Oscillations and Chaos in Ant Societies

Ricard V. Solé†, Octavio Miramontes‡ and Brian C. Goodwin‡

† *Complex Systems Research Group, Departament de Fisica i Enginyeria Nuclear, Universitat Politècnica de Catalunya, Pau Gargallo 5, 08028 Barcelona, Spain and ‡ Department of Biology, Open University, Faculty of Sciences, Milton Keynes, Walton Hall MK7 6AA, U.K.*

A neural network-like model of collective short-time oscillations in ant colonies is presented. Such behaviour has been recently observed in some experimental situations. Each individual is here considered as a cellular automaton able both to move into a given available space and to interact with other (nearest) automata. As a consequence of non-linear interactions, the observed oscillations are an emergent property of the colony as a whole. Time series and Fourier spectrum are in agreement with real data. The internal dynamics of each individual is modelled either by random process or deterministic chaos.

1. Introduction

Among the complex phenomena observed in nature, social behaviour is probably the best example of what we call "complexity". Groups of several non-linear interacting elements evolve in space and time displaying new higher-order phenomena. Such phenomena are called *emergent properties*. In this context, self-organization arises from the interaction of individuals, through simple local rules which are able to generate new correlations at larger scales. Ant colonies are a particularly interesting class of these systems. Individuals are not able to do those tasks which are characteristic of the whole colony, as nest construction or trail formation. As Hofstadter (1987) points out: ". . . Here we come to the mysterious collective behaviour of ant colonies, which can build huge and intricate nests despite the fact that the roughly 100·000 neurons of an ant brain almost certainly do not carry any information about the nest structure. How, then, does the nest get created? Where does the information reside? (. . .) Somehow, it must be spread about in the colony, in the caste distribution, the age distribution and probably largely in the physical properties of the ant body itself".

Several interesting studies on ant dynamics have been developed in recent years. Major contributions have come from Prigogine's ideas on self-organization (Nicolis & Prigogine, 1977). In this context, amplification processes linked with the non-linear character of interactions lead to new collective phenomena such as foraging properties (Deneubourg *et al.*, 1986; Gordon *et al.*, 1992). Randomness at the individual level was suggested as an efficient response to environmental unpredictability. Further studies by means of Monte Carlo simulation (Deneubourg *et al.*, 1989)

343

showed how macroscopic activity (such as the army ant raid patterns or the aggregation of some insect larvae) can be explained as the result of simple microscopic rules (for a general discussion, see Prigogine & Stengers, 1984). In this context the emergent "collective mind" is the result of the amplification of fluctuations in systems which are far from equilibrium. A few "decisions" in an unstable situation channels the system formed by many interactive elements toward a global structure.

A very interesting phenomenon which has been recently investigated (Cole, 1991a) concerns the existence of short time activity cycles in the dynamics of experimental ant nests. The origins of these dynamics is not clear, and synchronization of activity as periodic waves was noticed by Franks & Bryant in *Leptothorax acervorum* (see Franks *et al.*, 1990 and references therein). In this species an approximate 15 min activity cycle has been observed. Further studies by Cole (Cole, 1991a, b) on *Leptothorax allardycei* also showed clearly defined rhythmic changes in movement-activity levels. In the second case a careful experimental study of the colony and individual dynamics was performed using a solid-state automatically digitizing camera. The activity of numbers of individual workers was recorded and several interesting results concerning the global colony dynamics were obtained:

(i) The activity of the whole colony was shown to be periodic with a range of values between 15–37 min per cycle.

(ii) The activity of single ants, recorded by using isolated individuals, is not periodic. Single ants have patterns of activity characterized by spontaneous bursts of activity followed by relatively long periods of inactivity. As further individuals are added some synchronization begins to appear, but periodic activity seems to takes place only for a number of workers similar to the normal colony size.

(iii) A careful study of the experimental data showed evidence of low-dimensional deterministic chaos in the dynamics of single ants and periodic activity in whole colonies. The attractor of single ant activity (reconstructed from the obtained time series) was shown to have a small non-integer dimension. The activity of the entire colonies yielded an integer dimension.

It is our belief that the analogy between neural systems and insect societies (Hofstadter, 1979; Prigogine & Stengers, 1984; Kephart *et al.*, 1990; Gordon *et al.*, 1992) is not trivial. The interaction between individuals can be studied as some kind of neural-like phenomenon. In this sense, there is experimental evidence that ant behaviour can be switched as a consequence of worker interaction (Gordon, 1989). The activity level of nearest ants can switch the state of an individual from active to inactive as in the communication between two (or many) neurons. As in neural systems, behavioural processes will be defined, to some extent, by the kind of connectivity between microscopic parts (ants or neurones). Some kind of collective emergent behaviour will be observed as the result of local coupling. In neural organizations, retrieval or associative memory (and maybe consciousness) can be thought of as emergent properties. In ant societies, such new properties are, for example, nest building, trail formation or foraging behaviour.

These properties can be modelled by using a cellular automata (CA) model of ants and a neural-like interaction rule between individuals. Our model, as we will see, is

robust and the results obtained are not dependent on the specific choice of the main part of rules and parameters.

2. Neural Network Models and Cellular Automata

CA models are based on the definition of a set of rules which are then applied to a discrete set of lattice sites (the automata) over a discrete time scale. The main part of CA models is based on a local interaction scheme in which the automata state $S(\mathbf{k}; t)$ is updated following a simple dynamical rule, i.e.

$$S(\mathbf{k}; t) = F_\mu\left[\sum_{\mathbf{k}'} \alpha(\mathbf{k})S(\mathbf{k}'; t)\right] \tag{1}$$

F_μ being the rules, $\{\mathbf{k}'\}$ the nearest neighbours of $\mathbf{k}$ and $\alpha(\mathbf{k}) \in \mathbf{Z}$ as a set of constants. In spite of the simplicity of these models, they are able to generate complex and intricate structures. These structures are then emergent properties of the CA models, including periodic and chaotic dynamics and propagating structures.

A specially important type of CA are formal neural networks, in which the elements (neurones) are defined by Boolean variables (Serra & Zanarini, 1990). A neural network (NN) is a large and more or less interconnected assembly of simple elements. The elements (neurones) are usually two-state automata. They can be "active" ($+1$) or "inactive" (-1) depending on the sum of the inputs from other elements. A NN is a simple model of co-operative behaviour in the nervous system, and gives new insight into the study of computational properties of such systems. The statistical properties of these models are very close to well-known disordered systems, and physicists' interest in NN stems largely from such an analogy (Sompolinsky, 1988; Amit, 1989).

In recent years, increasing attention to NN theory has been dedicated to Hopfield-like systems (Hopfield, 1982). The Hopfield model is defined over a set of elements

$$\Xi(n, t) = \{S_i(t), \ldots, S_n(t)\}$$

in which $S_i(t)$ is the neurone state at a given time step. In such systems $S_i \in \mathbf{R}$ and the dynamics is defined by a deterministic rule:

$$S_i(t+1) = \Phi\left[g \sum_{j=1}^{n} J_{ij}S_j(t)\right]. \tag{2}$$

Usually $\Phi(z) = \mathrm{Tan}h(z)$ which is represented in Fig. 1 for several g values. Other functions such that (i) $\Phi(0) = 0$, (ii) $\Phi(\infty) = 1$ and (iii) $\Phi(-\infty) = -1$ can be used with similar results. Equation (2) means that the i-th neurone state is updated depending upon the state of other neighbouring neurones. The so-called gain parameter g is a measure of the degree of non-linearity of interactions. For $g \to \infty$, the Φ-function converges to the well-known step function, i.e.

$$\lim_{g \to \infty} \Phi(z) = \mathrm{Sign}\,(z) = \begin{cases} +1 & \text{if } z > 0 \\ -1 & \text{otherwise.} \end{cases} \tag{3}$$
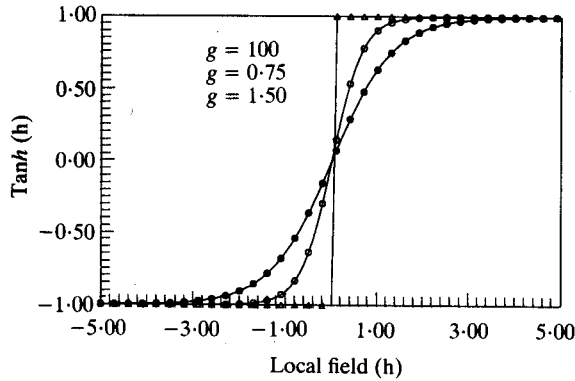
FIG. 1. Interaction function of neural network (NN) elements for several gain parameter (*g*) values.

Here $\{J_{ij}\}$ is the coupling matrix, which gives the kind of interaction between each (i, j)-pair of neurones. In the Hopfield approach, the matrix is assumed to be symmetric, i.e. $J_{ij} = J_{ji}$, $\forall i, j = 1, \ldots, n$, and there is no self-interaction, $J_{ii} = 0$. Under these restrictions, and a fully connected network, an energy-like function can be defined as:

$$E(\{J_{ij}\}, \{S_j\}) = -\tfrac{1}{2} \sum_{i, j = 1}^{n} J_{ij} S_i S_j. \tag{4}$$

This has been shown to be a Lyapunov function and the network always moves "downhill" towards a local minimum. For a suitable choice of $\{J\}$, associative memory can be present and several properties of real neural systems can be modelled. From a dynamical point of view, only point attractors (the learned states) are present. Such results are in fact also present in short-range interacting neural nets. The so-called "cellular neural networks" (Chua & Yang, 1988) in which neurones are connected with only nearest ones (Fig. 2) also have an associated energy function.

Further studies revealed that oscillatory behaviour can be obtained from these networks by using delays. Collective oscillations can also be obtained in non-symmetric networks (Serra & Zanarini, 1990). Chaotic behaviour in neural assemblies has also been suggested (Skarda & Freeman, 1987) as an essential element in brain dynamics. We are particularly interested in this kind of behaviour in order to explore the previously mentioned experiments. As we will see, the colony behaviour shows global oscillations for a wide range of parameters, such behaviour being typical.

3. Ant Colony Model

In our study, we consider the state of an individual as a real continuous variable. Let $\Xi(n, t)$ be the global state of a colony of n individuals. Here $S_i(t) \in \mathbf{R}$ is the activity state of a given individual. A given ant is called active if $S_i(t) > \theta$ and inactive otherwise. Here θ is a threshold below which the ant becomes inactive. In order to compare our results with experimental data, we study the (observable) number of
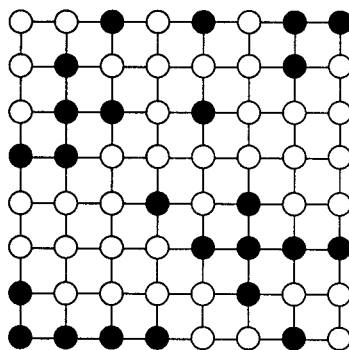
FIG. 2. Neural network (NN) structure. A network of fixed elements is defined on a lattice. Each element interacts with some of their neighbours through a coupling matrix J_{ij}. The value of J_{ij} defines the kind of global behaviour observed. For symmetric matrices and no self-interaction, the steady state is a given point attractor. Here black and white circles are, respectively, active and inactive neurones.

active elements, $n_a(t)$. Clearly, the "activity" is restricted to $0 \leq n_a(t) \leq n$ with $n_a(t) \in \mathbf{Z}$.

The experimental observation that a single ant (without other neighbours) can show spontaneous activation can be described in two ways, either

(i) Random activation: If $S_k(t) < \theta$ then $S_k(t+1) = S_m$ with some probability of activation p_a,

or

(ii) Low-dimensional deterministic chaos: Here the internal state is controlled by a deterministic function: $S_k(t+1) = F_\mu(S_k(t))$ in which $F_\mu(s)$ is a given continuous one-dimensional chaotic map. Here μ is a fixed bifurcation parameter.

In our model ants are a set of automata moving on a given spatial domain. Space is considered as a square lattice (the nest):

$$\Lambda(L) = \{\mathbf{k} = (i, j) \mid 1 \leq i, j \leq L\} \tag{5}$$

and each ant is placed at a given position $\mathbf{k} \in \Lambda(L)$ (see Fig. 3). Each $\mathbf{k} \in \Lambda(L)$ can be occupied by only a single ant. In our model we take rigid walls as boundary conditions. We usually take $n < L^2$; the extreme situation $n = L^2$ corresponds to a cellular NN.

Movement rules are simply stated. If a given ant is active, each time step a deplacement towards an empty neighbouring point will occur. The movement rule is then defined as

$$S_k(\mathbf{r}; t) \rightarrow S_k(\mathbf{r}'; t+1).$$

If the ant is inactive or all nearest points are occupied, no movement takes place.

The previous rules are very simple and clearly satisfied in real systems. The main assumption of our work concerns interaction rules. As previously mentioned, ant
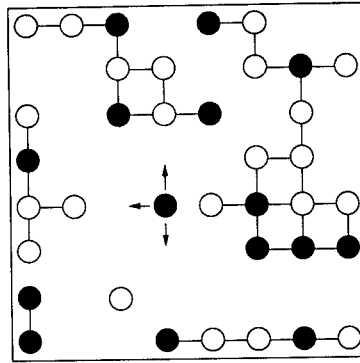
Fɪɢ. 3. Neural-like structure of the insect social structure. Elements can move around towards nearest positions. The elements (ants) are active (black circles) or inactive (white circles) and their state will be updated by interaction with nearest individuals. Here the coupling coefficient depends on the elements under interaction.

societies and neural structures share several qualitative common properties. Following this approach, a neural-like scheme will be used.

Let $C(\mathbf{r}) \subset \Lambda(L)$ be a neighbourhood of a given ant $S_k(\mathbf{r}; t)$. In our study, only the eight nearest lattice points are considered. Then the dynamics of ant states will be described by:

$$S_k(\mathbf{r}; t+1) = \mathrm{Tan}h\,[gh_k(t)] \tag{6}$$

where $h_k(t)$ is the local field of the k-th ant, i.e.

$$h_k(t) = \sum_{\mathbf{q} \in C(\mathbf{r})} J_{km} S_m(\mathbf{q}; t) \tag{7}$$

for those individuals whose spatial co-ordinates $\{\mathbf{q}\}$ fall into $C(\mathbf{r})$.

A more general hypothesis is a restriction of $h_k(t)$ to only some of the nearest individuals, perhaps with only one of those. An extensive study has shown that the observed qualitative properties are the same in both cases. In the following, only single-ant-to-single-ant interaction is used. Such a situation seems more realistic from a biological point of view.

The numerical value of the gain parameter g can be taken as a constant for all the individuals but experimental evidence (Cole, 1988) suggests that each individual has specific characteristics linked with actual age, status, etc. A distribution of g values i.e. $\{g_k\}$, $k = 1, \ldots, n$ can also be used, and the interaction rule is then generalized to:

$$S_k(\mathbf{r}; t+1) = \mathrm{Tan}h\,[g_k h_k(t)] \tag{8}$$

and equivalent results are obtained.

The set of matrix elements $\{J_{km}\}$ defines the specific kind of interaction and dynamics. For simplicity, we take in our study $J_{km} \in \{-1, 0, +1\}$ and several matrices are used. A further and non-trivial assumption is also introduced: self-interaction of

individuals is present. Next we consider the dynamics of individual ants and the corresponding behaviour of colonies.

3.1. DYNAMICS OF SINGLE ANTS

Let $S_0(\mathbf{r}; t)$ be the state of a given single ant and $\mathbf{r} \in \Lambda(L)$. Following our previous scheme, the internal state of our individual will be defined by

$$S_0(\mathbf{r}; t+1) = \text{Tan} h \, [g_0 J S_0(\mathbf{r}; t)] \qquad (9)$$

in which $\{J_{ij}\}$ is restricted to a single element J that we can take as $J = 0$ or $J \neq 0$. The first case corresponds to absence of self-interaction and an activation event is followed by a sudden inactivation. Now the ant will be "frozen" at a fixed lattice position. If $1 > J > 0$, self-interaction gives us an exponential decay of activity. In such a case, the ant will move around until activity disappears.

Equation (7) defines, for $\forall J \in (0, 1]$ a one-dimensional discrete map with a unique fixed point $S_0 = 0$ obtained from $S_0 = \text{Tan} h \, [g J S_0]$. Such a point is stable and for $t \to \infty$ the activity decays to zero. In our model we consider a threshold $\theta \ll 1$ below which the ant is called "inactive". As the ant becomes inactive, a random activation event can take place, with some probability p_a. After an activation event, the individual state is $S_0 = S_m$, the maximum activity level [(see Fig. 4(a) and (b)]. As the ant is again activated, it moves across $\Lambda(L)$ until activity decays again to θ. An
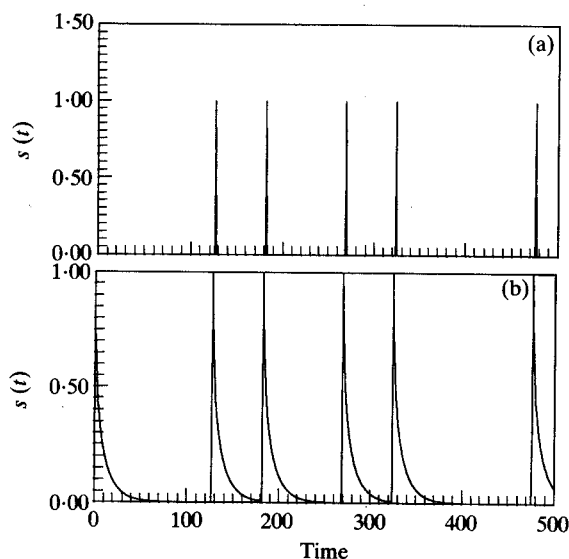

FIG. 4. Individual activity pattern. An active individual shows switches in its state (a). When active, it has an associated positive $S_i(t)$ and an exponential decay of activity (b) after each activation. As the activity moves to the threshold, θ, an activation event can occur with a fixed probability p_a.

exponential decay following

$$S(t) = S_m \exp(-gt) - 1$$

(using $J = 1$) will be observed for an isolated ant. For a given θ, the individual state will be "active" for a period of time T given by

$$T = -\frac{1}{g} \log\left[\frac{\theta + 1}{S_m}\right].$$ (10)

For such a time interval, the ant will move into $\Lambda(L)$ as a random walk. Clearly, T is a refractory period, during which no spontaneous activation can take place.

An example of the activity pattern is shown in Fig. 4(a) and (b). The activity is here restricted to $n_a(t) \in \{0, 1\}$ and is shown in Fig. 4(a). The state dynamics $S_0(t)$ [Fig. 4(b)] is shown to be a set of randomly spaced exponential decays. The next step in our study is the analysis of the global behaviour of a given colony of n individuals.

3.2. DYNAMICS OF WHOLE ANT COLONIES

Now we consider the behaviour of a set of n interacting individuals. The interaction matrix is defined for active–inactive ants:

$$J = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix}$$

where: J_{11}, active–active coupling, J_{22}, inactive–inactive coupling and J_{12}, J_{21}, active–inactive coupling. Equivalently, we can write **J** as $J = \{J_{11}, J_{12}, J_{21}, J_{22}\}$. Several matrices have been used in our study. In the following we take one of the simplest ones i.e. $J = \{1, 1, 1, 0\}$ as a model of interaction. Those matrices such that $J_{11} = 0$ seems to be unlikely to show coherent oscillations. We also take $J_{22} = 0$, i.e. no interaction between inactive individuals (equivalent results are obtained for non-zero values). The cross-terms, i.e. J_{ij}, $i \neq j$ can have different values, and have been found to be less important in generating collective oscillations. The frequency and amplitude of such oscillations can be, on the other hand, changed depending on these cross-interactions.

In order to study and characterize the colony dynamics, we have applied several approaches. Our interest is in showing that all the observed dynamical properties of the above mentioned ant colonies can be well reproduced with our model. A first result is obtained by observing the qualitative shape of the colony dynamics as the number of individuals n is increased.

As we can see, from Fig. 5(a–k), a collective oscillation of the colony as a whole is observed as n is increased. We show here the number of active ants $n_a(t)$. We can characterize the periodicity of such time series $\{n_a(t)\}$ by using Fourier analysis.
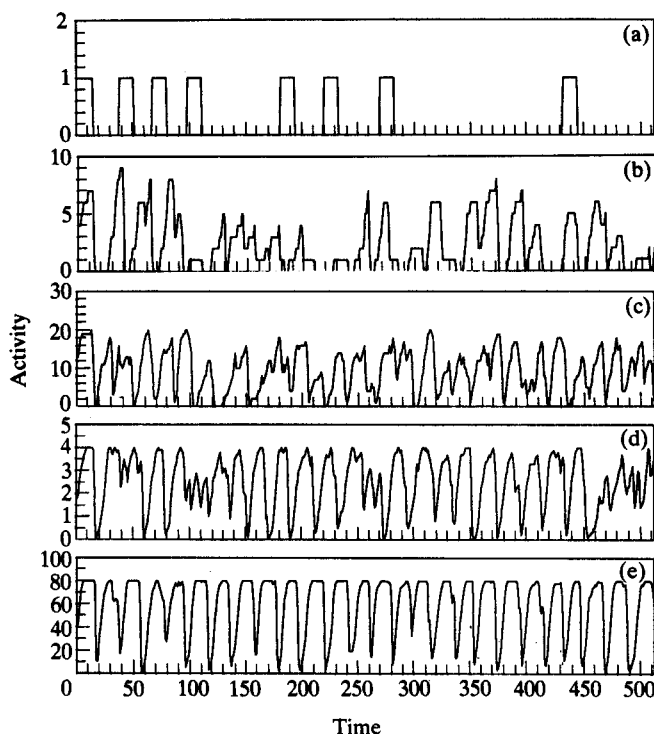
FIG. 5. Coherent oscillations obtained for increasing numbers of ants included in a 40 × 40 lattice. Here we have (a) $N = 1$ (single ant); (b) $N = 10$; (c) $N = 20$; (d) $N = 40$ and (e) $N = 80$. As N (and the colony density) increases, the collective periodic behaviour becomes more and more clear. In these cases we take a 10 × 10 lattice, a gain parameter g_i defined at random for each ant with $g_i \in (0.1, 0.2)$, $\forall i = 1, \ldots, N$, a ground activation state of $S_0 = 0.01$ and a probability of activation of $p_a = 0.01$.

The fast Fourier transform was calculated for the previously shown series, and the corresponding squared spectra are shown in Fig. 6(a–e). As expected, an emergent dominant amplitude becomes more and more sharply peaked as the number of individuals increases. As in the results of Cole, the existence of a maximum in $P(\omega)$ for a given frequency ω_c is a first qualitative evidence of the collective oscillation.

The observed oscillations are obtained in our model for several matrix structures. A necessary condition for oscillation is that $J_{11} > 0$, i.e. interaction between active ants is a key condition. If there is no self-interaction, the activity pattern is not able to propagate effectively through the system and an irregular fluctuation pattern is observed [Fig. 7(a)]. As mentioned before, self-interacting individuals but with $J_{11} = 0$ (i.e. no communication between active ants) gives no pattern [Fig. 7(b)]. Our results suggest that self-interaction must be present as a key ingredient of colony dynamics in order to have robust oscillations.

In all these situations the density of individuals plays an important role in the qualitative and quantitative properties of the oscillatory behaviour. Two relevant
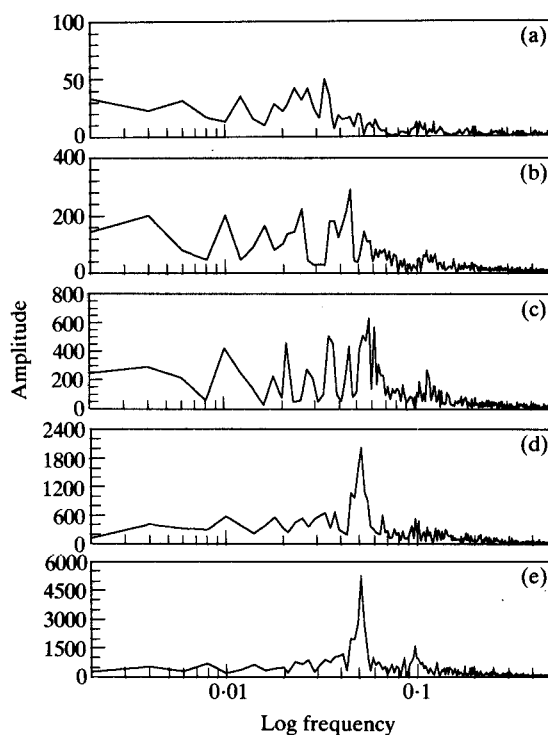
FIG. 6. Fourier spectrum corresponding to the time series shown in Fig. 3(a)–(e). We can see the appearance of a well-defined maximum in the amplitude as the colony size is increased.
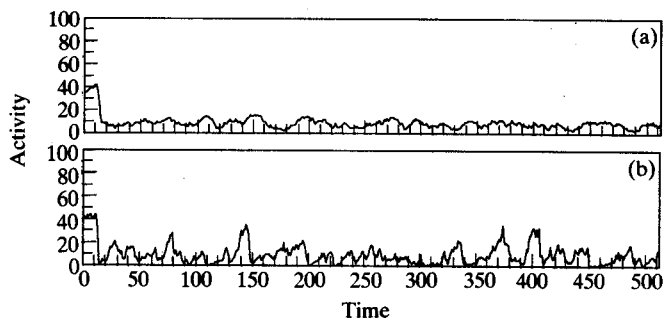

FIG. 7. Effect of no interaction between active elements (a) and absence of self-interaction (b). (These figures are under the same conditions as previous figures.) Oscillatory response is not present (a) and weakly observed (b). A high density level of individuals is necessary in (b) in order to observe oscillations. Such oscillations are never observed in (a).

parameters have been studied in this context: (i) the fraction of time in which elements are active (the so-called time budgets) and (ii) the period of oscillation as a function of colony density. The result of this study is summarized in Fig. 8(a) and (b). As we can see, the fraction of activity times $T_a \in (0, 1)$ increases with the colony density from $T_a \approx 0.25$ for low densities ($D = 0.1$) to an approximately constant activity level $T_a \approx 0.6$ for $D = 0.5$. In this sense, higher levels of individual activity are expected as the number of individuals inside the system is increased. Such a result is quite clear if we remember that activity is strongly dependent on interaction with nearest neighbours. The second result concerns the period of oscillation. As the density is increased, a nearly exponential decay of period is observed, with a high level of variability for $D < 0.5$. For higher densities, the period of oscillation is nearly constant. In our figure we also show a square around the zone of low density levels,
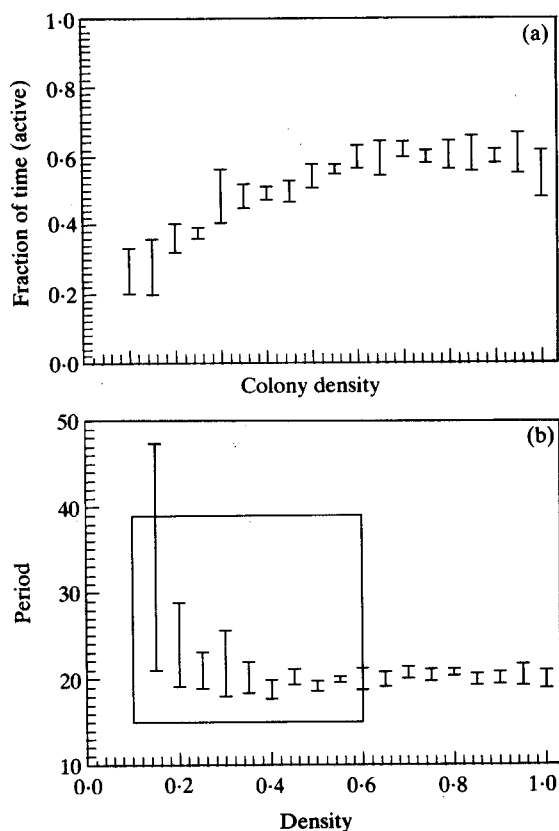

FIG. 8. (a) Distribution of time budgets for several values of colony density. Here we use the colony shown in previous figures. Calculations are made over five replica using 500 time steps. (b) Relation between period of oscillation (computed from the Fourier spectrum) and the colony density shows an exponential decay toward a nearly constant value. See text for comments.

in which the error bars are important. This zone is probably close to that observed in Cole (1991*a*), in which a strong variability of periods was reported.

3.3. CHAOTIC ANTS

In recent years, it has been shown that chaos is widely present in natural systems. Many studies on chaotic behaviour in biological systems have been made, showing how such dynamics can be described (see, for example, Glass & Mackay, 1988 and references therein). In population biology, these kind of dynamics are shown to be present even in the simplest models of population growth (May, 1986). Recent studies have also shown that chaos can be a typical phenomenon in spatially distributed ecosystems (Solé & Valls, 1992). On the other hand, and as pointed out by Conrad (1986), chaotic mechanisms of adaptability can be present at the level of search processes (genetic or behavioural). The implicit richness of chaotic behaviour can provide a given (simple) individual the necessary diversity of behaviour to explore, or avoid predators. In fact, recent studies have shown how chaotic elements can perform efficient parallel synchronous computation (Inoue & Nagayoshi, 1991). For our system under study, the existence of social interactions produce an additional degree of complexity. Nevertheless, we will see that non-linear chaotic individuals lead to predictable behaviour under spatial interaction.

Let us now consider the case of a deterministic chaotic dynamics of individual ants. The essential idea is that the internal state of each individual is given, when isolated, by a deterministic map $x_{t+1} = F_\mu(x_t)$, $x_t \in \mathbf{R}^+$ being a continuous variable. In our case, we take a one-dimensional map with a single maximum:

$$x_{n+1} = x_n\, e^{\mu(1 - x_n)}. \tag{12}$$

As it is well known, one-dimensional maps with a single locally quadratic maximum as above have an associated period-doubling route to chaos as μ grows enough (see for example May, 1976 and references therein). The corresponding bifurcation diagram for our map is shown in Fig. 9(b). For $\mu = 5\cdot5$, chaotic dynamics are obtained, as is shown in Fig. 9(a). For an isolated ant, we can use eqn (12) in order to describe the activation process as a deterministic (but chaotic) phenomenon. The deterministic rule is defined for an inactive ant as:

$$S_0(t+1) = S_m \quad \Leftrightarrow \quad x_{t+1} > \theta^*. \tag{14}$$

Here θ^* is a new threshold $0 < \theta^* < \max\{F_\mu(x)\}$. An example of such a threshold is also shown in Fig. 9(a). Now, the chaotic automaton will be used as the unit of our ant colony. The essential structure of our previous approach remains intact, but a non-trivial difference is present: the activity of individuals is predictable here at short time scales and the behaviour is deterministic. In this context, the "probabilistic behaviour" of ants (Deneubourg *et al.*, 1983) can be seen as the result of deterministic chaotic phenomena with only a few degrees of freedom. We did not reproduce all our results here, because of the equivalent structure of oscillations. An example of the colony behaviour is shown in Fig. 10 together with the behaviour of one of the
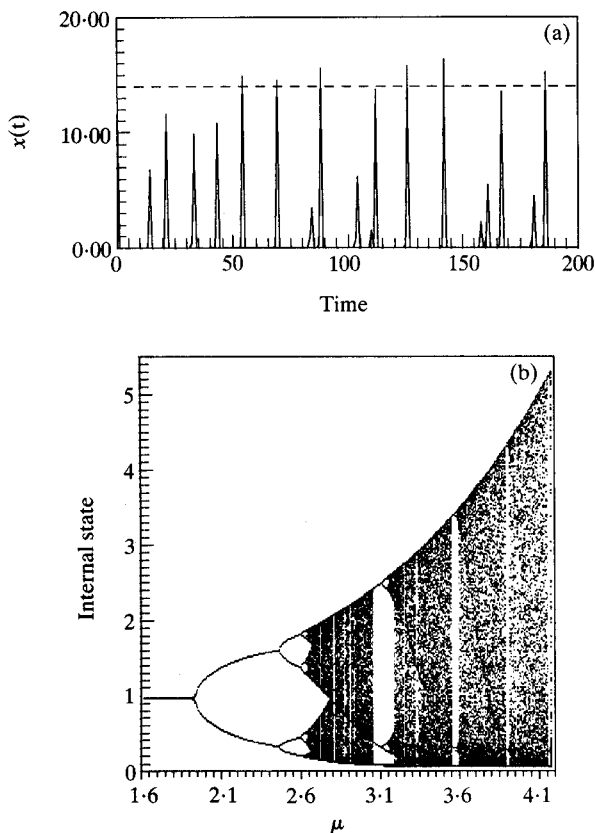
FIG. 9. (a) Dynamics of a chaotic map [eqn (13)] with $\mu = 5 \cdot 5$, and the corresponding threshold θ^*. As the threshold is reached, an inactive chaotic ant became activated and the internal state decays exponentially. In (b), the corresponding bifurcation scenario for our discrete map is also shown. We can observe a period-doubling cascade as μ is increased.

chaotic ants. As we can see, there is no direct relation between the individual and the collective dynamics.

4. Summary and Discussion

We have presented a neural-like CA model of interactions in ant societies. The model is inspired by both theoretical studies of neural organization and experimental observations. Using a simple model, emergent properties of the dynamics of some ant colonies have been carefully reproduced, in particular the emergence of periodic global oscillations. Such oscillations are present in several species of ants and would be present in other related situations. The obtained results were found to be robust on a wide range of parameter combinations and matrix structure; such robustness will be extensively analysed in a further paper. The global periodic motion emerges
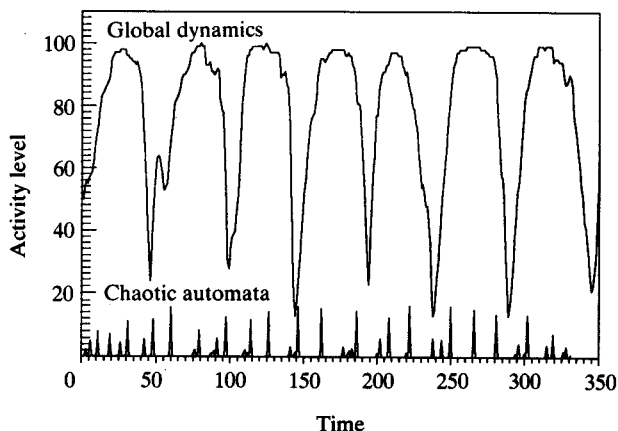
FIG. 10. Dynamics of a network of chaotic mobile automata. In this system we have $N = 100$ individuals on a 30×30 lattice and identical parameters as before. The internal threshold is $\theta^* = 16$. Both global dynamics and individual internal state are shown.

from the local interaction of (two or more) non-periodic elements. The matrix structure **J** has only few restrictions on the dynamical oscillatory behaviour: $J_{11} > 0$ appears to be a necessary condition, together with self-interaction. It also seems reasonable to use $J_{22} = 0$ and cross-interactions operate on the frequency and/or amplitude of oscillations. The unpredictability of single ants is, from our point of view, an element of internal "randomness" which can be useful for colony flexibility. On the other hand, global low-dimensional dynamics such as oscillatory behaviour can be an element of predictability. An additional approach using a set of chaotic automata also showed collective oscillations. In this model, ant states are internally determined by a chaotic one-dimensional map and as a consequence the dynamics of individual ants is low-dimensional chaos. This is then in agreement with Cole's studies on the dimension of activity patterns in ant colonies (Cole, 1991*b*): individuals are chaotic despite the existence of global periodic behaviour.

As a result of our study, some predictions can be made. First, a nearly negative exponential dependence of oscillation period in relation to density is expected to be present. In previous experiments (Cole, 1991*a*), no pattern was observed, but this could be linked with both low-density levels and with a lack of a representative statistical average. Concerning spatial patterns, several simulations have shown that our system is able to display non-homogeneous spatial patterns of activity. Recent studies suggest a good agreement between the spatiotemporal structures obtained from our model and patterns of activity in ants nests (Franks, 1992; Cole, B. J., personal communication). In this sense, experiments with higher densities of individuals will be very useful in order to test the present model and to suggest new ideas on order and chaos in insect societies.

REFERENCES

AMIT, D. J. (1989). *Modelling Brain Function.* Cambridge: Cambridge University Press.

CHUA, L. O. & YANG, L. (1988). Cellular neural networks: theory. *IEEE Trans. Circuits Syst.* **35,** 1257–1272.

COLE, B. J. (1991a). Short-term activity cycles in ants: generation of periodicity by worker interaction. *Am. Natur.* **137,** 244–259.

COLE, B. J. (1991b). Is animal behaviour chaotic? Evidence from the activity of ants. *Proc. R. Soc. Lond.* B **244,** 253–259.

COLE, B. J. (1988). Individual differences in social insect behaviour: movement and space use in *Leptothorax allardycei.* In: *Interindividual Behavioral Variability in Social Insects.* Boulder, CO: Westview.

CONRAD, M. (1986). In: *Chaos* (Holden, A. V., ed.). Manchester: Manchester University Press.

DENEUBOURG, J. L., PASTEELS, J. M. & VERHAEGHE, J. C. (1983). Probabilistic behavior in ants: a strategy of errors? *J. theor. Biol.* **105,** 259–271.

DENEUBOURG, J. L., GOSS, S., PASTEELS, J. M. & DUERINCK, G. (1986). Random behavior, amplification processes and number of participants: how they contribute to the foraging properties of ants. *Physica D* **22,** 176–186.

DENEUBOURG, J. L., GOSS, S., FRANKS, N. & PASTEELS, J. M. (1989). The blind leading the blind: modelling chemically mediated army ant raid patterns. *J. Insect Behav.* **2,** 719–725.

FRANKS, N. R., BRYANT, S., GRIFFITHS, R. & HEMERIK, L. (1990). Synchronization of the behavior within nests of the ant *Leptothorax acervorum I. Bull. math. Biol.* **52,** 597–612.

FRANKS, N. R. & SEMLOVA-FRANKS, A. B. (1992). Blood sorting by ants distributing the work load over the work surface. *Behav. Ecol. Sociobiol.* **30,** 109–123.

GLASS, L. & MACKEY, M. C. (1988). *From Clocks to Chaos.* Princeton, NJ: Princeton University Press.

GORDON, D. M. (1989). Dynamics of task switching in harvester ants. *Anim. Behav.* **38,** 194–204.

GORDON, D. M., GOODWIN, B. C. & TRAINOR, L. E. H. (1992). A parallel distributed model of the behavior of ant societies. *J. theor. Biol.* **156,** 293–307.

HAKEN, H. & STADLER, M. (eds) (1990). *Synergetics of Cognition.* Berlin: Springer-Verlag.

HOFSTADTER, D. (1979). *Godel, Escher, Bach.* Brighton: Harvester Press.

HOPFIELD, J. K. (1982). Neural networks and physical systems with emergent collective computational abilities. *Proc. natn. Acad. Sci. U.S.A.* **79,** 2554–2557.

INOUE, M. & NAGAYOSHI, A. (1991). A Chaos Neurocomputer. *Phys. Lett.* **A158,** 373–376.

KEPHART, J. O., HOGG, T. & HUBERMANN, B. A. (1990). Collective behavior of predictive agents. *Physica D* **42,** 48–65.

MAY, R. (1976). Simple mathematics models with very complicated dynamics. *Nature, Lond.* **961,** 459–467.

MAY, R. (1986). When two and two do not sum four: nonlinear phenomena in ecology. *Proc. R. Soc. Lond.* B **228,** 241–266.

NICOLIS, G. & PRIGOGINE, I. (1977). Selforganization in nonequilibrium systems. New York: Wiley and Sons.

PRIGOGINE, I. & STENGERS, I. (1984). *Order out of Chaos.* W. Heinemann.

SERRA, R. & ZANARINI, G. (1990). Complex systems and cognitive processes. Berlin: Springer-Verlag.

SKARDA, C. A. & FREEMAN, W. J. (1987). How brains make chaos in order to make sense of the world. *Brain Behav. Sci.* **10,** 161–195.

SOLÉ, R. V. & VALLS, J. (1992). On structural stability and chaos in biological systems. *J. theor. Biol.* **155,** 87–102.

SOMPOLINSKY, H. (1988). Statistical mechanics of neural networks. *Phys. Today* 70–88.