

# The Computationally Complete Ant Colony: Global Coordination in a System with no Hierarchy

Michael Lachmann<sup>1</sup> and Guy Sella<sup>2,3</sup>

<sup>1</sup> Department of Biological Sciences, Stanford University  
Stanford CA 94305, USA

e-mail: dirk@charles.stanford.edu

<sup>2</sup> Interdisciplinary Center for Neural Computation  
The Hebrew University of Jerusalem, Jerusalem, Israel

<sup>3</sup> School of Physics and Astronomy  
Raymond and Beverly Sackler Faculty of Exact Sciences  
Tel-Aviv University, Tel-Aviv 69978, Israel  
e-mail: guy@math.tau.ac.il

**Abstract.** We present a model inspired by task switching of ants in a colony. The model consists of a system composed of many identical ants. Each ant has a finite number of internal states. An ant's internal state changes either by interaction with the environment or by interaction with another ant. Analyzing the model's dynamics, we prove it to be computationally complete. This gives us a new perspective on the sophistication a colony can display in responding to the environment. A formalism for measurement and response in the framework of the model is presented. A few examples are studied. The model demonstrates the possibility of inducing very complex global behavior without any hierarchical structure.

## 1 Introduction

Understanding the dynamics of ant colonies is a classic problem in sciences that try to understand the behavior of “complex systems.” It is a clear example of a system in which the complex behavior of the whole arises from the interactions of many parts, so that the whole seems to be more than the sum of its parts. What kind of behavior of the single ant creates the complex behavior of the whole colony ?

In many systems consisting of a multitude of entities, the composite behavior of the individuals creates a coordinated complex behavior of the whole system. There are two possible ways to achieve such a coordination – the top-down approach, and the bottom-up approach. In the top-down approach, a hierarchy in the entities creates a control structure that guides the behavior of the system. This approach is for some reason is the one easier to understand, perhaps because of the similarity between the apparent structure, and its manifestation in the causal structure of events. A manifestation of this approach is found in the way an

army is coordinated, through a hierarchical command structure. In the bottom-up approach, the rules followed by the individual entities bring a self-organization of the system. Most systems in nature have elements of both approaches in them. The behavior of a modern free-market economy is composed both of some hierarchy imposed by corporations and the government, and of self-organization resulting from the action of independent agents in the free market.

In this paper we present a model that is inspired by the behavior of ants in a colony. The aim is twofold. The first is to show what level of coordination might be expected from an ant colony, even under very simplistic assumptions about the behavior of the ants. Thus, it is not claimed that an ant colony is fully described by the model, rather, as the ingredients of the model are contained in an ant colony, the colony will surely be able to achieve at least a response which is as sophisticated as the one described by our model. The second aim is to show one way in which a system can perform certain tasks or computations using the bottom-up approach. This insight will be useful in studying systems other than ant colonies.

Understanding the behavior of an ant colony requires understanding of global coordination without hierarchy. Even though the reproducing ant in the colony is called the queen, empirical work shows that in many cases she does not seem to be at the top of a hierarchy which rules the colony. The behavior of the colony seems to simply arise from the behavior of the individual workers. There are many other cases in nature where we face the same phenomenon. These include the behavior of colonies of other social animals such as bees or termites, but also the understanding of the action of the immune system or the interactions of the proteins and other molecules which make up the cell.

There are several approaches to studying the behavior of a colony of social insects. One is through understanding how the behavior of the colony might be affected by pheromone trails laid by ants (see Deneubourg and Gross, 1989). Several models show how this might lead to optimal, or observed, foraging patterns of the colonies (Deneubourg et al. 1989, 1990; Gross et al. 1990; Millonas 1994). Another approach is to understand the allocation of individuals to tasks in the colony. Individuals in a colony often engage in different tasks – foraging, nest-maintenance, brood care, etc. It has been shown that social insects may react to the environment by changing the proportion of individuals allocated to the various tasks in the colony (Calabi 1987; Gordon 1989; Robinson 1992). An example of this is recruiting ants for nest maintenance when there is a need to remove obstacles from the neighborhood of the nest. In this paper we follow the trail laid by the second approach, trying to understand mechanisms underlying the task allocation. It will, of course, be worthwhile to synthesize this work with the first approach in further research.

How does an ant colony react to its environment? Let us examine a reaction of a multi-cellular organism, such as our body, to the environment. Light signals are absorbed by photo-receptors in the retina cells. These signals are then transmitted through the central nervous system (CNS) to the brain, where they are assessed using information about the environment currently stored in the

brain. A signal for a reaction is then transmitted through the CNS to regulating neurons controlling a muscle in the hand, for example. The ant colony might face a similar task. Some ants – patrolers – might gain information about a food source, and other ants will then need to be recruited to forage at that food source, potentially bringing into account some information about the current state of the colony, the hunger level in the brood for instance. This has to be achieved without a CNS connecting the various ants, and without a brain to store and assess the information.

Gordon et al. (1992) showed how certain behaviors of individuals in the colony may enable the colony to process information like a Hopfield net. The model assumed, however, that individual ants are able to measure global states of the colony, such as the proportion of ants allocated to certain tasks. Our model is based on the model presented by Pacala et al. (1994). In this model ants can engage in a task or be inactive. Ants doing a task can also be either “successful” or “unsuccessful” and can switch between these two according to how well the task is performed. Unsuccessful ants also have a certain chance to switch to be inactive, and successful ants had a certain chance to recruit inactive ants to their task. This is an example of how certain interactions of ants can give rise to global behavior in the colony.

In the model presented in this paper, the notion of a “successful” or “unsuccessful” ant engaging in a certain task is expanded to a general notion of a state that the ant is in. An ant in the colony can be in one of a finite number of states. Ants doing different tasks are always in different states, but ants doing the same task could also be in different states. Such a state might correspond, for example, to an ant foraging while hungry and successful. It is assumed that there are many more ants in the colony than states, so that it makes sense to talk about the fraction of ants in a certain state. The ways in which an ant can change its state are through interaction with the environment and through meeting another ant. The model is aspatial, and thus does not regard the place of ants in the colony or the pheromones left by the ants in certain places in the environment.

In Sect. 2 we present the master equation for this model, assuming an infinite number of ants in a colony. Then in Sect. 3, we show that this model can lead to a very complex behavior, including amplification, cycling, and potentially the performance of any computation that can be done by a finite Boolean network or by a finite Turing machine. We also present a different formulation of the model, in which the interaction with the environment is separated to “measurement”. In Sect. 4 we present two examples. One is a test of how well a finite colony fits the predictions of the model. The other presents a model developed by Seeley et al. (1991) in order to show a possible solution to choosing between two alternate foraging sites in bees. It is shown how this solution can be stated within the framework of our model.

## 2 The Infinite-size Model

Our infinite-size model consists of the following assumptions:

- At any time, each ant can be in any of  $M$  states. Let  $p_i(t)$ , where  $i = 1, \dots, M$ , be the fraction of ants in the colony that are in state  $i$ . Different tasks correspond to different states, but different states can correspond to the same task.
- An ant can switch tasks either spontaneously, or through social interaction. The probability of spontaneous switching is dependent on the environment. The probability per unit time for an ant in state  $i$  to switch to state  $j$  in an environment  $s$ , is denoted  $A_{ij}(s)$ . In a social interaction in which an ant in state  $i$  encounters an ant in state  $j$ , this ant has a probability  $B_{ijk}$  of switching to state  $k$ .
- The number of ants is large enough, and the number of states small enough, that  $p_i(t)$  can be treated as a real number.

Under these assumptions, the master equation is<sup>1</sup>:

$$\frac{dp_i}{dt} = - \sum_{j=1}^M A_{ij}(s)p_i + \sum_{j=1}^M A_{ji}(s)p_j + \alpha(N) \left( - \sum_{j,k=1}^M B_{ijk}e_{ij}(s)p_i p_j + \sum_{j,k=1}^M B_{jki}e_{jk}(s)p_j p_k \right), \quad (1)$$

where  $i = 1, \dots, M$ , and  $e_{ij}(s)$  is the probability per time unit for an ant in state  $i$  to encounter an ant in state  $j$ . This probability can be a function of  $s$ , the environment. We will not deal with the determination of  $e_{ij}$ , and for the simplicity of the analysis it will be subsumed by  $B_{ijk}$ .  $\alpha(N)$  is a factor to scale the speed at which ants meet relatively to the speed at which they switch states spontaneously, as the density changes as a result of a change in the number of ants in the colony,  $N$ .

Because  $p_i$  is the fraction of ants in state  $i$ , it is subject to the constraints  $\sum_{i=1}^M p_i = 1$ ,  $p_i \geq 0$ . In Appendix A, it is shown that, assuming  $A_{ij} \geq 0$  and  $B_{ijk} \geq 0$ , these constraints are maintained by this master equation.

In this model we omit the effects of space and finite size. These are briefly addressed in the example in Sect. 4. Furthermore, in the initial study of the model we have not included the changes to the environment resulting from its interactions with the ants, such as foraging, nest maintenance, and pheromone

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<sup>1</sup> In general all variables in this equation could depend on the environment and on the density of the ants, but we believe the formulation given in the equation covers a wide range of cases. Thus  $B_{ijk}$  could depend on the environment, but we separated out cases in which this change could simply be called a change of the ant's state, or a change caused by changing the chance of the ants to meet (which is included in  $e_{ij}(s)$ ), or a change caused by the effect of the number of ants in the colony on the density of the ants (which is included in  $\alpha(N)$ ).

marking. In the following sections we show the dynamics of this model to be very rich, even without these feedback mechanisms. Nevertheless, we believe understanding these mechanisms is important for understanding the behavior of an ant colony.

### 3 Interpreting the Master Equation

As we show in Sect.3.3, a colony in the model be *computationally complete* just as a computer or a neural network. This means that the colony can respond to the environmental input in a complex way. It is also shown that in this model the colony may exhibit stable fixed points, or periodic cycles.

The systems studied in the following sections are defined by the specific choices of  $A$ 's and  $B$ 's. Using the notation illustrated in Fig. 1 will be helpful in studying specific examples. An arrow (see Fig. 1a) shows that an ant in state 1 has a certain non-zero chance of going over to state 2; in other words,  $A_{12} \neq 0$ . The number under the arrow indicates the value of  $A_{12}$ , in this case 0.64. An arrow with a dashed line connected to it (see Fig. 1b) means that if an ant in state 1 meets an ant in state 2, the former has a non-zero chance of changing to state 3;  $B_{123} \neq 0$ . Again, the number under the arrow shows the value of  $B_{123}$ , 0.7.

#### 3.1 Amplifier

In this section we consider a colony that exhibits a behavior like an amplifier. Two states (state 1 and 2) are affected by the environment, so that under certain conditions ants in state 1 tend to go to state 2, and under other conditions ants in state 2 tend to go to state 1. These will be called input states. This colony will behave like an amplifier, because the ratio of the ants in the input states will be amplified to states 3 and 4; thus, if  $p_1/p_2 > 1$ , then  $p_3/p_4 > p_1/p_2$ , and if  $p_1/p_2 < 1$ , then  $p_3/p_4 < p_1/p_2$ . The relationship of the states is illustrated in Fig. 1c. The equations for this system are

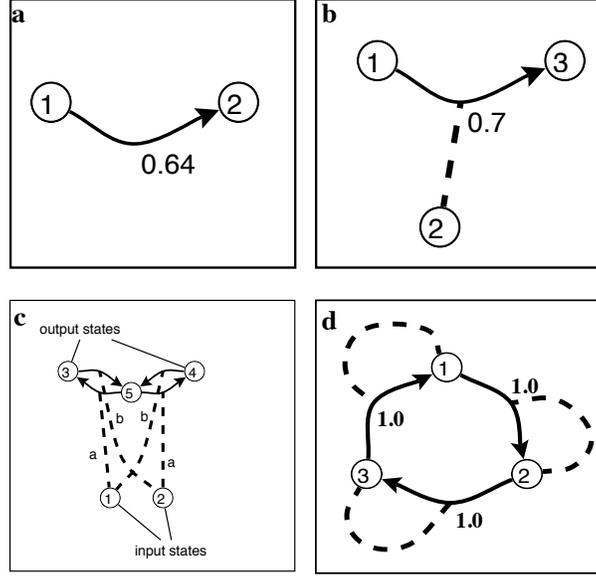
$$\frac{dp_1}{dt} = \frac{dp_2}{dt} = 0 \quad , \quad (2)$$

$$\frac{dp_3}{dt} = -bp_3p_2 + ap_5p_1 \quad , \quad (3)$$

$$\frac{dp_4}{dt} = -bp_4p_1 + ap_5p_2 \quad , \quad (4)$$

$$\frac{dp_5}{dt} = -ap_5p_1 - ap_5p_2 + bp_3p_2 + bp_4p_1 \quad . \quad (5)$$

They can be derived from the figure by adding, for each arrow with a dashed line that goes from  $i$  to  $j$  and has a dashed line at  $k$ , and a weight  $B_{ikj}$  – the



**Fig. 1.** a) Arrow representing spontaneous state transition. b) Transition through an encounter. c) Transition diagram of the amplifier. d) Transition diagram of the oscillator.

term  $-B_{ikj}p_i p_k$  to  $dp_i/dt$  and the term  $B_{ikj}p_i p_k$  to  $dp_j/dt$ . Given the initial conditions  $p_i(0), i = 1, \dots, 5$ , the system will converge to the solution

$$p_1 = p_1(0) , \quad (6)$$

$$p_2 = p_2(0) , \quad (7)$$

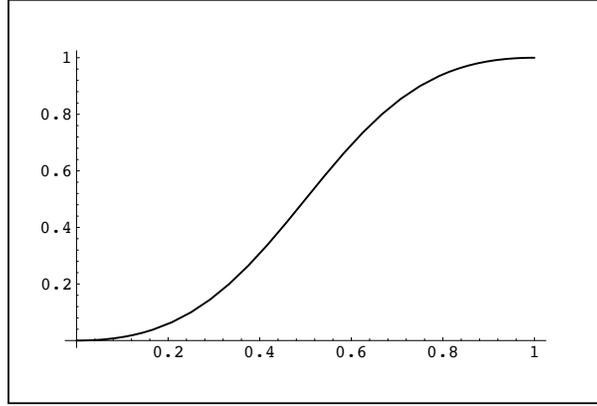
$$p_3 = s \frac{a}{b} \left( \frac{1}{\alpha^2 + \alpha + 1} \right) , \quad (8)$$

$$p_4 = s \frac{a}{b} \left( \frac{1}{\alpha^{-2} + \alpha^{-1} + 1} \right) , \quad (9)$$

$$p_5 = s - p_3 - p_4 , \quad (10)$$

where  $\alpha = p_1(0)/p_2(0)$ , and  $s = p_3(0) + p_4(0) + p_5(0)$ . For this point one gets

$$\frac{p_3}{p_4} = \left( \frac{p_1}{p_2} \right)^2 . \quad (11)$$



**Fig. 2.**  $\beta_{in}$ , the input to the amplifier at time 0, vs.  $\beta_{out}$  the output of the amplifier at equilibrium.

Thus, the ratio of  $p_1$  to  $p_2$  was amplified. If we define the input to the amplifier as  $\beta_{in} = p_1/(p_1 + p_2)$ , which will be a number between 0 and 1, and the output of the amplifier as  $\beta_{out} = p_3/(p_3 + p_4)$ , then the colony will settle on the equilibrium

$$\beta_{out} = \frac{\beta_{in}^2}{2\beta_{in}^2 - 2\beta_{in} + 1}. \quad (12)$$

The graph of  $\beta_{out}$  vs.  $\beta_{in}$  is shown in Fig. 2.

It can be seen that this function is similar to the sigma function used in neural nets. Thus, the relation between the number of ants in states  $p_1$  and  $p_2$ , which is represented by  $\beta_{in}$ , was amplified in a sigmoid-like manner to the relation between the number of ants in states  $p_3$  and  $p_4$ , represented by  $\beta_{out}$ . By connecting several amplifiers “sequentially”, by having the output states of one amplifier act as the input states of the other, one can approximate a step function, building a unit that acts much like a neuron.

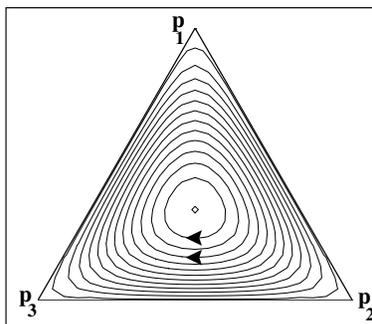
### 3.2 Oscillator

The following colony has a periodic trajectory as a solution. The dynamics are depicted in Fig. 1d. The equations for this system are

$$\frac{dp_1}{dt} = -p_1p_2 + p_1p_3, \quad (13)$$

$$\frac{dp_2}{dt} = -p_2p_3 + p_2p_1, \quad (14)$$

$$\frac{dp_3}{dt} = -p_3p_1 + p_3p_2. \quad (15)$$



**Fig. 3.** Trajectories of solutions to equations 13–15 on the simplex.

This is an equation in the two-dimensional simplex  $p_1 + p_2 + p_3 = 1$ . It has four fixed points:  $(1, 0, 0)$ ,  $(0, 1, 0)$ ,  $(0, 0, 1)$ ,  $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ . For solutions of these equations,  $d(p_1 p_2 p_3)/dt = 0$ , and therefore the trajectories lie on lines with constant  $p_1 p_2 p_3$ . From this it follows that all solutions, except for the four fixed points and the boundary of the simplex, are periodic. Figure 3 shows the trajectories on the simplex.

### 3.3 NOR-gate

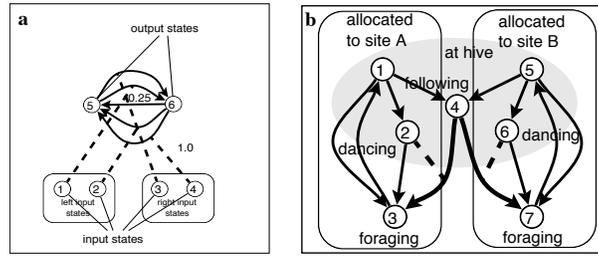
The last example for possible behaviors of an ant colony under the assumptions of the model can be interpreted as a NOR-gate. A NOR-gate is a Boolean gate and has the property that with it any Boolean network can be built. Appendix B describes this gate. The relations of the states in the gate are depicted in Fig. 4. The full gate needs to feed the output through three amplifiers. The equations for this system are

$$\frac{dp_1}{dt} = \frac{dp_2}{dt} = \frac{dp_3}{dt} = \frac{dp_4}{dt} = 0 \quad , \quad (16)$$

$$\frac{dp_5}{dt} = -p_1 p_5 - p_3 p_5 + p_4 p_6 + p_2 p_6 + \frac{1}{4} p_6 \quad , \quad (17)$$

$$\frac{dp_6}{dt} = -p_4 p_6 - p_2 p_6 + p_1 p_5 + p_3 p_5 - \frac{1}{4} p_6 \quad . \quad (18)$$

The inputs are defined as follows:  $p_1 + p_2 = p_3 + p_4 = \frac{1}{3}$ ; if  $p_1/p_2 > 3$ , then the left input is 0 (see Fig. 4); if  $p_1/p_2 < \frac{1}{3}$ , then the left input is 1. If the ratio is between these two values, the input is undefined. The right input is defined similarly. The output is defined in the same way: if  $p_5/p_6 > 3$ , the output is 0; and if  $p_5/p_6 < \frac{1}{3}$ , the output is 1. In Appendix B it is shown that in all cases of a well-defined input (that is  $p_1/p_2, p_3/p_4 < \frac{1}{3}$  or  $p_1/p_2, p_3/p_4 > 3$ ), the output behaves as it should for a NOR-gate.



**Fig. 4.** a) Transition diagram of a NOR-gate. b) Transition diagram for choosing a foraging site by bees.

### 3.4 Computation Completeness and other Conclusions

The NOR-gate of Sect. 3.3 concludes the tools we need to prove that the system is computationally complete. Using this NOR-gate, one can build any Boolean circuit. Using a Boolean network of polynomial size (in the input size), with a clock of the sort built in Sect. 3.2, one can compute anything that a finite computer can (see Borodin 1977; Parbery 1994). Thus, such a system can do computation as much as silicon computers can.

A potential problem might arise because as the size of the memory of the system scales up, the number of potential states of each ant goes up, and with them the size of the transition matrices  $A$  and  $B$ ; one might say that the individuals are not simple anymore. If we build the system with NOR-gates, then for an ant in a certain state, the number of other states it needs to interact with and that it can potentially reach, is small and does not scale up as the system scales up. Thus, most of the entries in these matrices are 0, and the ant just has to be supplied with the rule “do not interact with an ant in a state you do not know”; this might restore the “simplicity” of the ants.

By showing computational completeness of the model, we do not mean to say ant colonies perform universal computation. Computational completeness is a property characterizing the complexity of the dynamics, like being chaotic (discussion on the dynamical implications of systems with computational power could be found in C. Moore 1990). A use for the computational abilities described is briefly addressed in the discussion. Another implication of the computational completeness is that it can give us a new perspective on the level of sophistication an ant colony can display in its interaction with the environment. In Sect. 4.2 we describe a model presented by Seeley et al. for explaining the behavior of bees, in deciding between alternative foraging sites. The computational completeness tells us that even a more elaborate response, taking into account more inputs from the environment should not be surprising.

### 3.5 A Mechanism for Measurement and Response

Further understanding of the model can be reached by showing that for certain choices of  $A$ 's and  $B$ 's, one can interpret the dynamics as consisting of two processes: one in which the colony measures the environment, and another in which it uses the information from the measurement for a computation. Such a computation can result in a response to the measured environment.

A simple formalism is to denote each state, using two indices:  $i = (m, n)$  where  $(m = 1, \dots, M$  and  $n = 1, \dots, N.)$  The first index,  $m$ , will be related to the measurement, and the second,  $n$ , to the computational state. We further assume that the  $A$  elements mediate the measurement:  $A_{(m,n)(m',n')} = A_{m',m}\delta_{n,n'}$  ( $\delta$  is the Kronecker delta function,  $\delta_{ij} = 0$  when  $i \neq j$ ,  $\delta_{ii} = 1$ ), i.e the  $A$  elements do not change the computational index of the state, and

$$B_{(m,n)(m',n')(m'',n'')} = B_{n(m',n')n''}\delta_{m,m''} . \quad (19)$$

That is, the  $B$  elements do not change the measurement state. This assumption is made in order to simplify the following equations. Defining  $P_m^{\text{mes}} = \sum_n p_{(m,n)}$  and  $P_n^{\text{com}} = \sum_m p_{(m,n)}$ , leads to the following equations for the change in  $P_m^{\text{mes}}$  and  $P_n^{\text{com}}$ :

$$\frac{dP_m^{\text{mes}}}{dt} = \sum_{m'} A_{m',m} P_{m'} - A_{m,m'} P_m , \quad (20)$$

$$\frac{dP_n^{\text{com}}}{dt} = \sum_{n',m'',n'''} B_{n'(m'',n''')n} P_{n'}^{\text{com}} p_{(m'',n''')} - B_{n(m'',n''')n'} P_n^{\text{com}} p_{(m'',n''')} \quad (21)$$

The first set of equations are like standard master equations in statistical mechanics for  $P_m^{\text{mes}}$ s. One can interpret it as the colony measuring the environment with the result represented by the vector  $(P_1^{\text{mes}}, \dots, P_M^{\text{mes}})$ . The second set of equations describes change in the computational states according to both the computational states and the measurement states.

It may be claimed that the term measurement is not simply a mathematical definition, that when one speaks of measurement one assumes the intervention of some intelligent entity that performs it. We do not claim that an ant colony does a measurement in this respect. Nevertheless, following a line of argument set by J. von Neumann (1955), we demonstrate the existence of a process having the physical manifestation of a measurement: One feature of measurement is the correlation induced between the state of the measuring apparatus and the state of the system measured. Furthermore, when a human performs a measurement, the perception of its result induces a correlation between the state of the brain and the state of the system. Another feature related to the process of measurement is the possibility of its result affecting the actions of whoever performed it. The possibility of these two features in the framework of the model was demonstrated.

As for the existence of "real" measurement, one may conceive an ant colony as an entity with purpose, and as such it might "qualify" to perform "real" measurements. Whether this is the case, is an interesting question, but beyond the scope of this work.

## 4 Examples

In this section we present two examples of systems exhibiting a behavior that can be explained by the described model. Only the first is an ant colony. The second is a bee colony, from a model done by Seeley et al. (1991).

### 4.1 Discrete Spatial Model

A first step in testing the applicability of this model to an ant colony is to change the model to a finite-size population. Another step is to take into account each individual ant's spatial position.

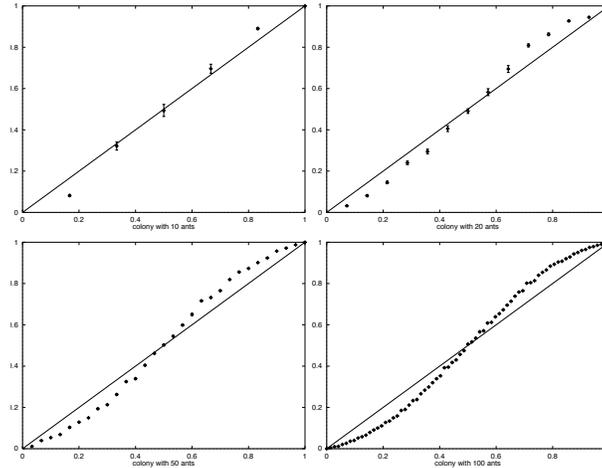
$A_{ij}$  of (1) is interpreted now as the probability that any single ant in state  $i$  will change to state  $j$  per time unit.  $B_{ijk}$  is the chance for an ant in state  $i$  to go over to state  $k$  during an encounter with an ant in state  $j$ . A simulation was done using the following additional assumptions.

- $N$  ants were put on a rectangular grid with cyclic boundary conditions.
- Each ant did a random walk with equal probabilities of walking in the eight possible directions (the eight nearest cells on the grid) and staying in its place. An ant never walked to a position already occupied by two other ants.
- The ants could be in  $M$  possible states. In each time unit, ants had a chance of changing their states according to  $A_{ij}$ . If two ants occupied the same grid point, they changed states according to  $B_{ijk}$ .

The simulation was run for the amplifier colony. Figure 5 shows  $\beta_{in}$  vs.  $\beta_{out}$  for colony sizes of 10, 20, 50, and 100 ants on a square grid of size 20. It can be seen that in this case the colony acts like an amplifier even when colony size is small.

### 4.2 Allocation of Bees to Alternate Foraging Sites

The model in this section is adapted from a model by Seeley et al. (1991), which explains how a bee colony can consistently allocate more foragers to the richer site, as they showed empirically. When the colonies were presented with two food sources at equal distances, more foraging effort was directed to the site with the richer food source. In the model, each foraging bee can be in one of seven states. A bee associated with a particular site can be in three states – at the hive, at the hive dancing, or foraging at that site. A bee can also not be associated with any site, in which case it is called “following” (see Fig. 4). The only difference between the models is that in the original model the bees spend a certain time at the site, whereas we use a Poisson process for the transition between foraging and being at the hive; at each moment a bee has the same chance of deciding to return to the hive. The results for this model are then, of course, exactly like those of Seeley et al. This model also demonstrates how a model with spatial components can be fit into the scheme of the model described here.



**Fig. 5.**  $\beta_{in}$  vs.  $\beta_{out}$  for a finite-size colony of size 10, 20, 50, and 100. Each point represents the mean of 10 simulation runs. The simulation was run on a square grid of size 20 by 20.

## 5 Discussion

Motivated by the manner in which an ant colony displays a highly coordinated global behavior in the absence of a hierarchical control structure, we studied a model system consisting of many identical units with a finite number of internal states. The state of the whole system is then determined by the fraction of units in each internal state. Following the bottom-up coordination scheme, the internal state of each unit was updated following a local rule. In this framework we demonstrated how such local rules can induce globally coordinated behavior. Furthermore, we addressed the question of how complex the global dynamics of such a system can be in this bottom-up approach. It is important to notice that even though the coordination is induced bottom-up, the collective complex behavior induced cannot be reduced to the level of the individual unit. Stated in computational terms, even though the system as a whole could perform a complex computation, no computation is performed by the single unit. This is necessary in the model (and maybe in an ant colony), since a single unit has no information on the state of computation. This information is coded in the state of the system, i.e. in the distribution of the units to the different states. In this sense, the whole is more than the sum of its parts.

The global behavior of computation resulting from a local rule has counterparts in neural networks (NN) and cellular automata (CA) models. These differ conceptually from this model, however, in that in this model the state of the whole system is defined by the fraction of units in the different states. This means an individual unit has no identity, in contrast to NN – in which the label

of the firing neuron is crucial, and to CA – where the relative spatial position of cells is likewise crucial.

This characteristic makes the ideas of the model relevant not only to ants, but also to other partly non-hierarchical systems such as the immune system, or a complex chemical system, which could be interpreted as performing computations, or could even be designed to do so. Indeed a model resembling the one presented was explored by Hjelmfelt et al. (1991), in which it was shown that a chemical reaction can potentially perform any computation a finite Turing machine can. In their model it is quite apparent that a single molecule does not have an identity, and only the interaction and relation of the molecules holds information and has computational power.

This model can be used as a basis for further research. One direction is to develop more elaborate models to study ant behavior. Spatial effects could be brought into consideration, and their effect on the encounter rate should be studied. An interesting question would be to study the complexity of response possible with respect to the number of ants in the colony (see also Gordon 1989, Pacala et al. 1994). A prediction which can be inferred from the model is that the statistics of task switching should show that when switching between tasks the ants must be going through some minimal number of intermediate states, which might or might not be measurable otherwise.

Three related challenging questions are : Where are the local rules instructions (the analogs of the *A*'s and *B*'s), kept? How can these rules change (i.e. changing the *A*'s and *B*'s) so the colony can learn to react correctly to its environment? How did such a coordination evolve in the first place?

For the version of the model studied here it was assumed that ants are identical units. It seems to be the case that for many social insects, the genetic composition of the colony is not uniform. If the transition rates are genetically governed, this could potentially pose a problem to selection on these genes. One might think that selection would have minimized the genetic variation in the colony, but this is not the case, and some colonies even have multiple queens. From this we expect that ants have solved this problem in a different manner.

A principle we believe should be incorporated in the study of these questions, is closing reaction loops to enable feedback (in our case feedback to the colony through the environment). A schematic description of such a loop is: 1. The colony measures the environment (as described in Sect. 3.5). 2. The measurements outcome induces a coordinated response (as described in Sect. 3.5). 3. The colony responds by acting on the environment. 4. The action causes changes in the environment in a way correlated to the state of the colony, thus closing a loop. (Which is, in a sense, a loop in which the order in the whole system grows.) In this respect, incorporating pheromone trails laid by the ants seems natural. The time-wise separation drawn above between the different stages is, of course, artificial.

Considering the colony as a selection unit, the evolution of *A*'s and *B*'s could be studied by applying a selective pressure on a population of colonies. We believe the study of such an evolution, should also include a closed loop

of reaction. Thus, not only having the selective pressure act on the population of colonies, but having the population of colonies change the selective pressure. How this should be done is indeed a challenging question.

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### Appendix A

In this appendix it is shown that for the model described in Sect. 2, if the constraints  $\sum_{i=1}^M p_i = 1$  and  $p_i \geq 0$  hold for  $t = 0$ , then they will hold always.

$$\frac{d}{dt} \sum_{i=1}^M p_i = \sum_{i=1}^M \frac{dp_i}{dt} \quad (22)$$

$$= \sum_{i=1}^M \left( - \sum_{j=1}^M A_{ij}(s)p_i + \sum_{j=1}^M A_{ji}(s)p_j + \alpha(N) \left( - \sum_{j,k=1}^M B_{ijk}p_i p_j + \sum_{j,k=1}^M B_{jki}p_j p_k \right) \right) \quad (23)$$

$$= - \sum_{i,j=1}^M A_{ij}(s)p_i + \sum_{i,j=1}^M A_{ji}(s)p_j + \alpha(N) \left( - \sum_{i,j,k=1}^M B_{ijk}p_i p_j + \sum_{i,j,k=1}^M B_{jki}p_j p_k \right) \quad (24)$$

$$= - \sum_{i,j=1}^M A_{ij}(s)p_i + \sum_{j,i=1}^M A_{ji}(s)p_i + \alpha(N) \left( - \sum_{i,j,k=1}^M B_{ijk}p_i p_j + \sum_{k,i,j=1}^M B_{ijk}p_i p_j \right) \quad (25)$$

$$= 0 . \quad (26)$$

Hence  $\sum_{i=1}^M p_i = 1$  always.

Next it will be shown that if  $p_i = 0$ , then  $\frac{dp_i}{dt} \geq 0$ , so that if initially  $p_i \geq 0$ , this will hold for later time also.

$$\frac{dp_i}{dt} = - \sum_{j=1}^M A_{ij}(s)p_i + \sum_{j=1}^M A_{ji}(s)p_j + \alpha(N) \left( - \sum_{j,k=1}^M B_{ijk}p_i p_j + \sum_{j,k=1}^M B_{jki}p_j p_k \right) \quad (27)$$

$$= \sum_{j=1}^M A_{ji}(s)p_j + \alpha(N) \left( \sum_{j,k=1}^M B_{jki}p_j p_k \right) \quad (28)$$

$$\geq 0 . \quad (29)$$

This is because all quantities in the last expression are non-negative.

## Appendix B

In this part it will be shown that the colony described in Sect. 3.3 behaves like a NOR-gate. For this, it has to have the following relations between the input and the output:

$in_1$	$in_2$	out
1	1	0
0	1	0
1	0	0
0	0	1

The input and output were defined such that, for example if  $\frac{p_1}{p_2} > 3$  the first input is 0, and if  $\frac{p_1}{p_2} < \frac{1}{3}$  the first input is 1. We also have  $p_1 + p_2 = p_3 + p_4 = p_5 + p_6 = \frac{1}{3}$ . This translates the same table to the following inequalities, which must hold at the steady state of the system.

$$\begin{aligned}
 p_1 < \frac{1}{12} \quad p_3 < \frac{1}{12} \quad \text{output} &= 0 \\
 p_1 > \frac{1}{12} \quad p_3 < \frac{1}{12} \quad \text{output} &= 0 \\
 p_1 < \frac{1}{12} \quad p_3 > \frac{1}{12} \quad \text{output} &= 0 \\
 p_1 > \frac{1}{12} \quad p_3 > \frac{1}{12} \quad \text{output} &= 1
 \end{aligned}$$

At a steady state (16)-(18) give the following:

$$p_5(p_1 + p_3) = p_6(p_4 + p_2 + \frac{1}{4}) , \quad (30)$$

or

$$\frac{p_5}{p_6} = \frac{p_4 + p_2 + \frac{1}{4}}{p_1 + p_3} . \quad (31)$$

If we apply the first line of table 6 we get

$$\frac{p_5}{p_6} > \frac{\frac{3}{12} + \frac{3}{12} + \frac{1}{4}}{\frac{1}{12} + \frac{1}{12}} = \frac{9}{2} . \quad (32)$$

If this were amplified through three amplifiers, the relation between the output states will be  $(\left(\frac{9}{2}\right)^2)^2$  which is greater than 3, so the output is 0, as required. The second line of the table gives

$$\frac{p_5}{p_6} > \frac{0 + \frac{3}{12} + \frac{1}{4}}{\frac{1}{3} + \frac{1}{12}} = \frac{6}{5} . \quad (33)$$

Amplifying this three times will give  $(\left(\frac{6}{5}\right)^2)^2$  which is also greater than 3, so the output is again 0. The last line of the table gives

$$\frac{p_5}{p_6} < \frac{\frac{1}{12} + \frac{1}{12} + \frac{1}{4}}{\frac{3}{12} + \frac{3}{12}} = \frac{5}{6} . \quad (34)$$

and amplifying this three times gives  $(\left(\frac{5}{6}\right)^2)^2$  which is smaller than  $\frac{1}{3}$ , so the output is 1.