Social Integration of Robots in Groups of Cockroaches to Control Self-organized Choices

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Collective behavior based on self-organization has been shown in group-living animals from insects to vertebrates. These findings have stimulated engineers to investigate approaches for the coordination of autonomous multi-robot systems based on self-organization. In this experimental study, we show collective decision-making by mixed groups of cockroaches and socially integrated autonomous robots, leading to shared shelter selection. Individuals, natural or artificial, are perceived as equivalent and the collective decision emerges from nonlinear feedbacks based on local interactions. Even when in minority, robots can modulate the collective decision-making process and produce a global pattern not observed in their absence. These results demonstrate the possibility of using intelligent autonomous devices to study and control self-organized behavioral patterns in group-living animals.

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Self-organization is a central coordination mechanism exhibited by both natural and artificial collective systems. Collective behavior and decision-making based on self-organization occur in eusocial insects (*1-3*), gregarious arthropods (*4,5*) and vertebrates (*6-8)*. Self-organized mechanisms are characterized by nonlinear responses to stimulus intensity, incomplete information and randomness (*1*). Self-organization coexists with guidance from environmental templates, networks of interactions among individuals and various forms of leadership or pre-existing individual specialization (*9, 10*). Studies of animal societies (*1-8)* show that self-organization is used to coordinate group members, to reach consensus, and to maintain social coherence when group members have to choose between mutually exclusive opportunities.

These biological findings have stimulated engineers to investigate novel approaches for the coordination of autonomous multi-robot systems (*11-14*). Swarm-robotic systems, in contrast with other multi-robot systems, explicitly exploit self-organization as a main coordination mechanism. Often, the controller of individual robots is designed using reactive, behavior-based techniques (*15*): robots act and interact with their close environment that sends immediate feedback to their receptors in response to their own actions and the actions of others. Behavior-based techniques allow for real-time implementation of the social nonlinear feedbacks influencing the whole system, minimization of on-board computational resources under tight volume constraints, and suitable support for the injection of stochastic behavioral rules.

Autonomous robots, perceived as congeners and acting as interactive decoys are interesting research tools. By their ability to respond and adapt to animal behavior they open possibilities to study individual and social animal behaviors. Robots, or any artificial agents, could then be used to implement new feedback loops leading to new collective patterns in these mixed natural-artificial systems. Here we show an experimental study that makes a step towards building such mixed societies of artificial and natural agents, using real and robotic cockroaches.

Our experimental set-up consists of a circular arena endowed with two shelters (Fig. 1). In the presence of two identical shelters, large enough to host the entire group, all the cockroaches choose collectively to rest under one of the shelters (*16, 17*). When one shelter is darker than the other, cockroaches select the darker shelter by amplifying their individual preference through inter-individual interactions. This self-organized choice does not require leadership, reference to the final pattern, or explicit comparison between the shelters. This mechanism leads to shelter selection and optimal group formation (*17*).

A mathematical model in quantitative agreement with the experiments was developed (*17*) considering the following experimental facts: (i) individuals explore their environment randomly and thus encounter sites randomly; (ii) they rest in sites according to their quality, in this case determine mainly by darkness; (iii) they are influenced by the presence of conspecifics through social amplification of resting time, all individuals being considered equal. This model also forms the core behavioral module of the robots enabling them to respond stochastically to social stimuli according to eq. 2b (below). The robots are designed to discriminate: (i) cockroaches from other robots, these two types of agents being considered here as conspecifics; (ii) shelters from the rest of the arena and shelter darkness; (iii) the wall around the circular arena and other obstacles (*18*). The model is used as a quantitative explanation as well as overall guidance for the design of the robot.

The model describes mixed groups where robots and cockroaches exhibit similar behavior. The differential equations giving the time evolution of the number of individuals in the shelters and outside are:

$$\frac{dx_i}{dt} = R_i x_e - Q_i x_i \qquad i = 1,2 \quad (1a)$$

$$\frac{dr_i}{dt} = R_{ri} r_e - Q_{ri} r_i \qquad i = 1,2 \quad (1b)$$

$$C = x_e + x_1 + x_2 \quad (2\mathrm{a})$$

$$M = r_e + r_1 + r_2 \quad (2\mathrm{b})$$

Variables x_i and r_i represent the number of cockroaches and robots present in the shelter i respectively and x_e and r_e outside the shelters. Parameters C and M correspond respectively to the total number of cockroaches and robots. The functions R and Q giving respectively the rate per individual of entering or quitting shelters are:

$$R_i = \mu_i (1 - \frac{x_i + \omega r_i}{S_i}) \quad (3a)$$

$$R_{ri} = \mu_{ri} (1 - \frac{x_i + \omega r_i}{S_i}) \quad (3b)$$

$$Q_i = \frac{\theta_i}{1 + \rho (\frac{x_i + \beta r_i}{S_i})^n} \qquad (4a)$$

$$Q_{ri} = \frac{\theta_{ri}}{1 + \rho_r (\frac{\gamma x_i + \delta r_i}{S_i})^{n_r}} \qquad (4b)$$

Each cockroach or robot outside shelters has a rate of entering shelter i R_i (R_{ri}) (R=1/mean exploring time). Because these functions (3a,b; 4a,b)) take into account a crowding effect, they decrease with the ratio between the number of individuals present in site i and its carrying capacity S_i. The carrying capacity corresponds to the maximum number of cockroaches that can be hosted in the shelter i. In equations (*3a,b*), parameter ω represents the surface of one robot expressed as a multiple of the surface of one insect. μ_i (μ_{ri}) represents the maximal kinetic constant of entering the shelter for insects (robots).

Each cockroach (robot) in shelter i has a rate Q_i (Q_{ri}) of leaving it and to start exploring (Q = 1/mean resting time). Parameters θ_i (θ_{ri}) are the maximal rate of leaving a shelter. Parameters ρ and n (ρ_r and n_r) take into account the influence of the conspecifics. When both shelters are identical, the parameters characterizing them are equal: $S_1=S_2$; $\mu_1=\mu_2$; $\mu_{r1}=\mu_{r2}$; $\theta_1=\theta_2$; $\theta_{r1}=\theta_{r2}$. In case shelters are of different darkness: $\theta_1 \neq \theta_2$; $\theta_{r1} \neq \theta_{r2}$. Parameters γ, β and δ correspond respectively to the influence of insects on robots, of robots on insects and of robots on robots. The greater they are, the greater the mutual influences. The influence of insects on insects is imposed by biology and is not modulated in our experiments. However parameters γ, δ and β could be modulated by changing the hardware and/or software of the robots. As in insect societies, the inter-attraction between cockroaches is chemo-tactile and mainly based on a blend of hydrocarbons coating their body (*19-22*). The robots are coated with this blend and the higher the pheromone concentration the higher β.

Acceptance of robots within a cockroach group is related to the ability of robots to bear the correct chemical signal and to behave appropriately. Chemical analyses and behavioral tests were performed to identify the main molecules composing the odor that carries cockroach identity (*18*). This odor was then collected from male cockroaches and calibrated to a known concentration used to condition filter papers dressing the robots. The concentration per cm^2 on the filter paper and on one cockroach were the same. Therefore natural and artificial agents were equally attractive to one another. Tests with encounters between robots and cockroaches showed that cockroaches were lured to, and interacted with, chemically dressed robots. Comparisons with unmarked robots showed the importance of this chemical message (*18*).

Pheromone luring is used here to allow acceptance of the robot in the group and not to attract the insects to a specific shelter. As robots become members of the group, they can take part and influence dynamically the collective decision making process. Not only do these robots explore their environment autonomously but they are also able to tune their resting time in relation to the presence of cockroaches, as cockroaches do (*16, 17*). In turn, the insects are influenced by the presence of robots closing the loop of interactions between animals and machines. The shelter selection emerges from the social interactions between natural and artificial individuals.

The first set of experiments showed the sharing of the collective decision-making for shelter selection in mixed cockroach-robot groups. The robots were programmed to select dark shelters as cockroaches do. Interactions between robots and cockroaches lead to the selection of a common shelter (Fig. 2). Given the choice between two identical dark shelters, both types of groups chose to rest under one of the shelters and behaved as a whole, irrespective of their natural or man-made origin. In most trials, both cockroach groups and mixed groups selected one of the shelters. In 93% of the trials (28 of 30 trials), mixed groups presented a clear choice for one of the shelters and 75% of cockroaches and 85 % of robots aggregated under the same shelter. Comparisons of these results with computer simulations of the model confirmed that the choice corresponds to the coexisting stable states of a nonlinear system (Fig. 2A, C).

The second set of experiments was designed to show the control of the collective choice by mixed groups when shelters differ in attractiveness - in this case darkness (Fig. 3). Cockroaches prefer to aggregate under the darker shelter (brown bars in Fig. 3A). This selection process is explained by the same model as above with a bias induced by the darkness level of the shelters ($\theta_1 \neq \theta_2$; $\theta_{r1} \neq \theta_{r2}$, Fig. 3C). When cockroach groups selected one of the shelters (22 of 30 trials), the darker shelter was selected in 73% of the cases and the lighter one in only 27% of the cases (Fig. 3A). As in the first set of experiments with two identical dark shelters, these proportions correspond to the coexistence of multiple stable states in a nonlinear system.

In the case of mixed groups (yellow bars in Fig.3A), the robots were programmed to prefer the lighter shelter, contrary to the cockroaches. This effect was obtained by keeping the same behavioral model and swapping the parameters controlling the robot response to darkness with respect to those measured for cockroaches. Given the choice between a dark and a light shelter, robots were able to induce a change of the global pattern by inverting the collective shelter preference. Under these conditions, the shelter less preferred by the cockroaches (i.e. the lighter one) was selected by mixed groups in 61% of the trials compared to only 27% of the trials done without robots. Despite the individual preference of robots for lighter shelters, they were socially driven by the cockroaches into the darker shelter in 39% of the trials (Fig. 3A). These results are explained by the nonlinear mechanism governing the self-organized choice as shown by stochastic simulation of the model (Fig. 3B). In some trials, the choice was induced by the robots and in others by the cockroaches. The robots did not act as a mere attractant but were integrated in the decision-making process of the society.

These experimental results show the possibility of shared and controlled collective actions between machines and animals. At the technical level, we introduce lures able to perceive animal response and able to respond to it. The robots were designed to interact and to collaborate autonomously both with the animals and with one another. This work could be extended to vertebrates taking into account sound, visuals cues and social organization. Possible ways to identify individual behavioral algorithms could be to replace some animals within a group by robots or other artificial devices and to compare collective responses in “mixed” and “natural” groups (*23-26*). They could also be used to test hypotheses about the origin of cooperation among group members. At the conceptual level, we exploit the nonlinear dynamical properties of regulatory feedbacks to introduce a form of control that can require only a small number of social lures. Artificial agents such as robots or networks of sensors and actuators could also be used to introduce new regulatory feedback loops (or modulate existing ones) at the social level (27, 28), inducing new patterns of collective behavior. Animal societies could be one of the first biological systems where autonomous artifacts cooperate with living individuals to solve problems.

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Supporting Online Material (www.sciencemag.org)**:** materials and methods, text, tables and figures.

Figure 1. Experimental set-up showing the cockroaches (*Periplaneta americana*) and the robots. Two shelters (150mm) made of plastic disks covered by red film filter are suspended (30mm) above the floor of a circular arena (1m diameter). The darkness under the shelter is controlled by the number of layers of red film. Cockroaches aggregate under the shelters (18).

Figure 2. Shared collective choice between two identical shelters: (A,B) Experimental results for 30 trials; (C,D) Computer simulations of Eqs. 2 (18). Groups of 16 cockroaches (brown bars) selected one of the two shelters. Mixed groups of 12 cockroaches plus 4 robots (yellow bars) presented the same distribution, demonstrating that the mixed groups made the same collective decision as cockroaches alone. The probability of selecting one of the shelters is about 0.5 in accordance with a dynamics leading to stable multiple states (*16, 17*). (B, D) Fraction of the group present under the shelters (mean +/- s.d.) in relation to time showing that selection has similar dynamics in both types of groups. Green lines represent the selected shelter (randomly shelter 1 or 2 in different trials), the red lines the not selected one.

Figure 3. Controlled collective choice between dark and light shelters. (A,B) Experimental results and (C, D) computer simulations (18). (A) Groups of cockroaches without robots (brown bars) select the dark shelter in 73% and the light shelter in 27% of the trials. Mixed groups with robots programmed to prefer the light shelter (yellow bars) select it in 61% of the trials. The robots induce a change of the collective choice by modulating the nonlinear collective mechanism. Nevertheless, the dark shelter is still selected in 39% of the trials because the robots also socially respond to the cockroaches. In all selections, robots and

cockroaches shared the same shelter. (B-D) Fraction of the group present under the shelters (mean +/- s.d.) as a function of time showing that the selection has similar dynamics in both types of groups (dark blue: dark shelter; light blue: light shelter). (B) In red, number of selections out of 30 trials.

Supporting online text

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1- Materials and methods

Prototyping the robot and experiments with cockroaches and mixed groups required about 600 3-hour trials. Experiments were performed with *Periplaneta americana* cockroaches. They were bred in large cages with water and dog food pellets provided *ad libitum*. The temperature in the breeding room was 298±1 K with a 12h:12h light-dark cycle. Adult males were taken randomly from the breeding cages 48 hours before each trial and put at rest. Individuals with any external damage were discarded. During day time (09h00-12h00; 14h00-18h00), each individual was tested only once.

Groups of 16 individuals, including 16 cockroaches or 4 robots plus 12 cockroaches, were given a choice between two shelters in a large circular arena. For each trial, a group was placed in a circular arena delimited by a black polyethylene ring (diameter: 1 m, height: 0.2 m) (Fig. 1). Cockroach escape was prevented by an electric fence placed on the inner lower-side surface of the arena.

The experimental setup was maintained at 293±1 K. The white paper sheet covering the floor of the arena was replaced before each trial to avoid chemical marking. Lights placed over the centre of the arena produced 355 ± 5 lux at the ground level. The centre of each shelter was 230 mm from the edge of the arena and 30 mm above the ground. A shelter is made of Plexiglas disc (diameter: 150 mm) suspended by nylon threads and covered with red filter (Rosco color filter, E-Colour #019: Fire). One layer of red filter was used to obtain a light shelter (100 ± 5 lux), and two layers for a dark shelter (75 ± 5 lux). Discs were cleaned with denatured alcohol (97.1% of ethanol + 2.9% of ether) between each trial. To avoid bias, the setup was surrounded by an opaque white enclosure to prevent perception of potential external visual landmarks. The angular position of each shelter pair was randomized between replicates.

Before each trial, robots were wrapped with filter paper (Whatman, grade 1) that covered their entire surface except for the sensors. This paper was conditioned with the recognition odor. It was collected by extracting cuticular hydrocarbons (S1,S2) from adult males in dichloromethane. Each robot was conditioned with 60 μl of the blend concentrated so that the robot carried the same concentration per cm² as live cockroach cuticle. A trial began when cockroaches and robots were placed in the arena. All individual movements were recorded for 3 hours by a video camera (Fire-I Digital camera, Unibrain). The recordings were analyzed with a tracking software (S3) giving the position of each individual every 1/25 s.

2- Mobile robot technology

Many robot developments have tried to mimic animals in their morphology. For instance, the legged walking system of cockroaches has inspired several legged robot designs (S4-S8).

Some research work has been done on the combination of artificial and natural devices in the same body. Nagasawa *et al.* (S9) equipped their PheGMot-III robot with real cockroach antennas. Holzer and Shimoyama (S10) kept the real cockroach but replaced antenna feedback by artificial electrical stimulation, thus controlling some movements of the cockroach.

The goal of our development is different from other studies, aiming to have robots that integrate into a group of animals, live inside their society and interact with them. The focus of this work is on social interaction, which does not necessarily correspond to the reproduction of body structure and appearance. The goal here is to reproduce some mechanisms that are crucial for social interaction and will allow the robot (i) to be fully accepted and integrated in the society and (ii) to participate in the social decisions. These artificial mechanisms must permit the robots to, for instance, statistically produce the same patterns as animals do. To achieve this goal, the robot main behavioral module incorporates the model for shelter selection presented below.

The main robot requirements defined by the biological modeling are:

- Size: Robots have to be of similar size (not shape) to the cockroaches.
- Motion and behavior: Robots have to move and react to cockroaches and other robots like a real cockroach among its group. Their movements are designed to avoid excessive bumping into insects and display similar speed and movement as insects.
- Environment perception: Robots have to distinguish between walls or obstacles and shelters of different darkness.
- Experimentation tools: Each robot is equipped with a radio link for monitoring and debugging facilities.

To satisfy these requirements we developed the InsBot robot (Insect-robot). The global technical design principles of the InsBot robot can be found in (S11). An overview of the robot design process can be found in (S12) and a detailed description of hardware and software of the final version of the robot used for experiments can be found in (S13).

3- Semiochemical coating of robots

In insect societies, chemical cues allow individuals to recognize their conspecifics and to communicate with them (S14-S16). In the tested cockroach species, recognition among individuals is mainly based on chemical compounds present on their body surface (S1, S2, S16). This study on *Periplaneta americana* included three parts.

Firstly, we identified the chemical compounds of the cuticular blend acting during aggregation. The blend extracted in dichloromethane contains mainly hydrocarbons (section 3.1).

Secondly, the aggregative efficiency of these dichloromethane extracts was tested on groups of cockroaches by quantifying their response to an immobile chemically coated robot. This classical luring method based on chemical communication was used to induce interactions between cockroaches and robots (section 3.2).

Thirdly, we investigated whether the coupling of this semiochemical coating with movement of the robot favored its integration. Therefore, we tested the influence of these two factors on the duration of encounters between two cockroaches or between a robot (coated or not) and a cockroach (section 3.3).

We aimed to demonstrate that mobility of the coated robot was a key element in the control of the collective choice of a mixed robot-cockroach society. Classical luring methods are based on the intervention of a human operator who influences the response of the tested subjects by the way he manipulates them. For example, an operator can influence cockroach shelter choice by placing an immobile robot under a specific shelter. In this case, shelter choice by cockroaches is influenced by the decision of the human operator who positioned the lure as we did in section 3.2 below. In the third part, as positioning of the autonomous robot is influenced by cockroaches and influences at the same time cockroach positioning, shelter selection was not induced by a human operator but emerged from interactions between cockroaches and robots in a dynamic way based on self-organization. Moreover, as robots are autonomous and programmed to perceive and to react to the presence of cockroaches, they were able to induce new dynamics based on mutual influence leading to self-organized collective choices.

3.1 Chemical compounds mediating inter-individual recognition leading to aggregation

We identified the main chemical compounds that mediate inter-individual recognition leading to the formation of aggregates in *Periplaneta americana* by coupled gas chromatography-mass spectrometry (GC-MS) and coupled gas chromatography-electroantennography (GC-EAD) (see table S1, and ref. S1, S2). Identification required several types of behavioral bioassays to identify the molecules involved in the aggregation processes (S1, S2, S15, S16). Cuticular hydrocarbon profiles of *Periplaneta americana* were described (Table S1). Bioassays were based on the choice between two resting sites by groups of cockroaches. The presence of dichloromethane cuticular hydrocarbon extracts on one of the resting sites induced selection of that site (S2). Furthermore, other molecules with slightly lighter molecular weights (hexadecanoic acid, pentadecanoic acid and pentaethylene-glycol) attracted conspecifics in a non-random way. All these molecules are at the basis of aggregation formation in cockroaches.

Name	abb	Mean area (n=5)	SD (n=5)
3-Methyltetracosane	3 Me-C24	0.10	0.01
n-Pentacosane	nC25	10.34	2.33
3-Methylpentacosane	3 Me-C25	12.86	1.06
n-Hexacosane	nC26	0.31	0.12
Dimethylpentacosane	diMe-C25 mix	0.39	0.13
6,9-Heptacosadiene	6,9-C27:2	68.47	3.61
n-Heptacosane	nC27	1.35	0.48
13-Methylheptacosane	13 Me-C27	0.13	0.08
5-Methylheptacosane	5 Me-C27	0.10	0.02
3-Methylheptacosane	3 Me-C27	0.14	0.03
Octacosadiene	C28:2	0.12	0.03
n-Octacosane	nC28	0.10	0.02
Nonacosadiene	C29:2	0.20	0.17
n-Nonacosane	nC29	1.59	0.53
15-Methylnonacosane	15 Me-C29	0.29	0.52
5-Methylnonacosane	5 Me-C29	0.03	0.02
3-Methylnonacosane	3 Me-C29	0.08	0.03
n-Triacontane	nC30	0.10	0.06
n-Hentriacontane	nC31	0.11	0.04
13-Methyltriacontane	13 Me-C39	0.13	0.05
Hentetracontene	C41:1	1.10	0.29
13-Methylhentetracontane	13Me-C41	0.38	0.08
Tritetracontadiene	C43:2	0.26	0.10
Tritetracontene	C43:1	0.28	0.07

Table S1. Cuticular Hydrocarbon profile of *Periplaneta americana* (GCMS, area %, from (S2)). Legend: Abb: abbreviation of HC names. The mean area of the chromatogram peaks is proportional to the quantity of that molecule in the chemical spectrum.

3.2. Role of an immobile semiochemically coated robot in shelter selection

Groups of 10 *P. americana* adult males were tested in the experimental setup described in the methods section. Robots were dressed with a filter paper coated either with dichloromethane cuticular hydrocarbon extracts (60 µl, coated robot) or only with solvent (60 µl dichloromethane, uncoated robot). These dresses covered the whole robot, except all the sensors. Coated robots carried the same amount of cuticular hydrocarbons per cm² as a living cockroach. One coated and one uncoated robot were placed randomly under each of the two shelters.

The numbers of cockroaches under each shelter were recorded every 15 min for 3 hours to evaluate the role of the coated robot on collective shelter selection by a cockroach group.

More than 66% of the trials ended with at least 80% of the cockroaches under the shelter containing the coated robot. Analysis of the aggregation dynamics highlighted that the coated robot nucleated the aggregation right from the initial moment of a trial (Fig. S1). Numbers of cockroaches increased in relation to time until a plateau was reached before the end of a trial. These data demonstrated that cockroaches which easily explored the whole surface of the arena had stopped near the coated robot.

Therefore, we assumed that the presence of an immobile coated robot initiated the aggregation process and that the chemical compounds present on its surface are sufficient to be accepted by a cockroach group, while an uncoated robot was ignored.

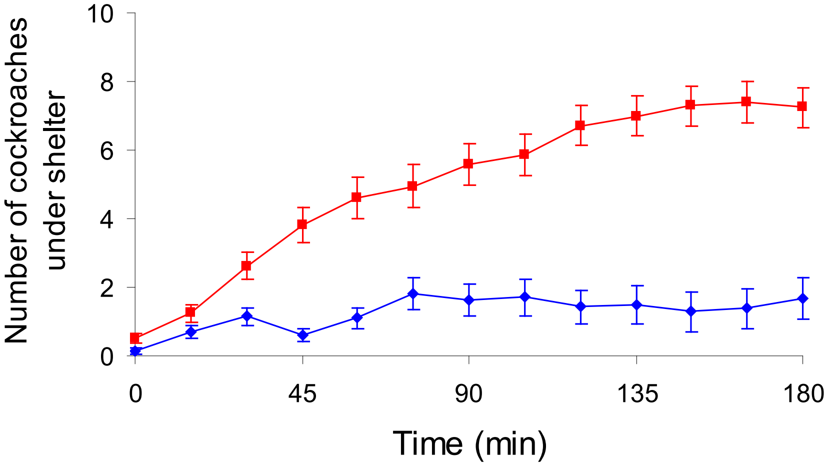

Figure S1. Number of cockroaches (mean ± S.E.) in relation to time under the shelter containing a coated robot (red) or an uncoated robot (blue). Total number of trials = 24.

3.3. Role of robot chemical coating on dynamics of cockroach-robot interactions

As demonstrated above, acceptance of robots by cockroaches was due to the odor coating of the robots and to appropriate behaviors. Robots are programmed to avoid excessive bumping and modulate their physical closeness of contact with insects. When encounters between cockroaches and robots occurred in the experimental arena, the mean contact duration was related to the chemical coating of the robots.

Groups of 10 *P. americana* adult males and one robot were tested in the previously described experimental setup. Mobile robots were programmed as described in the main text and the robot supplementary information. Robots were coated either with cuticular hydrocarbon extracts or only with solvent.

Type of contact	Mean contact duration, in s (± S.D.)
Cockroach-cockroach (n = 184)	9.45 ± 21.47
Cockroach-coated robot (n = 24)	7.48 ± 13.68
Cockroach-uncoated robot (n = 27)	2.54 ± 2.42

Table S2. Mean contact duration, in s (± S.D.) between one cockroach and either another cockroach or a coated robot or an uncoated robot.

Outside shelters, the duration of encounters between cockroaches and robots was measured during 3-hour trials. Encounters are defined by physical body or antennae contacts. Time spent by one cockroach with another cockroach or with a coated robot was not statistically different (Table S2, Mann-Whitney test, $U = 1739$, $p > 0.05$). Cockroaches spent significantly less time with an uncoated robot than with another cockroach (Table S2, Mann-Whitney test, $U = 1409$, $p < 0.001$).

The comparison between the log-linear survival curves of the cumulative fraction of contacts in relation to their duration highlighted a difference between tested conditions. We observed strong similarity between cockroach-cockroach and cockroach-coated robot contacts (Fig. S2, comparing of the linear regressions). On the contrary, the survival curve of contact durations between cockroaches and an uncoated robot is very steep due to the absence of long contact durations, which never exceeded 10s. Distribution of contact durations between two cockroaches or between a cockroach and an uncoated robot differed significantly (Fig. S2. Comparing slopes of the linear regression). A survival curve statistical analysis based on the log-rank test gives: cockroach-cockroach vs cockroach-coated robot: chi-square=0.63, df=1, P=0.42, NS; cockroach-cockroach vs cockroach-uncoated-robot: chi-square=21.68, df=1, P<0.0001, S. These tests confirm the visual analysis of the distributions Furthermore, the presence of an uncoated robot prevented cluster formation and led to spatial segregation between cockroaches and robots (S17).

As this chemical coating of robots induced long-lasting interactions between cockroaches and robots, these bioassays stressed the need for semiochemicals to lure cockroaches and validated the efficiency of our semiochemical coating.

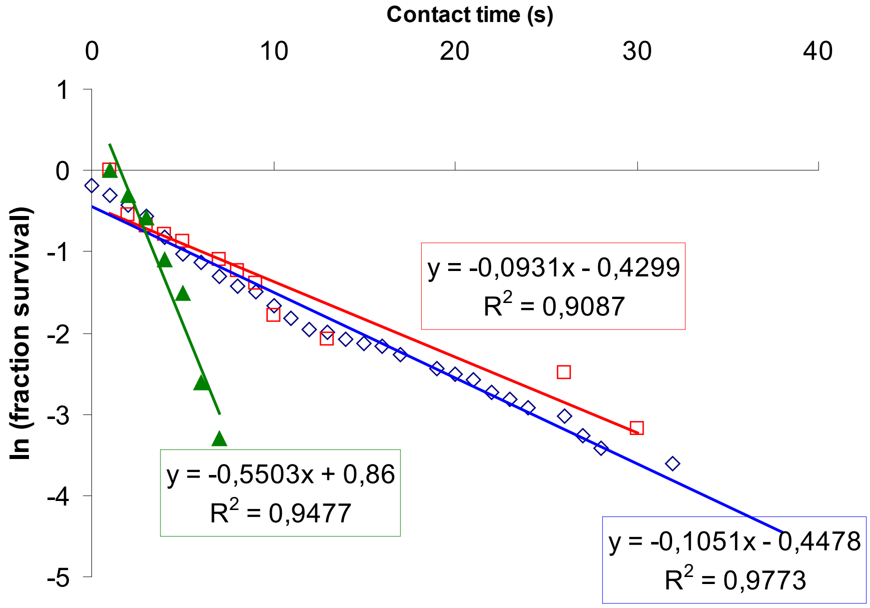

Figure S2. Survival curves (log-linear scale) for the three types of contacts: cockroach-cockroach (blue diamonds), cockroach-coated robot (red squares) and cockroach-uncoated robot (green triangles) in relation to contact time (s).

This study demonstrated that semiochemical coating of the robots facilitated their integration in cockroach groups by allowing their recognition as if they were conspecifics. Furthermore, the significant components of this blend have been identified and could be synthesized (S1, S2). Coating of a robot, presenting appropriate behavior, induced the formation of mixed groups under the same shelter and was the only instance where cockroaches accepted long-lasting contacts with robots.

4- Dynamical system model for mixed groups and statistical criteria

We make use of a dynamical system model for cockroach aggregation and shelter selection based on individual behavior (S18). The model is used (i) as a quantitative explanation, (ii) as design guidelines for the robots and (iii) as a behavioral module of the robot. This model has been validated experimentally for two species of cockroaches (*Blattella germanica, Periplaneta americana*), for juveniles and adults and for males and females. Here, we focus on mixed groups where robots and cockroaches exhibit similar behavior. The differential equations 1,a,b give the time evolution of the number of individuals on each site. Space is abstracted into three compartments i.e. shelter 1, shelter 2 and outside the shelters. Closely related model explicitly including space have also being developed (S19, S20). In the next section we present the experimental estimation of parameters involved in equations 1 and 2. Then we discuss the numerical results obtained with a stochastic version of eq.1 and 2 and presented in Fig. 2C, D and 3C, D.

4.1 Estimation of parameter values from experiments

4.1.1 Carrying capacity (*S*)

The carrying capacity can be estimated by the ratio between the shelter area (17 671 mm^2) and the average cockroach area ($\approx$ 600 mm^2) and corresponds to S=29.45. The robot area (30mm * 41mm = 1230 mm^2) is twice (ω =2.05) the average cockroach area. The value of S was confirmed by experimental tests showing that the maximal number of cockroaches under one shelter was always below 30.

4.1.2 Rate of entering *(R)*

Experimental tests showed that the cockroach probability of entering the shelter is independent of the darkness of the shelter. Observations (768 for the dark and 779 for the light shelters) showed that the mean number of entrance events in the shelters (± standard error) was 24 ± 3.43 for the dark and 24.34 ± 3.38 for the light shelters (Paired t test: t = 0.19, d.f.=31, p=0.85). Parameter μ is the inverse of the mean time needed to find an empty shelter and equals 0.0027 s^{-1} (estimated from 1572 observed events).

Similarly, for the robot, its maximal kinetic constant of entering a shelter was experimentally estimated, μ_r= 0.0094 s^{-1} (estimated from 76 observed events).

4.1.3 Rate of quitting *(Q)*

Fitting the cockroach rate of quitting (*Q)* (see supporting information of S18 doi:10.1073/pnas.0507877103), equation 2,b, and the data of Table S3) implies that for a light shelter, θ_{light} =0.544 s^{-1}, ρ = 4193, n= 2, (r^2 = 0.956). The ratio between the rate of leaving a dark and a light shelter is 0.77 and therefore θ_{dark} =0.44 s^{-1}.

The chemical marking of the robot was calibrated to correspond to the attractiveness of one insect, therefore β= 1. The probability of leaving for an insect associated with a robot (Q= 0.057 s^{-1} for a light shelter, based on 120 observed events) is close to the probability of an insect associated to another insect (Q= 0.041 s^{-1} based from 246 observed events).

The observed parameter values for the robots were $\theta_{rlight}= 0.04\ s^{-1}$, $\rho_r= 610$, $n_r= 2$. The ratio between the rate of leaving the dark and the light shelter was 0.38 and therefore θ_{rdark} = 0.015 s^{-1}. We consider that the influence of the insects on the robot rate of leaving (γ) was equal to the influence of another robot (δ) because robots are programmed to consider other robots or insects as equivalent. Perception of cockroaches and robots by the robots are described in S13.

In the experiments where robots have preference for the light shelter, parameters values are $\theta_{rdark}= 0.04\ s^{-1}$, and θ_{rlight} = 0.015 s^{-1}.

Number of cockroaches	Q (s^{-1})	Number of observations
1	0.066	779
2	0.041	246
3	0.017	137
4	0.008	95
5	0.004	82
6	0.003	69

Table S3. Probability of leaving a light shelter (Q) in relation to the number of cockroaches under the shelter.

All parameter values are summarized in table S4.

Parameter	**Value**
Carrying capacity (S)	30
Robot surface (ω)	2
Cockroach maximal rate of entering the shelter (μ)	0.0027 s^{-1}
Robot maximal rate of entering the shelter (μ_r)	0.0094 s^{-1}
Cockroach maximal rate of leaving a dark shelter (θ_{dark})	0. 44 s^{-1}
Cockroach maximal rate of leaving a light shelter (θ_{light})	0.544 s^{-1}
Influence of conspecifics on cockroaches (ρ)	4193
Exponent of the cockroach rate of leaving a shelter (n)	2
Influence of insects on robots (γ)	1
Influence of robots on insects (β)	1
Influence of robots on robots (δ)	1
Influence of conspecifics on robots (ρ_r)	610
Exponent of the robot rate of leaving a shelter (n_r)	2
Robots with preference for the dark shelter (same preference as the cockroaches)	
Robot maximal rate of leaving a dark shelter ($\theta_{r\ dark}$)	0.015 s^{-1}
Robot maximal rate of leaving a light shelter ($\theta_{r\ light}$)	0.04 s^{-1}
Robots with preference for the light shelter	
Robot maximal rate of leaving a dark shelter ($\theta_{r\ dark}$)	0.04 s^{-1}
Robot maximal rate of leaving a light shelter ($\theta_{r\ light}$)	0.015 s^{-1}

Table S4. List of the model parameter values as estimated from experiments

4.2. Stochastic simulation results

4.2.1. First set of experiments: two identical shelters (dark)

The model has been analytically assessed (S18). For the parameter values corresponding to our experiments with cockroaches (C=16, M=0), it shows two stable stationary states. These two solutions are asymmetrical meaning that one of the shelters is selected. In order to take into account the effects of fluctuations (or noise), we performed stochastic simulations of equations (1a,b).

These simulations confirm the analytical results (Fig.2C). Simulations of 5000 runs per condition were done. Their results allowed us to follow the time evolution of the number of individuals present on site 1, 2 and outside. At each second (time step), the position (in shelter *i*, i=1,2 or outside) of each cockroach and robot was checked. Then its probability of leaving from shelter *i* to outside is given by Qi (Q_{ri}). Its position at the next second (time step) depends on the comparison between the calculated value Q_i (Q_{ri}) and a random number sampled from a uniform distribution between 0 and 1. If its value is less than or equal to Q_i (Q_{ri}), the individual leaves shelter *i* and goes outside. If not, it stays in shelter *i*. The probability of joining one of the two shelters is implemented similarly using the function R_i or R_{ri}. The functions Q and R are updated at each time-step.

Simulations of duration of 3h show a frequency of shelter selection (0.9) higher than the experimental selection rate (0.65). This difference is in part explained by the fact that during the first 30 minutes of experiments, the insects are stressed by their introduction from the breeding boxes into the experimental setup. Of course, the model does not take into account this effect. Stochastic simulations, for durations of 2h30 instead of 3h, show a selection ratio closer to the experiments. In this type of simulations and in the case of two identical shelters, cockroach groups present a shelter selection frequency of 0.75. This frequency computed for a duration of 2h30 is not different from the experimental selection ratio after 3h (Chi-square test, $\chi^2 = 1.6$, df=1, NS, $p > 0.05$). This effect is also seen by comparing the experimental and simulated time evolution of shelter selection (compare Fig. 2 and 3).

In mixed groups (C=12, M=4), the model shows that most of the robots and cockroaches settle under the same shelter. The theoretical (0.9) and experimental (0.93) selection frequency are not statistically different ($\chi^2 = 0.27$, df = 1, NS, $p > 0.05$). For the parameter values used here, aggregation of cockroaches and robots under the same shelter is robust.

The model was used to explore the influence of the different parameters on the collective response. Surprisingly, it shows that, only for small value of β and γ, the two populations can segregate. In this case, the majority of the robots are on one site and the majority of the cockroaches are on the second site (data not shown).

4.2.2. Second set of experiments: two different shelters.

This section presents computer simulations corresponding to the selection experiment between a dark and a light shelter with the robots programmed to show a preference for the light shelter (Fig.3).

With cockroaches only, the majority of the simulations, as the majority of experiments, show the selection of one shelter (0.9 simulations vs 0.75 experiments). Among the simulations with selection, 0.89 of the groups select the dark shelter (vs. 0.73 in the experiments, Fig.3A, C). For mixed groups, despite the difference between robot and cockroach preferences, most of the simulations ended with aggregation of the robots and cockroaches under the same shelter (selection frequency of 0.9 vs 0.75 for the experiments). Among simulations with selection, most often the population selects the light shelter (0.6 vs 0.61 for the experiments, $\chi^2 = 0.01$, df= 1, NS, $p > 0.05$) (Fig.3 A, C).

4.3. Statistical criteria for shelter selection

Here, we only present the statistical analysis of the experimental data as computer simulations can produce significantly large amount of data allowing avoidance of statistical inaccuracy.

4.3.1 First set of experiments: two identical shelters (dark)

First we assessed whether shelter selection was significantly different from an individual random choice (Fig.2A). We tested if the repartition of the individuals between two identical shelters (x_1 and x_2) was different from a random distribution of individuals having all the same probability of being in shelter 1 or shelter 2 ($p_1 = p_2 = 0.5$). Thus, the null hypothesis is a binomial distribution of observing x_1 and x_2 individuals in shelter 1 and 2. Each experimental combination of x_1 and x_2 individuals (at 180 min) with a corresponding probability of an occurrence value of $p < 0.05$ was assumed to be different from the random expectation. Experiments show that groups of cockroaches and mixed groups select one resting site in respectively 20 and 28 experiments out of 30 replications.

Second: the model predicts that the self-organized selection between two identical shelters occurs with an equal probability i.e. 0.5 (S18). Therefore, we tested the lack of selection bias between shelter 1 and 2 (Fig.2A). For 30 trials, the total number of individuals under the two shelters were not statistically different (cockroaches: 173 individuals in shelter 1 and 186 in shelter 2, $\chi^2 = 0.47$, df= 1, NS, $p > 0.05$; mixed groups: 204 and 172, $\chi^2 = 2.72$, df= 1, NS, $p > 0.05$). Moreover, the number of experiments where shelter 1 was selected was not statistically different from the number where shelter 2 was selected (for cockroaches: 8 and 11, df=1, $\chi^2 = 0.47$, NS, $p > 0.05$; for mixed groups: 15 and 12, $\chi^2 = 0.33$, df = 1,NS, $p > 0.05$).

4.3.2 Second set of experiments: two different shelters (dark and light)

The same statistical tests were used for the experiments with two different shelters. In this case, we observed 22 selection cases out of 30 tested mixed groups (Fig. 3A).

The model predicts that the difference in darkness between the shelters induces a bias in favor of the dark one, i.e. a change of value for the steady states of the system (Fig. 3C). The observed selection of the dark shelter (0.73 dark vs 0.27 light, Fig. 3A,C) is significantly different from a random choice ($\chi^2 = 4.55$, df=1, S, $p < 0.05$).

In Fig. 3A, the selection frequency of the dark shelter by cockroach groups (0.73) is statistically different from the selection frequency for mixed groups (0.40) with robots preferring to settle in the light shelter ($\chi^2 = 11.23$, df=1, S, $p < 0.05$).

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