaptic connection is changed by the diffusive chemicals

1: Cross-links changed by the result of fight

2: The information is coded by oscillatory signals

2: Synchrony of oscillators determines the behaviour

Identification of brain functions involved in social-interaction-dependent behaviour

The purpose of the simple brain function model and robot was to elucidate the main factors governing environmentally dependent behaviours, in particular identifying correlations between brain mechanism and behaviour. We then tested whether the simple robot could induce variations in the number of winning crickets, depending on group density. We developed a computer model of a robot whose action algorithm corresponded to the action of a robot considering how each mechanical and electrical mechanism, such as the antenna and oscillators, contributed to the formation of the action of the robot and how these mechanism should be reflected in the action algorithm. This model is hereafter referred to as an 'agent', and we performed a computer simulation of a group of agents.

Four agents, whose shapes and sizes are shown in Fig. 2A, were placed in a two-dimensional square field matching the area used in the real cricket experiments (large, $1200\,cm^2$; medium, $300\,cm^2$; small, $75\,cm^2$). The simulated behaviour of agents was observed and the number of continuously fighting agents was recorded. Each agent moved using the rules described for the oscillator network robot; i.e. during agent encounters, each agent either fought or avoided fighting and a change in behaviour occurred if the charge level of a 'capacitor' exceeded 70%.

We focused on the effects of defeat as a key element for eliciting social behaviour. To simulate the memory of defeat, we provided a mechanism to accelerate the charge speed and reduce the discharge speed after an agent selected the avoidance behaviour, as shown in Fig. 2B. Fig. 2B shows that the recovery time was postponed by this operation.

The behaviour of agent groups equipped with a memory of defeat experience was compared with the behaviour of those whose actions were not affected by memories of past fights. This allowed us to test the effect of defeat memory on emergent social behaviour. The simulation was performed for four agents in order to compare their behaviour with that of real crickets; in order to elucidate the effect of field size on the number of winners in detail, simulation was also performed using 10 agents in 100 to 1600 cm^2 arenas.

RESULTS

Crickets change their behaviour depending on population density. To understand the neuronal mechanisms of decision-making underlying social interactions, we built simple robots that moved and interacted with other robots using the proposed mechanism governed by an analogue circuit. Group behaviour of the crickets was then simulated using a computer simulation of agents whose action algorithms corresponded to the action of robots in order to identify the mechanism required for the adaptive behaviour. The effect of memories of previous fighting experience on decision-making determines the interaction between robots (and also determines the interaction between simulated agents), so the behaviour of agents with and without memory was compared.

Behaviour of crickets under different population density conditions

The size of the experiment arena was varied to determine how local population density regulates male aggressiveness in cricket groups. Pairs of male crickets fought locally to establish a dominant–subordinate relationship. Once this relationship was established, victorious males (dominants) retained their aggressiveness but defeated males (subordinates) exhibited reduced aggressiveness. When victorious males encountered other victorious males, they fought to establish dominant–subordinate relationship. However, when defeated males encountered the same victorious males within a short period, they exhibited avoidance behaviour and retreated from the opponents. Defeated males also showed avoidance behaviour if they encountered males victorious in other fights, naive males or even males defeated in other fights. After repeated fights, a repeatedly defeated male lost its aggressiveness. In due course, one or more males were established as the dominant individual(s) in the group. Depending on the group density, the loss of individual aggressiveness limited the number of fighting crickets at any given time. Thus, overall aggressive behaviour in a group was changed as a consequence of group size, but was ultimately determined by individual fights (Fig. 3).

High population density increases the probability that individuals might encounter others and start fighting. High-density conditions
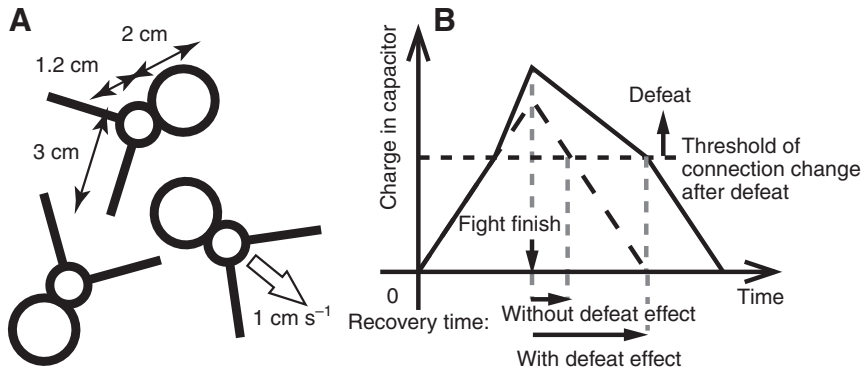
Fig. 2. Definition of the agents used in the simulation. Each agent was equipped with the same mechanism as the proposed robot model (Fig. 1). The agent had two states that alternated a specific period after fighting. The agent was composed of two antennae, a head and a body (A). Agents moved around with a fixed speed in three sizes of two-dimensional fields: 75, 300 and 1200 cm^2. We investigated the effects of a memory of defeats in fights. (B) The mechanism for modelling the memory of defeat. The charge speed of the capacitor equipped on the robot changed after defeat in a fight. This mechanism was implemented by varying the resistance in the real circuit of the robot.

were mimicked by placing four male crickets in a small arena (75×100 mm), as shown in Fig. 3A. Crickets were placed gently in the arena (separated from each other) and kept isolated in a separate room for 15 min to allow them to acclimatise to their new environment; the separator was then removed for the observation of the agonistic behaviour. Crickets typically wandered freely in the arena and encountered another male before commencing intensive fighting to establish the dominant–subordinate relationship. The victorious male vanquished all other males in a group. However, on some occasions, the victorious male lost aggressiveness within a few minutes and failed to attack other males in the group. If this occurred, the behaviour of all males became calm and settled. The dominance index of the highest-ranked cricket (the victorious cricket) was significantly higher than that of the lower-ranking crickets (P<0.05). However, the dominance index of the highest-ranked crickets was quite low, at only 0.31±0.14. This was because the victorious males exhibited aggressive behaviour at the start of the test but later exhibited avoidance behaviour, or no response, when they encountered other males. This indicates that victorious males suppressed their aggressiveness in higher population density conditions. The dominance index of other crickets was almost zero, i.e. the index of the second-, third- and fourth-highest ranked was 0.04±0.03, 0.02±0.02 and 0.01±0.02, respectively. This shows that subordinates mainly exhibited avoidance behaviour when they encountered other males. This suggests that the highest-ranked males could maintain the motivation to be aggressive more than other males, but that they suppressed aggressiveness in high population density conditions.

A decrease in local population density decreased the chance of individuals interacting. Local population density was decreased by placing four males in the medium arena (150×200 mm). In this arena, only one cricket maintained aggression during the behavioural test (Fig. 3B). Soon after the walls separating each cricket were removed, all crickets began fighting. Fights were settled within a few minutes and a single male became dominant. The dominant cricket always showed aggressive behaviour if it encountered other crickets in the medium arena. In contrast, all subordinate crickets showed avoidance behaviour when they encountered other males, even if it was a subordinate. The dominance index of the highest-ranked crickets was 0.94±0.1, which was significantly higher than the other ranked crickets (P<0.05). The dominance index of the second-highest-ranked cricket was 0.07±0.14, whereas that of the third- and fourth-highest-ranked crickets was zero. This indicates that dominant males established a despotic hierarchy within a group. This relationship might depend on local population density. In the next behavioural test, we further decreased local population density to examine whether the despotic relationship was maintained.

Group aggression in lower population density conditions was tested by placing four male crickets gently into a large arena (300×400 mm). As soon as the behaviour test began, all the crickets started wandering around the arena, but the probability of encountering other males was lowest in the large arena. Fights occurred if males encountered other males in the arena. One or two dominant crickets showed aggressive behaviour. The dominance index indicated that more than two crickets maintained
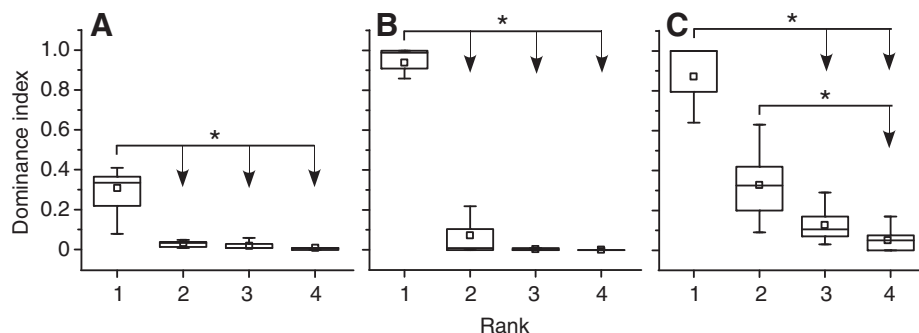

Fig. 3. Population density-dependent cricket behaviour. (A) Four male crickets were placed in a 75 cm^2 arena (N=12 groups tested). The dominance index of the highest-ranked cricket was 0.31±0.14, the second was 0.04±0.03, the third was 0.02±0.02, and the fourth was 0.01±0.02. (B) Four male crickets were placed in a 300 cm^2 arena (N=12). The dominance index of the highest-ranked cricket was 0.94±0.1, the second was 0.07±0.14, and the third and fourth were both zero. (C) Four male crickets were placed in a 1200 cm^2 arena (N=12). The dominance index of the highest-ranked cricket was 0.87±0.23, the second was 0.33±0.17, the third was 0.13±0.08, and the fourth was 0.05±0.05. *P<0.05, two-tailed Kruskal–Wallis ANOVA with Bonferroni-type multiple nonparametric comparison.

aggressiveness in the group. The dominance index of the highest-ranked crickets, 0.87±0.23, was significantly higher ($P<0.05$) than that of the third- (0.13±0.08) and fourth-highest-ranked crickets (0.05±0.05). However, the dominance index of the second-highest-ranked crickets, 0.33±0.17, was significantly higher ($P<0.05$) than the fourth-highest-ranked crickets. The second-highest-ranked crickets sometimes showed aggressive behaviour. In contrast, the third- and fourth-highest-ranked crickets mainly showed avoidance behaviour after the first or second contact with dominant crickets.

Behaviour of robots and simulation model of crickets

Robot model of behaviour switching using an oscillator network

The behaviour of the robot is shown in Fig. 4B. If there were no cross-links (dotted line in Fig. 1), the robot changed its direction and headed towards the obstacle (0–10 s, Fig. 4). This behaviour corresponded to the cricket behaviour of heading towards another cricket, which was regarded as aggressive behaviour. If cross-links were present (the neural network was transformed after a fight), the robot headed away from the obstacle (15–25 s, Fig. 4). Thus, the robot behaved in a submissive manner as a consequence of the structural change in the network. This indicates that we successfully achieved a change in robot behaviour as a consequence of network structure. The delay circuit alternated the connection after a certain period of fighting (Fig. 1B), so the robot initially exhibited aggressive behaviour by heading towards the obstacle, but then avoided the obstacle, as shown in Fig. 4B. Thus, the robot model simulated the individual interaction of crickets when the first contact with another cricket induced fighting, followed by avoidance behaviour with network transformation after a certain period.

Behavioural transitions in simulated agents with variable group density

Tests of group behaviour using four agents on the computer that possess the proposed mechanism implemented in the robots investigated the group behaviour of crickets, i.e. whether the number of aggressive crickets (or agents, in this case) changed depending on the arena size. Performance of the two agent groups was tested using simulation to compare group level behaviour.

Results indicate that the recovery time of one group was not affected by the outcome of the fight (without memory), whereas the recovery time of the other group was postponed in the defeated agent (with memory).

Without memory

No specific agent appeared dominant in the simulation and the aggressiveness of every agent was uniformly suppressed by reducing the field size. Fig. 5A–C shows the results of five trials in the same field with different initial conditions.

With memory

Fig. 5D–F shows the apparent effect of rank of agent on the decrease in aggressive time with a decrease in field size. Only the highest-ranking agent fought for most of the simulation period, whereas the other agents continuously avoided the highest-ranked agent (Fig. 5E). Results are from five trials with different initial conditions and the highest-ranked agent was alternated in each trial. With the large field (equivalent to the large arena), every agent fought continuously for most of the simulation time (Fig. 5F), whereas with the small field the agents stopped fighting (Fig. 5D). This differentiation among agents that possessed a memory of defeats was similar to that observed in real groups of crickets.

DISCUSSION

Integrating a constructivist approach into the results of behavioural experiments and observations can accelerate the understanding of biological systems. Crickets are good biomimetic models for extending our knowledge of aggressive behaviour because they change their aggressiveness depending on previous social interactions. We simulated aggressive–avoidance behaviour selection mechanisms in crickets to understand adaptive behaviours of animals in a changing environment. Our research proceeded according to three steps:

1. Experimental observation of cricket behaviour. Crickets changed their aggressiveness depending on their group size. In high-density populations, cricket aggressiveness was decreased and they avoided fights. In contrast, at a low population density, more than one cricket increased and maintained its aggressiveness in a group.
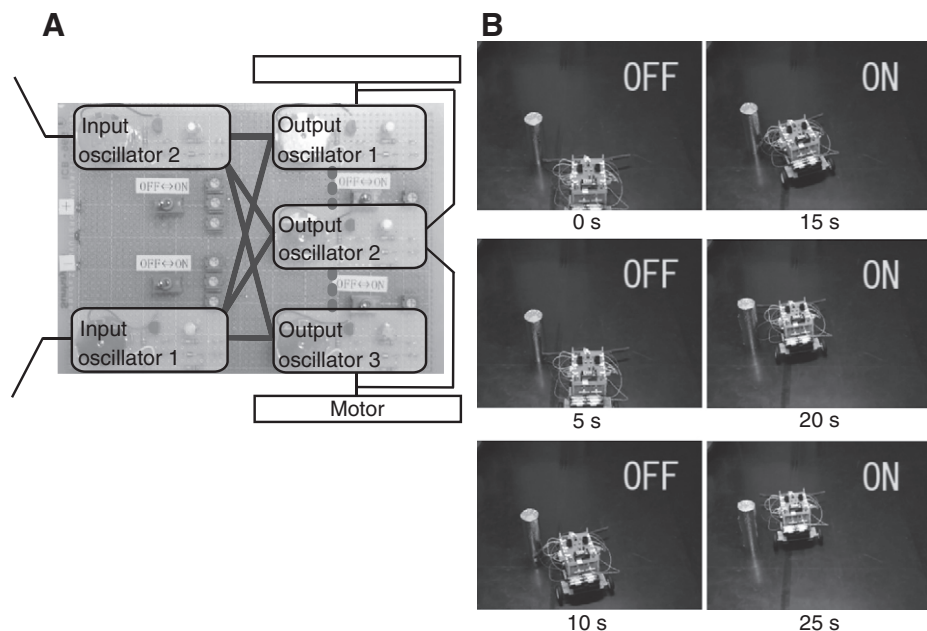

Fig. 4. Robot control circuit and behaviour of the robot. (A) The robot had two motors with wheels, two sensor inputs and a network based on the model of the chemical processing centre. The outputs of the oscillators were connected to motors such that they activated only when they were synchronised, making the robot move in the same manner as shown in Fig. 1. (B) The robot moved in the direction of the sensor input if the circuit had cross-links, but otherwise avoided the obstacle. When there was an obstacle in the way, the robot first moved towards the obstacle (0–10 s). Continuous contact with the obstacle changed the connection of cross-links after a certain period as a function of the delay circuit equipped on the robot, and the robot began avoiding the obstacle (15–25 s).
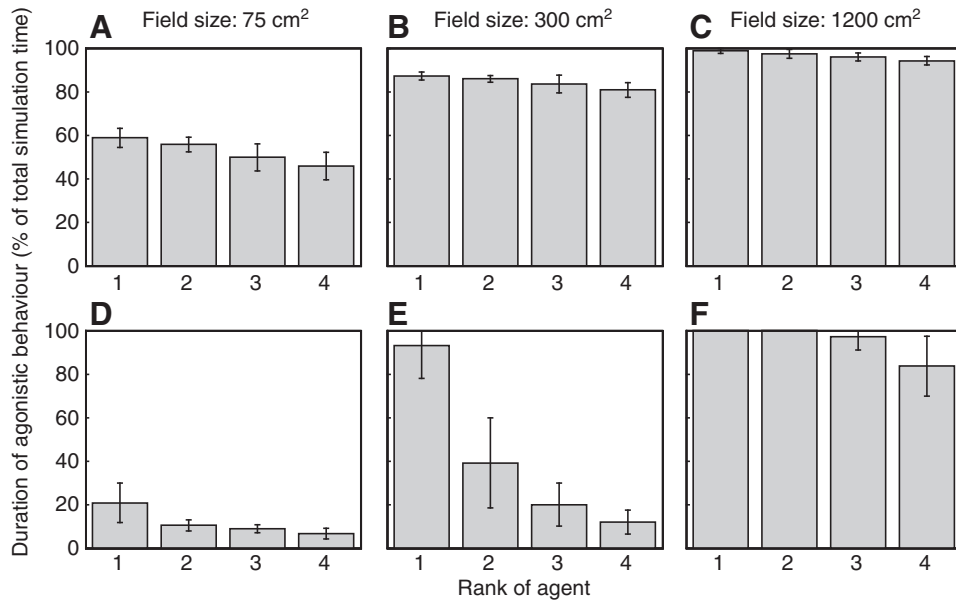
Fig. 5. Duration of agonistic behaviour (as a percentage of total simulation time) for each agent. The duration of agonistic behaviour includes the time that agents behave in an agonistic manner when they encounter other agents; this includes walking and fighting. The simulation was repeated five times with different initial conditions and the bars are shown in order of the rank (1–4) for each trial. Values are means ± s.d. for the five trials. (A–C) Results for agents using the memory of their previous fights to decide their behaviour, where aggression decreased at an almost equal rate according to the size of field. (D–F) Results for agents equipped with memory, where the number of aggressive agents changed depending on the field size. Only one agent was continually aggressive with the medium field (B,E), every agent was aggressive with the large field (C,F), and no agents were aggressive with the small field (A,D).

2. Modelling the behaviour transition of crickets. We constructed a robot that moved using an oscillator network algorism, which was inspired by oscillatory phenomena during chemical information processing in the brain. The robot decided whether to fight other robots based on the synchrony of oscillations.

3. Simulation of cricket group behaviour. Two agent groups, whose action algorithms corresponded to the action of robots, were simulated on the computer to compare their behaviour, one equipped with a memory of previous defeats and the other lacking any memory. The two agent groups were activated in a closed field with variable field sizes, but only the agent group with a memory of defeats showed a size-dependent change in aggressiveness matching that found in experiments with real crickets.

We discuss our results from both biological and robotic perspectives. First, the mechanism of group-size-dependent behaviour is discussed. The effect of size-dependent behaviour on the cricket group is then discussed from a systemic point of view. Finally, we discuss the advantage of the synthetic approach for understanding biological systems.

Why did agents without a memory of defeats reduce aggression at an equal rate independent of group rank?

Our results show that the memory of defeats affected the number of aggressive agents. We first consider this question from an engineering point of view. Fig. 6 shows the transition of the charge level of one agent without a memory of defeats during the simulation. The horizontal line in the centre shows the threshold for changing behaviour (70%), and the figure indicates that the change terminates soon after the level exceeds the threshold. This implies that the behavioural change suppresses the reduction in the extent of aggression afterwards, which enables the agent to regain its aggression within a short time. This reduces the number of agents that show avoidance behaviour. In contrast, Fig. 2B shows a mechanism that modifies the speed of change, where the repeatedly defeated agent shows avoidance and the tendency for avoidance behaviour does not decay rapidly. These experiences are stored and the agents are ultimately separated into continuous winners and losers. Our results suggest by analogy that a small change in the brain might change the entire behaviour of the group, i.e. the charging speed of the capacitor (Fig. 2B) in the case of the agent and the robot.

The functional role of variation in the number of aggressive agents and crickets

If we accept that a mechanism separates aggressive/dominant individuals and subordinates in a group, then the next question is why such a mechanism prevails and how it affects group activity. We discuss this issue from the viewpoint of energy consumption.

To discuss the energy consumption of the simulated agents in detail, we prepared 10 agents and modified the field size. Fig. 7A
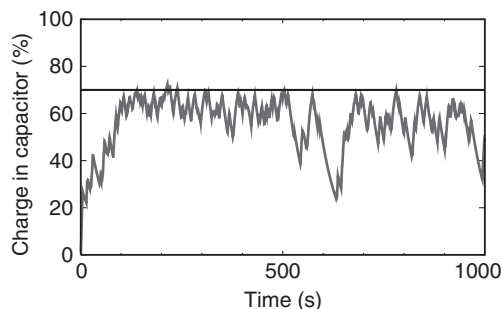

Fig. 6. Time series data of the charge of capacitor for one agent without memory of defeats. The horizontal line at 70% indicates the threshold between aggressive and non-aggressive behaviour. The charge was returned to below 70% immediately after it was exceeded, which led to a change in behaviour.
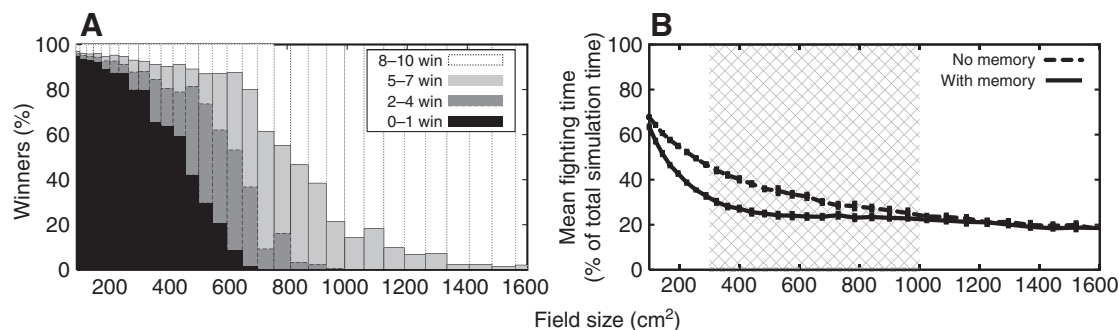
Fig. 7. Change in the percentage of winners and fighting time depending on field size. (A) Simulations where agents had a memory of defeats showed a change in the percentage of winners as a function of field size. By reducing the size of the field, the percentage of winners was reduced, particularly from 300 to 1000 cm^2. (B) The fighting time of agents with and without memory of defeats. The percentage of fighting time increased in response to a reduction in field size for the group with no memory, whereas a sustained increase was observed for the group using memory. Data are means of fighting time duration for 10 agents with 10 replicates. The most significant difference in mean fighting time was observed from 300 to 1000 cm^2 (hatched area).

shows the number of winners, depending on the field size. Fig. 7B shows the simulated duration of fighting in two agent groups. The number of winners in the agent group equipped with memory varied depending on the field size, whereas that in the agent group without memory did not vary. The duration of fighting tended to increase with a reduction in field size because agent encounters were more frequent. However, an increase in the duration of fighting was sustained as agent aggressiveness decreased (with memory). This was particularly evident with an arena size of 300–1000 cm^2 (Fig. 7B), where winners were most variable (Fig. 7A). The fighting is known to demand greater than five times more energy than normal behaviour (Hack, 1997). Thus, a lower level of fighting would reduce group energy use. This demand for energy reduction is best achieved by using the past experience, i.e. memory (Fig. 7B).

Thus, a neuronal mechanism might determine social characteristics, whereby a mechanism that utilises information from previous experience controls the number of aggressive crickets (or robots) and reduces fight duration in a small field to prevent excessive group energy consumption.

Understanding neuronal mechanisms underlying adaptive behaviour using a synthetic approach

The advantages of simulating biological systems using robotics include a better understanding of biological mechanisms and the possible application of biomimicry to engineering problems. We suggest a possible scenario where a mechanism inspired by cricket fighting might be effectively applied.

Passive cooperation, the execution of own duties while refraining from the interruption of other robots' activities, is an elemental ability for robot groups operated in a limited field (Yuta and Premvuti, 1991). The extent of the passive cooperation should be properly determined depending on the field size; if robots behave too carefully in the presence of other robots in a large field, the efficiency of their own tasks will decrease, and if they are not careful of other robots, they will prevent the work of other robots. An emergence of the social framework, i.e. the construction of winner–loser relationships without a blueprint, observed in the agonistic behaviour of crickets might reveal a key ability for providing a robot with the capacity for deriving the appropriate level of passive cooperation. The behavioural transition depending on the density of robots in the field, inspired by research into cricket behaviour, controls the number of active robots by identifying only aggressive robots as active. This tuning function is controlled by local interaction (fighting), so the robot requires no global information regarding field size or robot numbers.

Local interaction must be a key mechanism for the organisation of group behaviour in animals. For example, the schooling of fishes is believed to be governed by individual fish, which make behavioural decisions that are informed only by their neighbour's behaviour (Shaw, 1962; Partridge and Pitcher, 1980). Recognition is a crucial mechanism in the evolution of cooperative behaviour (Hamilton, 1964). In social insects, communication is highly developed. Ants use hydrocarbons on the body surface (cuticular pheromones) to distinguish nestmates (Singer, 1998). Nestmate recognition in the local area must be important to maintain ant societies. Some invertebrates might recognize conspecifics using facial patterns to establish and maintain social status after fights, such as paper wasps (Tibbetts and Lindsay, 2008) and crayfish (Van der Velden et al., 2008), but other animals, such as crickets, might not use individual recognition to maintain social status. Our behavioural experiments suggest that once a dominant–subordinate relationship is established, subordinate crickets avoid other crickets, even if subordinate crickets encounter unknown males. Our study highlights two main functions in local interactions: the automatic transition of behaviour and the memory of experience. These functions can solve problems in robot systems. Our findings also indicate the presence of adaptive mechanisms in the cricket nervous system in that social interactions are mediated by the actions of the nervous system to modify cricket behaviour. Fighting establishes dominant–subordinate relationship in crickets. Crickets losing fights must retain a memory of fighting loss, which makes them continually avoid other crickets. Even though they do not remember the dominant opponent's identity, subordinates can select avoidance behaviour depending on their memory of past fighting experience.

Conclusions

This research focused on a multi-scale phenomenon where individual crickets in a group changed their aggressiveness depending on the global characteristics of group density. The brain function that induces this phenomenon was investigated using a robot model and a simulation of group behaviour. The proposed robot model composed the behaviour using an oscillator network, where changes in behaviour resulted in changes in the connections in a neural network caused by fighting. By comparing the behaviour of simulation agents, whose action algorithms corresponded to the action of robots, with memories of past experience and ones with no memory, we showed that memory induced a depression in aggressiveness, as found in real crickets. This research employed a new strategy for analysing the mechanism of a biological system
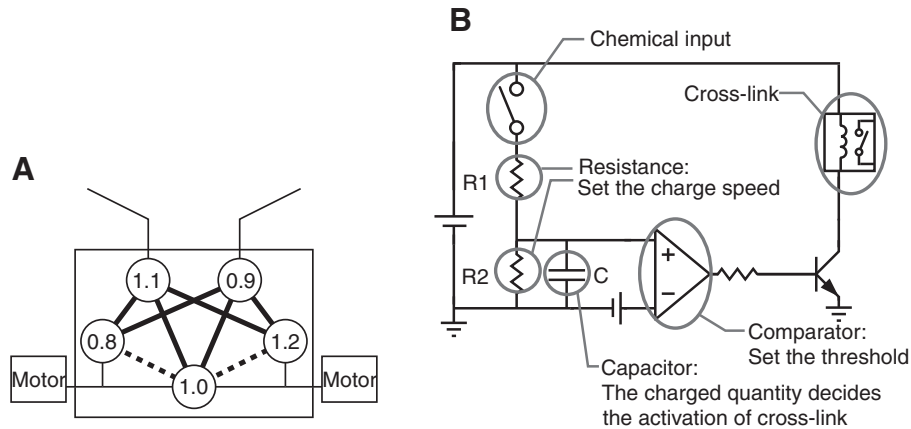
B

Fig. A1. Proposed robot model. The robot model was composed of an oscillator network (A) that converted the network structure to robot behaviour, and a delay circuit (B) that communicated sensory (chemical) inputs to effect network transitions. In A, the circles represent oscillators, the lines represent the connection between oscillators, and the numbers in the circles are the frequency of the oscillators. The robot had two states depending on the existence of cross-links (dotted lines). The activation of motors connected to the oscillators was modulated by the synchrony of the oscillators. The synchrony of the oscillators was controlled by cross-links to produce a change in robot behaviour. In B, the section labelled as a 'cross-link' corresponds to the dotted lines in A, which determines the network structure. The delay circuit allowed the cross-link connections to change after a certain period of fighting. The delay in the connection was achieved with the capacitor. A switch was connected during fighting (chemical input), resulting in electrical charge being stored in the capacitor. When the electricity stored in the capacitor reached a threshold value, the cross-link was connected and the robot changed its state.

by modelling the internal biological state using robots and studying interactions between members of a group of robots in different circumstances. Environmental adaptability emerged from interactions, as demonstrated by our effective analysis using robots.

APPENDIX 1
Detailed design of the robot

Movement of a robot called the Braitenberg vehicle is coordinated by its sensors and motors (Braitenberg, 1984; Pfeifer and Scheier, 1999). A Braitenberg vehicle with an ipsilateral connection between the sensors and motors moves the side opposite to the sensory input and avoids sensed objects, whereas a vehicle with a contralateral connection moves in the direction of the sensory input, as if it behaves in an aggressive manner. Funato et al. proposed a Braitenberg vehicle with an oscillator network (Funato et al., 2008), as shown in Fig. A1A. The activity of the motor equipped in the robot is determined by the synchrony of the oscillator network, based on the nature that the gain of mutually coupled oscillators is maximally reinforced when they are synchronized, and this robot switches between the aggressive and avoidance behaviour of the Braitenberg vehicle depending on the synchrony of the oscillator network. The circles in the figure denote oscillators, and the numbers inside them represent example eigenfrequencies, although the absolute values of the eigenfrequencies are unimportant. If there are no cross-links (dashed lines), this robot moves in the direction of the stimulated antenna. If cross-links are present, both motors are activated by a one-sided stimulus and the robot makes an avoidance manoeuvre because the oscillators with representative eigenfrequencies of 0.8 and 1.2 (Fig. A1A) approach 1.0 and all the three output oscillators are synchronized.

Thus, the robot exhibits aggressive or avoidance behaviour in response to the global connections of its inner network via the synchrony of the oscillators directly connected to its motors. A further mechanism communicates outer stimuli to the network structure and allows the robot to interact with the environment. In this study, we simulated a diffusive chemical that was discharged with the stimulation of a sensory input, changed the network structure and restored the network structure for a certain period. To achieve this, we equipped the robot with a delay circuit (Fig. A1B)

to alternate the network connection. The capacitors in this circuit charged during fighting and activated a cross-link once the charge level reached a certain value.

This mechanism allowed the robot to exhibit aggressive and avoidance behaviour in response to changes in the global connections of the inner network. A sensory mechanism supplied information to the network structure and allowed the robot to interact with the environment.

APPENDIX 2
Detailed design of the robot experiment

Fig. A2 shows the robot we constructed using an analogue circuit, which was based on the robot model proposed in Fig. 4A of the main text. The robot's oscillator network was inspired by oscillations that occur in the brain. The thick solid lines in Fig. 4A denote oscillator connections, and network structure change occurred with switches in the connections denoted by the dotted lines. The two input oscillators were connected to sensors. The sensors were equipped with mechanical switches to sense physical contact, which

Two wires connected to the input oscillators are mounted on the antenna. Obstacle is covered by aluminium.
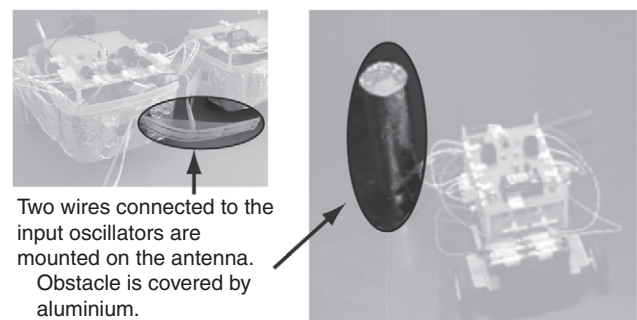
Fig. A2. The mechanism of fight initiation. Two wires were connected to the input oscillators and the robot started fighting when the wires were touched. These two wires were mounted in parallel on the antennae. The obstacle was covered by aluminium. The two wires on the antennae connected with each other when the robot touched an obstacle, thereby activating the input oscillators and initiating the fight.

Table A1. Parameters for oscillators used in the developed robot

A. Eigenfrequency ω and ε

Oscillator type	Input 1	Input 2	Output 1	Output 2	Output 3
ω^2	3,000,000/0.8	3,000,000/1.0	3,000,000/0.7	3,000,000/0.9	3,000,000/1.1
ε	125,700	125,700	125,700	125,700	125,700

B. Connection coefficient λ

	Fixed connection	Cross-link
λ	5000	3750

caused the input oscillators to oscillate. The other oscillators were connected to motors, and the motors were actuated when the two oscillators directly connected to the motors were synchronised.

The robot oscillators were comprised of van der Pol oscillators with a tunnel diode. The state of the van der Pol oscillators was determined by the following equation:

$$\ddot{x}_i - \varepsilon(1 - x_i^2)\dot{x}_i + \omega^2 x_i - \lambda(\dot{x}_j - \dot{x}_i) = 0 \qquad (A1)$$

where ω is the eigenfrequency, λ is the connection coefficient, ε is a parameter that determines the nonlinearity of the van der Pol oscillator, and x_i and x_j are the states of the oscillator i and the connected oscillator j, respectively, obtained as voltage. The oscillator parameters ω, λ and ε were set according to the list shown in Table A1. The parameters for connection λ were set by selecting the appropriate circuit elements, i.e. resistance, capacitance and inductance.

The robot had two wires, mounted in parallel on the antenna, which connected to input oscillators and actuated the oscillators when the two wires made electrical contact. The obstacle was a pole covered in aluminium and the wires connected when the robot touched the obstacle. The obstacle was positioned on the side of the robot's path, so the antenna of the robot could touch the obstacle first. As soon as the robot contacted the obstacle, the input oscillator connected to the antenna began oscillating and guided the robot towards the obstacle, thereby simulating fighting. After a few seconds of fighting, the function of the cross-link led to a behavioural change in the robot, making it exhibit avoidance behaviour, i.e. turning in the direction opposite to the obstacle.

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