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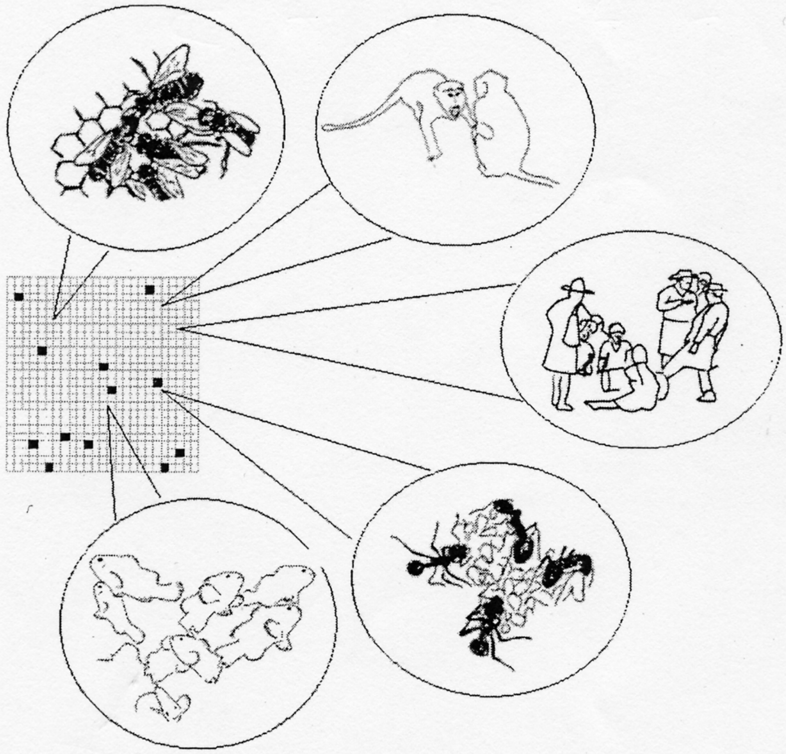
Charlotte K. Hemelrijk
AI Lab, University of Zurich, Switzerland

Papers and Abstracts



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Modelling of the chemical recognition system of ants

N. Labroche[1], F.J. Richard[2], N. Monmarché[1], A. Lenoir[2], G. Venturini[1]

[1] Laboratoire d'Informatique de l'Université de Tours
École d'Ingénieurs en Informatique pour l'Industrie
64, avenue Jean Portalis 37200 TOURS, France
labroche,monmarche,venturini@univ-tours.fr
[2] Institut de Recherche sur la Biologie de l'Insecte
CNRS UMR 6035, Université de Tours
Faculté des Sciences et Techniques, Tours, France
freddie-jeanne.richard@etu.univ-tours.fr, lenoir@univ-tours.fr

In this paper, we introduce a new mathematical model of the chemical recognition system of ants. This mechanism of colonial closure, can be observed when real ants need to discriminate between nestmates and intruders. Many works already describe this phenomenon for distinct species, but none of them formalises it from a computational point of view. In this work, we aim at reproducing experiments that are performed by biologists with real ants and testing hypothesis that may explain biological results. To reach our goal, we first model the individual and social behaviours that are involved in the establishment of a Gestalt odour in the colonies. We then simulate these behaviours in an artificial laboratory. For the time being, our results confirm the role of food in the divergence of cuticular odours profiles for the fungus growing ant species. Moreover, our system allow one to better appreciate the role of external cues such as queen and environmental odour as their influence is fully parameterised by the user.

Many biologists described the recognition system of social insects such as wasps, bees, termites and ants. This paper focuses on the colonial closure mechanism in the ants societies. It allows ants to discriminate between conspecifics and heterospecifics but also between nestmates and non-nestmates. According to the "Gestalt odour" theory, the colonial closure is achieved by the existence of a colonial odour that is built by continuous exchanges of chemical substances between the nestmates. Despite the importance of this phenomenon, no work managed to model the underlying chemical interactions of such mechanism as far as we know. Other studies modelled the foraging behaviour of ants and its emergence according to a genetic algorithm in Ant Farm [2] or the emergence of social structures in artificial ants populations in the Manta project [3]. Other works have proposed models inspired from the ants to solve computer science problem [10]. We may cite: the ability of ants to sort their brood in [8][9] and the use of pheromones trails in the algorithmic approach Ant Colony Optimization (ACO) [5]. Our goals are to propose a mathematical model of the colonial closure in the ant societies and to use it to deepen our understanding of the chemical recognition system of ants by evaluating biological hypothesis in an artificial framework. The paper is organized as follows: the recognition system of ants is introduced in section 2 while the third section describes the mathematical modelling. The fourth section presents the application of the model in an artificial life simulator and the results that have been obtained when studying the fungus growing ants. Finally, the conclusion discusses the future evolutions of the model and the simulator.

About real ants

Each time they meet, ants are able to identify the encountered odour to detect intruders. The mechanism by which an ant decide to accept or reject an other has led biologists to develop four hypothesis to explain its origin.

- Ants may use spatial discriminators. In this case, an ant would recognize an intruder if it does not own the right environmental odour. This may be the case for the *Pachicondyla apicalis* species.
- Ants may use purely genetic discriminators. It would mean that each ant is able to innately understand the genome of the encountered ant via its cuticular odour and then to decide if it should be accepted or not. This is not a valuable hypothesis because some ants can change their belonging nest only if their cuticular hydrocarbons are replaced by those of an other colony.
- Ants may use a "phenotype matching" mechanism, in which each ant has to learn the distinctive signs of its colonies (in term of appearance, size, odour), to recognize intruders.
- Ants may learn, at each contact with a nestmate, its odour and build a sort of template of what should smell a nestmate. In this hypothesis, each ant has its own representation of what should be the odour of a nestmate but has to update it continuously to be aware of changes that may occur.

The two last hypothesis are the more likely to fit the biological reality: the recognition between two ants relies mainly on the detection of phenotypic differences [7]. The recognition system, for each ant, can be seen as follows [6]: each ant emits an odour called label, that is composed of chemical substances spread over its cuticle. Similarly, each ant has a chemical reception system that allows it to perceive the encountered labels. To decide if it should accept an encountered ant or not, during its youth each ant learns a template representative of what should smell a nestmate. Thus, the recognition problem is resolved by the comparison of the perceived label to its template and the reaction is triggered by behavioural rules.

Composition and evolution of the label of ants

The identity of an ant is characterized by its label. It is mainly composed by hydrocarbons generated by the ant and also by chemical substances that originate either from the food or the nest's materials of the ant. There are also many external factors that can induce changes in the label and modify the recognition system. The influence of these factors has been highlighted by some experiments that are summed up in the next section . We may cite among these, species that may induce quantitative and qualitative changes in the concentration of hydrocarbons of the label. We may also notice the particular role played by the queen. In some species, the queen is a major discriminator of the recognition system because the queen adds its own chemical substances to the labels of its nestmates, whereas in some other species, it only helps spreading the colonial odour to a maximum number of nestmates.

When born, ants can not distinguish between nestmates and non-nestmates and their label is reduced to a simple "brood masking odour". This odour plays two major roles: first it prevents young ants from being eaten by the others and second it makes them smell attractive to the nestmates [7]. As the nestmates take care of them , the young ants learn how to recognize the ants of their colony. They develop their first template by physically impregnating other colony members labels by repeated social contacts such as feeding and grooming. After a short time, ants are able to synthesise their own cues and can exchange them with other ants. According to the Gestalt odour theory, the homogeneous sharing of all nestmates odours leads to the establishment of the colonial odour. It is achieved by trophallaxis (an ant decants its post-pharyngeal gland (PPG) content in an other one), by "allo-grooming" (each ant decants a portion of its PPG over the other's cuticle) or by simple contacts (only cuticular substances are exchanged).

Typical experiments and their conclusions

Before detailing the model, we quickly describe some experiments that highlight interesting properties of the recognition system of ants.

In [4], the authors study a polydomous colony of *Cataglyphis iberica* in which the nestmates are isolated in different nests during the winter. It is known that after the separation, ants of this colony have to exchange more chemical substances to accept each others again, because a divergence in the label of the different groups has appeared. In the experiments, the authors changed the external factors of hibernation of each sub-nests of the colony and showed that ants were more aggressive after the separation period. These experiments prove that when a colony is separated in several sub-colonies there is a divergence in the sub-colonial odours and that some external factors (such as temperature) can increase this divergence.

In [6], the authors tested the modalities of acceptance of an intruder in a nest by taking an ant from a colony and by confronting it to ants from other nests. They showed that if the intruder is washed so as to "erase" the label spread over its cuticle and if its label is replaced by the label of a new nest, the ant can be accepted in the new nest. The integration can be so successful that the intruder can also participate to the defence of its new nest against its old nestmates. This experiment demonstrates the importance of the label in the recognition system and proves that the recognition relies more on chemical cues than on other communications ways (hearing, eyesight, gesture).

Other experiments show the importance of the food (in this case, vegetable fragments) in the discrimination between fungus growing ants where changes in the diet can modify dramatically the discrimination process [11].We will develop further these experiments in the result section because we use them to evaluate our model.

About artificial ants

Our model derivates from the scheme introduced by Carlin and Hölldobler in [1]. This scheme presents the colonial and the internal relations (between members of the nest and between internal organs) that lead to the establishment of a colonial odour for each ant. The authors define an ant as a set of biological entities (the label, the template and the genome) that interact with each others and with the environment. Similarly to this work, we introduce a scheme that represents the chemical relations between an ant and the external entities that may influence the recognition process (Fig. 1-left). The considered ant is drawn in the centre of the figure with bold lines that represent its cuticle and its internal organs that participate to the establishment of the individual odour. The main external entities that can modify the recognition system are the queen, the food, the environment, the nest materials and the other ants. The major differences between the new model and the model of Carlin and Hölldobler are that in the new model, all the entities have been detailed more accurately (for instance, the food and environment are modelled in 2 distinct entities) and each relation associates 2 entities to a probability of appearance, a proportion of chemical substances exchanged and is modelled by a mathematical function.

Entities of the model

We choose to represent in (Fig. 1-left) an ant as a set of entities that play a role in the establishment of the colonial odour. These entities exist for every ants of the simulation and may evolve with time. They are detailed hereafter at time t for an ant k.
The label is modelled as a vector $Label_k^t$ of $m = n + e + f$ components where the n first components LH^{tk} represent the concentration of the hydrocarbons of the ant, the following e components LE^{tk} stand for the chemical substances extracted from the environment and finally the f last components LF^{tk} correspond to the substances absorbed with the food. The label fluctuates with the time t and is formalized as follows:

$$Label_k^t = \left(LH^{tk}, LE^{tk}, LF^{tk}\right) \tag{1}$$

$$LH^{tk} = \left(LH_1^{tk}, \dots, LH_n^{tk}\right) \tag{2}$$

$$LE^{tk} = \left(LE_1^{tk}, \dots, LE_e^{tk}\right) \tag{3}$$

$$LF^{tk} = \left(LF_1^{tk}, \ldots, LF_f^{tk}\right) \tag{4}$$

The neuronal template $Template_k^t$, the post-pharyngeal gland content PPG_k^t and the nest materials $NMat^t$ are modelled similarly to the label to facilitate chemical exchanges in the model. They are all dynamic:

$$PPG_k^t = \left(PH^{tk}, PE^{tk}, PF^{tk}\right) \tag{5}$$

$$Template_k^t = \left(TH^{tk}, TE^{tk}, TF^{tk}\right) \tag{6}$$

$$NMat^t = \left(NMatH^t, NMatE^t, NMatF^t\right) \tag{7}$$

The genome of the ant Gen_k and its biosynthesis organs Bio_k are formalized only with n components relative to the hydrocarbons that compose the label and can not evolve (they are set at birth):

$$Gen_k = \left(Gen_1^k, \ldots, Gen_n^k\right) \tag{8}$$

$$Bio_k = \left(Bio_1^k, \ldots, Bio_n^k\right) \tag{9}$$

The queen is represented as any other ant but is defined separately because of its specific role in the model. The queen can be simply seen as 2 main entities. The first, $QueenGEN$, corresponds to the genome of the queen and is used to determine partially the genome of the nestmates. The second, $QueenPPG^t$ models the post-pharyngeal gland content of the queen. In many studies, the queen is said to approximate the colonial odour because it exchanges much more chemical substances than the other members of the nest.

$$QueenPPG_k^t = \left(QPH^{tk}, QPE^{tk}, QPF^{tk}\right) \tag{10}$$

$$QueenGEN_k = \left(QueenGEN_1^k, \ldots, QueenGEN_n^k\right) \tag{11}$$

The environment Env^t and the food $Food^t$ are represented respectively with e and f components to fit the definition of the label. Both entities evolve as the ant moves or changes its diet:

$$Env^t = \left(Env_1^t, \ldots, Env_n^t\right) \tag{12}$$

$$Food^t = \left(Food_1^t, \ldots, Food_n^t\right) \tag{13}$$

Relations between the entities of the model

We are going to translate the relations between biological entities to mathematical equations. All the relations rely on a function called Φ. This function is presented in the following equation 14 and models the influence α of a quantity Q_2 over a quantity Q_1 (with $0 \leq \alpha \leq 1$).

$$\Phi\left(Q_1, \alpha, Q_2\right) = (1-\alpha)Q_1 + \alpha Q_2 \tag{14}$$

This function converges to $\frac{Q_1+Q_2}{2}$ when it is repeated many times over the same quantities Q_1 and Q_2 with $\alpha \ll 1$.

We now describe the biological relations of the model whith respect to the parameters that appear on the edges of figure (Fig. 1-left).

(1) The environment substances are spread over the cuticle of ants when they move. The environment plays a role in the discrimination between two ants that live in distinct territory and do not "wear" the same territorial odour. This influence can be translated as follows:

$$LE^{t+1,k} = \Phi\left(LE^{tk}, \alpha_{Env}, Env^{tk}\right) \tag{15}$$

(2) The diet influences directly the content of the PPG and has indirectly an impact on the label. We choose to represent the influence of the food as follows:

$$PF^{t+1,k} = \Phi\left(PF^{tk}, \alpha_{Food}, Food^{tk}\right) \tag{16}$$

(3) The queen has a major role in the model: it gives birth to the nestmates and influences directly their genomes with its own. To characterize the genome of a new nestmate k we introduce the notion of genetic variance G_v that reflects the maximum deviation allowed between the genome of the queen and the genome of the considered nestmate k:

$$\forall i \in [1,n], Gen_k(i) = U(QueenGEN_k(i) - G_v, QueenGEN_k(i) + G_v) \tag{17}$$

where $U(a,b)$ generates a random number between a and b with a uniform distribution.

(4)(5)(5') The biosynsthesis organs product hydrocarbons according to the genome of the ants (eq. 18). For the time being, our knowledge does not allow us to decide if other substances can be generated by these organs, so the equation 18 is voluntary simple. The new substances are then distributed to the ant's cuticle (eq. 19) and to its PPG (eq. 20).

$$Bio_k = Gen_k \tag{18}$$

$$LH^{t+1,k} = \Phi\left(LH^{tk}, \alpha_{BSL}, Bio_k\right) \tag{19}$$

$$PH^{t+1,k} = \Phi\left(PH^{tk}, \alpha_{BSP}, Bio_k\right) \tag{20}$$

(6) We consider in the model that the PPG content is used to update the neuronal template because it is a place where all the substances capted from the other ants are gathering.

$$Template^{t+1,k} = \Phi\left(Template^{tk}, \alpha_{Temp}, PPG_k^t\right) \tag{21}$$

(7)(8)(8')(9)(10) There are many ways for an ant to exchange chemical substances. The ant can reinforce its label by spreading its PPG content over its cuticle: it is a self-grooming (7). The ant can also give a part of its odor to a nestmate either by allo-grooming (8)(8'), by trophallaxy (9) or by cuticular contacts (10), depending on the ants

species and their similarity.
A self-grooming can be modelled as follows:

$$PPG_k^{t+1} = \Phi\left(PPG_k^t, \alpha_{PPG}, Label_k^t\right) \tag{22}$$

$$Label_k^{t+1} = \Phi\left(Label_k^t, \alpha_{Label}, PPG_k^t\right) \tag{23}$$

An allo-grooming between ants f and g can be formalized as follows (the equations are only written for ant f but should be used similarly for ant g):

$$PPG_f^{t+1} = \Phi\left(PPG_f^t, \alpha_{PPG}, Label_g^t\right) \tag{24}$$

$$Label_f^{t+1} = \Phi\left(Label_f^t, \alpha_{Label}, PPG_g^t\right) \tag{25}$$

A trophallaxy from the ant f to the ant g can be modelled as follows:

$$PPG_g^{t+1} = \Phi\left(PPG_g^t, \alpha_{PPGt}, PPG_f^t\right) \tag{26}$$

A cuticular contact can be modelled as follows (the equation is given only for ant f but is similar for ant g):

$$Label_f^{t+1} = \Phi\left(Label_f^t, \alpha_{N_C}, Label_g^t\right) \tag{27}$$

The main principles of our model are now detailed. We describe hereafter the first results that we obtain using this model.

Virtual Ants Laboratory Simulator

In this section, we introduce the simulator *Virtual Ants Laboratory Simulator (VALS)*, that allows to test biological hypothesis concerning the chemical recognition system mechanisms, in a short time and with a high number of colonies and ants. We briefly present the way the simulator works and the behavioural scheme for each artificial ant in the simulation. We then detail the experiments we conducted and the results we obtained.

The simulator

The simulator models colonies that are defined mainly by a queen (if there is one in the nest), a set of ants, a diet that indicates the type of food the nestmates consume, the influence of each main source of hydrocarbons (”genetic”, environment and food) in the estimation of similarity between ants and a set of probabilities that define the behaviour of the ants for this colony (probabilities to meet the queen, meet a nestmate, be in the nest or outside, find a source of food, ...). As the simulator acts as a general framework, it has to be adapted to different species by setting these parameters.
The only thing that is common to all the species is the structure of the behavioural scheme of the ants as in figure (Fig. 1-right). In this stochastic view, all the boxes with round corners represent a state of the ant (searching food, trying to meet the queen,

. . .) and the arrows model the probabilities to perform the action and go to a new state. The rectangular boxes represent chemical exchanges (”O. exchanges”, ”Allo-grooming”, ”Trophallaxy” and ”Self-grooming”) or odour learning (”O. learning”). Our simulator

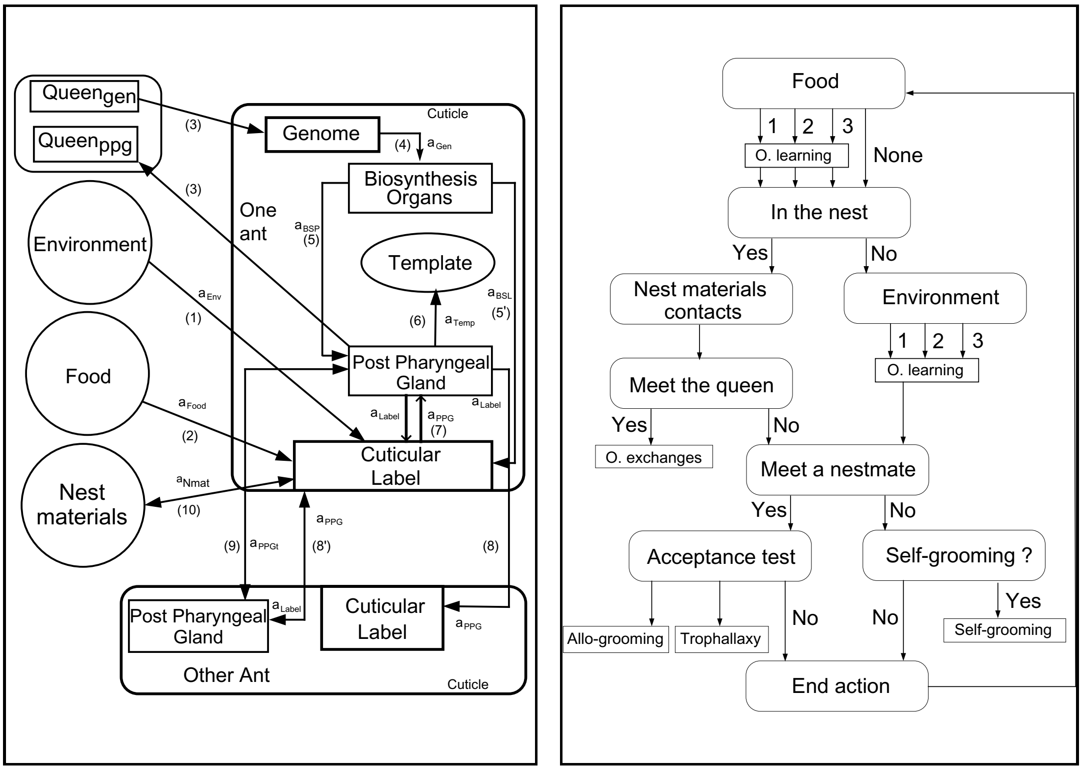

Figure 1: Left: new relational model of the recognition system of ants. Right: behavioural scheme for an ant in the model

gives a measure of distance between colonies that takes as input the mean chemical profile of each nest (computed with the post-pharyngeal gland content of each ant) and the influence of food, genetic and environment for the colonies. This measure is a value between 0 and 100 that correspond to a weighted Minkowsky distance at order 1.

Experiments

To see the efficiency of our simulator we aim at modelling colonies for which the diet has a bigger influence in the recognition process than other cues (”genetic” and environment). The protocol that we propose is the following: we generate a mother colony that consumes one food type and we split it in 3 sub-colonies. The first group (a) keeps the queen of the mother colony and its original diet, the second group (b) only keeps the original diet whereas the third group (c) changes the diet. If the predictions of the model are pertinent, then we expect that, after a time of separation that allows the odours of the sub-colonies to converge, we will obtain the following results. The distance between (a) and (b) should

Table 1: Results of the simulation over 2 runs and with 33 ants in each colony. The first columns "Genetic", "Environment" and "Food" indicate the influence of these factors in the discrimination process and the last columns present the distance observed between colonies (a),(b) and (c).

"Genetic"	Environment	Food	$(a)(b)$	$(a)(c)$	$(b)(c)$
$0,5$	$0,5$	1	0	5	6
1	1	1	1	3	3

not be significant because they have the same diet and the queen has no influence on discrimination for these colonies. The distances between (a) and (c) and between (b) and (c) should be more important according to the fact that the groups do not share the same diet.

In order to be able to evaluate our simulator in a real framework, we consider neotropical fungus growing leaf-cutting ants from the tribe Attini *Acromyrmex subterraneus subterraneus* which discrimination process seems to rely rather on food than on other cues. In fact, these ants live in obligatory symbiosis with a fungus that they grow on fresh leaves harvested by workers. Colonial recognition is likely based on chemical cues provided by cuticular hydrocarbons that have been found to be partly influenced by environmental sources. In [11], the authors tested the impact of different plant diets on colonial recognition. We use in our simulator the real chemical profiles extracted from the post-pharyngeal gland of these fungus growing ants, to set the odour of the food found by the ants. The table (Table. 1) sums up the results of our experiments. The columns headings "Genetic", "Environment" and "Food" indicates the influence of these factors, and $(x)(y)$ represents the distance observed between colonies (x) and (y). The results are given for two sets of parameters: one that gives more influence to the diet in the discrimination system and one that has no preference. As expected, the model predicts a significant increase in the distance between the groups that do not share the same odour (6 instead of 3) and allow to attenuate the distance due to the separation between groups (a) and (b) (distance equals 0 instead of 1).

Discussion

As the first results show, our model seems to be promising. For the time being, its allows to predict results that are similar to those obtained with the chemical study of the fungus growing ants, when we define colonies that favours food discrimination. However, we are not able yet to link chemical studies with behavioural studies as biologists usually do. We plan to model the scale of aggression used by biologists to realise complete prediction for the parameterised species. Moreover, we plan to enhance our model by adding a weighted queen odour, that acts as a marker on the nestmates and which has been described for some species.

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