



NEURAL NETWORKS AS SOURCES OF CHAOTIC MOTOR ACTIVITY IN ANTS AND HOW COMPLEXITY DEVELOPS AT THE SOCIAL SCALE

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We discuss a Neural Network model generating activation signals for locomotion in ants. The signals are chaotic and so are the temporal patterns of spontaneous activations in single ants. Active ants are able to move and interact with other nest mates. This process of movement-interaction generates periodic pulses of activity once the number of individuals reaches a certain density value. An algorithmic complexity measure is used for identifying accurately the transition from chaos into order. Finally, an Iterated Function System analysis reveals the richness of dynamical behavior that emerges when ant colonies are self-poised near such a transition.

1. Introduction

Mobility is a characteristic of all adult insects, it allows them to perform a range of vital activities such as feeding, dispersal, mating, defense, etc. and it has been suggested that the success of insects as terrestrial organisms may be in part due to their high degree of mobility [Chapman, 1991]. In ants, as in all other groups of social insects, mobility of individuals is fundamental for the coordination and maintenance of their highly structured and organized societies: mobility makes possible widespread

dissemination of information, correct task allocation and an efficient dynamics of interactions, among other essential activities.

It is now well established that the temporal patterns of movement and activity in ants reveal a clear pattern of discontinuity suggesting that individuals spend a significant portion of their time in a state of quiescence (e.g. [Sudd, 1967; Chauvin, 1970; Herbers, 1983]). Recently, it has been reported that temporal patterns of movement inside the nest of *Leptothorax* ants show periodic

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cycles of activity alternating with periods of inactivity [Franks *et al.*, 1987; Franks *et al.*, 1990; Cole, 1991a]. The initiation of a cycle of movement is due to the spontaneous activation of a few — or just a single — individuals and subsequent activation of the motionless ones by interaction. Detailed studies of single isolated workers show that the pattern of individual activity is characterized by low-dimensional chaos and that chaotic behavior tends to vanish once the ants are allowed to interact in a colony [Cole, 1991b]. This means a phase transition from a chaotic disordered temporal regime into a periodic ordered one driven solely by the process of interactions among the social units [Miramontes, 1995; Solé & Miramontes, 1995].

This collective phenomenon has been modeled in the past using a variety of formalisms [Goss *et al.*, 1988; Hemerik *et al.*, 1990; Tofts *et al.*, 1992; Cole, 1992; Miramontes *et al.*, 1993; Solé *et al.*, 1993a, 1993b]. We will use the formalism of mobile automata as in [Miramontes *et al.*, 1993] and [Solé *et al.*, 1993a, 1993b] but with the innovation that spontaneous activations at the individual level are driven by a chaotic neural circuit in each ant. Before introducing the model, we discuss some relevant aspects of the biology of *Leptothorax* ants in order to show how well the essential aspects of the problem are conveniently incorporated in the model.

2. The Basic Behavioral Biology of *Leptothorax* ants

Worldwide there are around 350 named taxa within the Hymenopteran genus *Leptothorax*. They are quite small in size and their natural colonies rarely exceed a few hundred individuals, the typical size being around one hundred. The colonies of these ants are very compact and the individuals live in close proximity to each other. *Leptothorax* nest commonly in small closed preformed cavities like hollow seeds, cracks on rocks or under stones. Colonies may have one or multiple queens but queenless colonies are common in nature suggesting that the queen has no other role but reproduction and that the colony is not centrally ruled by a single individual.

The ants in this genus are monomorphic and no castes exist in their societies except by some degree of labor specialization that develops with age. The individuals are quite homogeneous and can engage

easily in different tasks not belonging to their specific age groups. Being compact and living in close proximity suggests that communications are mostly short-range and in fact the most common form is direct contact through antennation [Herbers, 1983].

Cole [1991b, 1994] has established that the process of spontaneous activations in *Leptothorax* ants is chaotic and has suggested that this may have considerable consequences for the social behavior since movements are strongly correlated with activity. Hence the study of how locomotion in ants is generated is of relevance as well.

2.1. Locomotion and the central nervous system in ants

Locomotor activity in all animals is under direct control of the central nervous system (CNS). Motion results after muscles receive signals from the motor neurons that innervate them. Motor neurons in turn are coupled via axons to neurons situated in the nervous ganglia, the nervous cord or the brain, depending on the anatomical and physiological details of the animal in question.

Physiological rhythms, that are translated into motor activity through activation of specific motor programs, are generated by single cells or by networks of coupled cells known as central pattern generators (CPG). CPGs are in control of many important autonomous processes involving muscular activity such as cardiac pulses, breathing, intestinal contractions, swimming, escape movements, flight, etc.

One of the most well-known CPGs in invertebrates is the R15 neuron of the *Aplysia* mollusc. R15 is a single-cell with intrinsic rhythmic activity but subject to modulation by synaptic input and hormonal influence [Rinzel & Lee, 1987]. A single-cell CPG exists in the mollusc *Tritonia* [Katz & Frost, 1995]. In this case, three different cells are known for their property of endogenous rhythmic firing patterns. In *Tritonia*, these CPGs are known to be involved in locomotor control of swimming. Another case of single-cell CPG is known as the AB neuron in the lobster *Panulirus interruptus*. In this case the AB neuron may show, under diverse conditions, a rich variety of firing patterns [Guckenheimer *et al.*, 1993].

A number of CPGs are formed by a few interconnected neurons via electrical synapses. The simplest of these cell aggregates are those formed by only two single neurons. An example, is the

neural oscillator in the snail *Lymnaea stagnali* where the neural oscillator, known as VD1/RPD2, is a pair of electrically coupled peptidergic cells that fire in close synchrony [Kerkhoven *et al.*, 1992]. The VD1/RPD2 system has external excitatory and inhibitory inputs but the rhythmic activity is endogenous to the coupled pair.

Many neural circuits are known to generate electrical activity without any external input from the sensory organs and rhythmic patterns can arise from the network architecture itself [Glass *et al.*, 1988, and references therein]. This seems to be the case in ants where they show spontaneous motor activity without any external stimulus.

The nervous system in ants is organized as a network of interconnected ganglia that are located in specific regions along the body and with direct connection to the brain. The brain is located inside the head and is the largest aggregation of neural tissue wired directly to the eyes and the sense organs in the antennae, being for this reason involved in complex information processing and control tasks.

Apart from the basic anatomy, the CNS in ants is very poorly understood. This is due to the obvious difficulty posed by the size of an ant and by the fact that any experiment involving surgical manipulation with the purpose of studying social behavior will be hindered since any abnormally behaving ant is quickly disposed off by its colony fellows. Another reason has to do with the generalized belief that ants are capable of only quite simple individual behavior due to the simplicity of their nervous system (typically formed by about 100 000 neurons). It is widely accepted, though not rigorously probed, that ants have very limited neural plasticity and that almost all of its behavior is stereotyped and pre-programmed.

It is a reasonable hypothesis that the ant's locomotory system involves a neural network architecture. Evidence exist that certain neural regions have the typical parallel-distributed-system property that confer robust performance and fault-tolerance. For instance, it is known that ants have a number of neural circuits that are involved in orientation and locomotion and that experimental damage to these regions cause disorientation only after a number of them have been impaired. Disabling of only a few does not cause any noticeable loss of orientation or movement [Dumpert, 1981].

As already stated, the temporal patterns of spontaneous activation in some of the species of *Leptothorax* ants exhibit low dimensional chaos. We

model this individual behavior by means of a very simple neural network that generates low dimensional chaos.

2.2. A neural network model for individual chaotic activations

Neural networks of only a few elements may exhibit very complex dynamical behavior and models of four, two and even one single element able to generate chaos have been studied elsewhere [Das II *et al.*, 1991; Wang, 1991; Chay, 1985; Aihara *et al.*, 1990; Kurten *et al.*, 1986; among others]. For simplicity, we will use a two-neurons fully interconnected NN without controlling external inputs. One neuron is excitatory and the other inhibitory. The network is a discrete time two-dimensional map with a sigmoid coupling function. Wang [1991] has studied analytically, and in a very elegant way, an equivalent network and has shown that this quite simple arrangement of two interacting elements exhibits period-doubling route to chaos.

Consider the network formed by neuron x and neuron y as is shown in Fig. 1. The time evolution of the system is given by the following parametric map:

$$\begin{aligned} x(t+1) &= F_{\mu}(w_{11}x(t) + w_{12}y(t)) \\ y(t+1) &= F_{\mu}(w_{21}x(t) + w_{22}y(t)) \end{aligned} \quad (1)$$

where

$$F_{\mu}(z) = \tanh(\mu z) \quad (2)$$

μ is the *neuron gain*, and the w coefficients are the entries of the interaction matrix \mathbf{W} that codifies the strength of the neuron's connections. Following

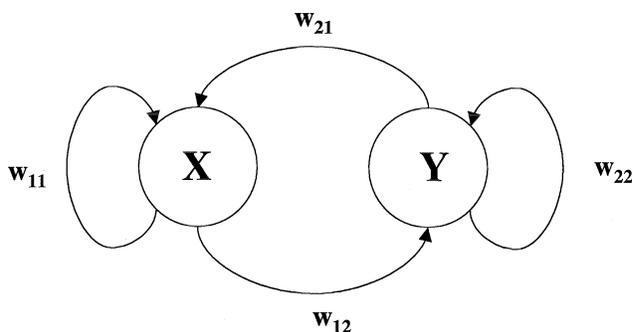


Fig. 1. Connection diagram of the neural network model used for generation of chaotic signals. The NN is a two-neuron discrete-time coupled map acting as a Central Pattern Generator for locomotion. Each ant, modeled as a mobile automata, has its own neural network.

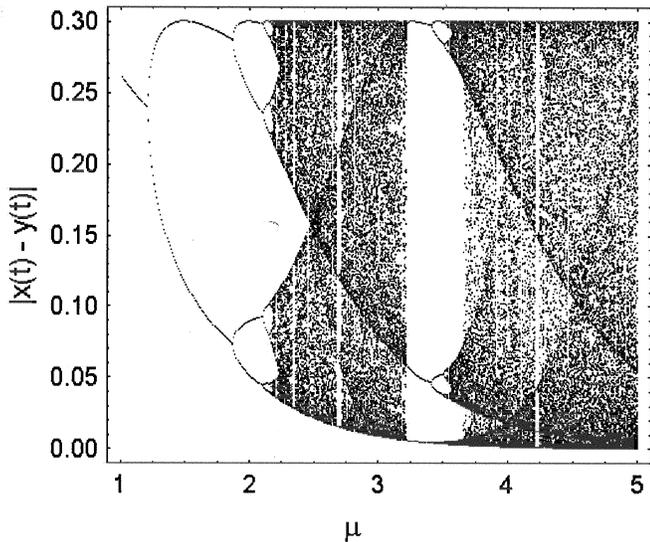


Fig. 2. Bifurcation diagram of $|x(t) - y(t)|$ and μ as a bifurcation parameter. System parameters are: $x(0) = 0.9$, $y(0) = 0.6$, $w_{11} = -3$, $w_{12} = 3$, $w_{21} = -6$, $w_{22} = 6$.

Wang [1991], the network shows chaos for a suitable value of μ and when the entries of \mathbf{W} are of the form:

$$\mathbf{W} = \begin{pmatrix} -a & a \\ -b & b \end{pmatrix}.$$

Each neuron in the network exhibits chaotic motion in its temporal evolution and the bifurcation diagram can be easily constructed taking μ as the bifurcation parameter. Here we use the absolute value of the difference of the two neurons' states as

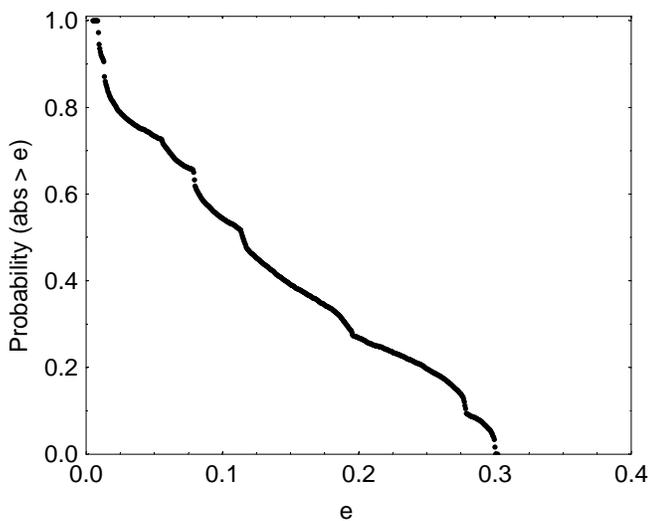


Fig. 3. Probability distribution obtained from the condition $|x(t) - y(t)| > e$, where e represents a positive firing threshold value, NN parameters as in Fig. 2.

the signal for locomotion activation and the resulting bifurcation diagram appears in Fig. 2. A signal for spontaneous chaotic activation is transmitted to a hypothetical motor program each time the absolute difference exceeds a given threshold value e (that is, the signal is produced depending on the degree of the network synchrony):

$$|x(t) - y(t)| > e. \tag{3}$$

The use of this convention allows fine control of the network's firing rate and hence the probability of having an spontaneous activation in the individual governed by its neural network. The probability distribution resulting from the above expression, is depicted in Fig. 3.

3. Collective Behavior in Artificial Societies

An ant colony is a highly integrated structure and this colony-level order is the result of coordinated massive individual interactions that are facilitated by the existence of effective communication links among the members of the colony. We explore now the extent at which social behavior can be understood as inevitable emergent properties of interactions between simple elements. We will use here the term "artificial society" in the narrow sense of a collection of individuals (the mobile automata) that can interact and modify their individual behavior because of the interactions. The coupled collective will be able to exhibit global dynamics and in the case reviewed here will be able to reproduce the self-organized order-disorder transition observed in real ants.

3.1. Social interactions and global dynamics

The colony-level dynamics is implemented here by means of an interacting set of *mobile automata* that have a range of features capturing closely the basic biology of the ants [Miramontes, 1995]: (1) a set of identical elements reflecting the fact that *Leptothorax* ants are monomorphic and casteless; (2) there are no "privileged" individuals dictating the dynamics to follow (no queens ruling centrally); (3) first neighbor interactions that capture the known fact that communications among ants are basically based on direct antennations (information is generated and transmitted locally but globally distributed in space); (4) the automata can

change their activity-movement status because of the interactions; (5) isolated individuals can activate spontaneously and the activation process is chaotic (the signal triggering activation is generated by the individual's own neural network).

3.2. Mobile automata

Mobile automata are space-extended discrete dynamical systems with mobile elements [Miramontes *et al.*, 1993; Solé *et al.*, 1993a, 1993b]. In the particular case discussed here, the automata are two-dimensional and interactions are restricted to the first neighbors in the nine-cells square around each automaton. The movement pattern of the automata (objects) are random walks with two constraints: two objects cannot be at the same place at the same time and new positions are selected only among the first-neighborhood square. The objects perform a maximum of six searching attempts until a free cell is found. In case of not available space, the objects remain still.

The activity state S_i of each object a_i is given by a function that couples the object's own activity with that of the other objects in the first neighborhood:

$$S_i^{t+1} = \tanh \left\{ g \left(\left(\sum_{j=1}^k J_{ij} S_j^t \right) + J_{ii} S_i^t \right) \right\} \quad (4)$$

where J_{ij} are coupling coefficients taken from the colony interaction matrix \mathbf{C} and k is the number of

neighbors of a_i . Note that term $J_{ii} S_i^t$ represents the contribution of the self-interaction. \mathbf{C} is the square interaction matrix defined as follows:

$$\mathbf{C} = \begin{pmatrix} c_1 & c_2 \\ c_3 & c_4 \end{pmatrix}.$$

c_1 represents active-active interactions, c_3 and c_2 represent active-inactive and inactive-active interactions, while c_4 represents inactive-inactive interactions. The activity value of the i and j elements are considered together. For instance, if $S_i > 0$ and $S_j > 0$ then the interaction is of the active-active type and $J_{ij} = c_1$. Detailed experiments have validated the mobile automata approach and have indeed measured in great detail the values of the interaction matrix for real ants [Cole & Cheshire, 1996].

The parameter g (gain) controls the slope of the hyperbolic tangent function and determines the rate of activation and deactivation of the mobile objects. If the activity of a given object is greater than zero then it is regarded as active and able to move, otherwise it will be inactive and motionless.

An isolated inactive object will remain so until activated by one of the two following processes: (1) it is spontaneously activated by a signal coming from its neural network and when this happens S_i is assigned with a fixed positive initial value (in all our simulations this value was arbitrarily taken as 0.1); (2) activated after contact with an already active object.

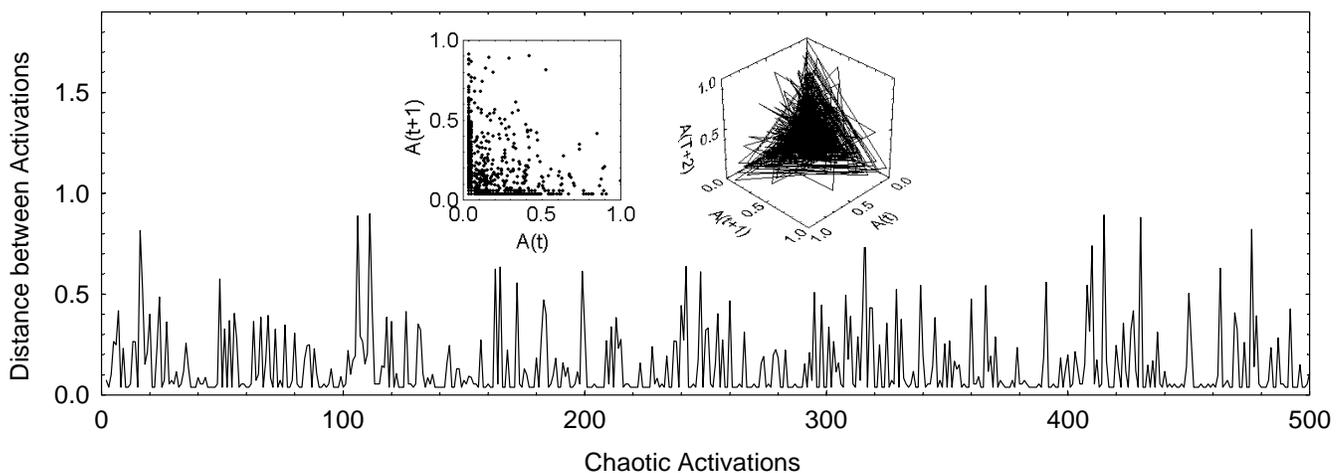


Fig. 4. Reconstructed chaotic time series for a single isolated object. Lattice size 10×10 , $g = 0.05$, \mathbf{C} matrix entries all one. $\mu = 3$, $\varepsilon = 0.3$, the rest of the NN parameters as in Fig. 2. The first return map of the series and a 3D attractor reconstruction are also shown. Notice the qualitative similarity of the graph and attractors with those in [Cole, 1991b] reported for real ants.

Consider a given lattice with a single isolated object on it. This automaton will activate spontaneously and will keep moving for an interval of time, as long as the S_i keeps greater than zero (S_i as defined in (4) is monotonically decreasing to zero for an adequate choice of g (see [Miramontes *et al.*, 1993]). We can plot the time series of the activations we obtained with this system (see Fig. 4). The time intervals between successive peaks is chaotic and it is possible to apply a linear transform to this series in order to show, in another way, that single isolated automata are indeed chaotic. The transform is quite simple and consist of the following: we take the time difference Δt_i between two successive activation peaks over a given time interval. The maximum of these Δt_i intervals is found (Δt_{\max}) and the Δt_i are normalized to Δt_{\max} . A new time series is reconstructed with this normalized data as successive points. One of these series (500 chaotic activations out of an original series 10 000 time steps long) is shown in Fig. 4 together with the reconstructed attractors in two and three dimensions. We compared the qualitative aspect of this series with the data for real ants as in [Cole, 1991b] and we found a good agreement.

3.3. *Social complexity at the edge of chaos*

After adding more and more objects to the lattice, we observed the same disorder–order transition phenomena reported by Cole [1991a, 1991b] in ant colonies and the same dynamic behavior reported for random-activated objects [Miramontes *et al.*, 1993]. The density-dependant phase transition was accurately pinpointed elsewhere in model ants using information theory measures [Miramontes, 1995; Solé & Miramontes, 1995] and the experimental work of Franks *et al.* [1992] showed that ants self-organize to attain a nest density value that correspond to the value predicted, the nest density value being around 0.2. In the present study, an algorithmic complexity measure (ACM) was used to explore and characterize the dynamical behavior of the lattice objects as a function of the density as shown in Fig. 5. This complexity measure refers to Kolmogorov’s complexity and it is regarded as the minimum information effort needed to simulate a given process, or in other words, the shortest computer algorithm than can generate or recreate it [Kaspar & Schuster, 1987]. The first and most important finding here is that the curve has a maximum that

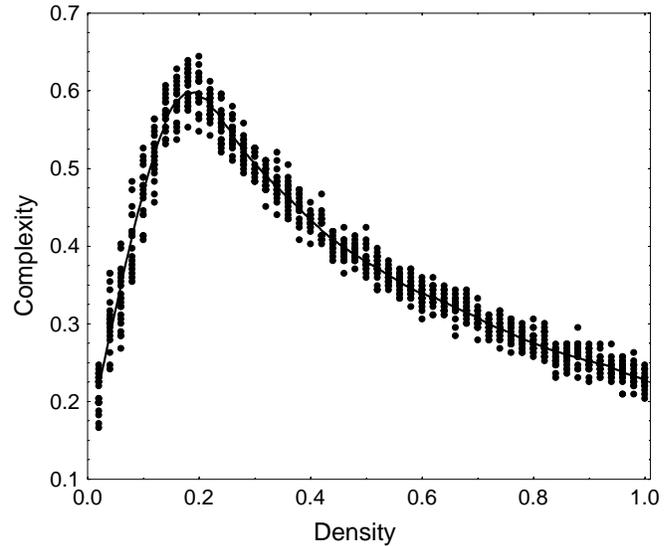


Fig. 5. Normalized algorithmic complexity (AC) as a function of the lattice density. Notice the bell-shaped curve with a maximum that corresponds to a density of around 0.2. Ant colonies at such densities would exhibit the most complex behavior and it is now known that real ants self-organize to attain a nest density close to this predicted value. Each point in this graph represent the measured algorithmic complexity of a single 2000 long time-series. For each value of density, 20 replicas were considered. Notice that the peak value of the AC is around 0.6 falling well below the maximum value of 1.0 that corresponds to a pure random process. NN parameters as in Fig. 2.

corresponds to a density value of around 0.2, so that the maximum algorithmic complexity is found at the same density where the maximum of entropy was previously detected [Miramontes, 1995; Solé & Miramontes, 1995]. This density is, indeed, the one that separates the region of chaos, linked to low density states, from the one where periodic oscillations, linked to high density states, emerge. This frontier, separating chaos from order, is commonly known as the *edge of chaos* [Langton, 1990] and it is widely thought that this state has a range of very interesting dynamical properties including the development of critical fluctuations [Haken, 1988].

Critical states associated to phase transitions are often characterized by $1/f$ noise-like scaling and $1/f$ power spectra have been reported to exist in ant colony dynamics [Miramontes, 1995]. Here, we have used an Iterated Function System (IFS), for proper visualization of the fine details that are present in $1/f$ dynamics including self-similarity [Jeffrey, 1992; Peak & Frame, 1994; Sprott & Rowlands 1995; Mata-Toledo & Willis, 1997; Miramontes & Rohani, 1998]. The IFS applied to both real and simulated ant colonies are pictured in Fig. 6. In

these graphs, it is clear that our model reproduces very well the patterns observed in the experiments. When the colonies (both artificial and real) are at densities around 0.2, the fluctuations in the temporal activity generate identical IFS maps having the characteristics of a self-similar process with triangle-like structures repeating at different spatial scales [Figs. 6(a) and 6(b)]. When the colonies

are in the chaos-dominated low density region, the patterns obtained for simulated and real colonies are also very similar and distinctive [Figs. 6(c) and 6(d)]. Finally, the high density states in artificial colonies generate peculiar IFS patterns that, however, are not possible to compare with real colonies since real ants do not attain such high density states.

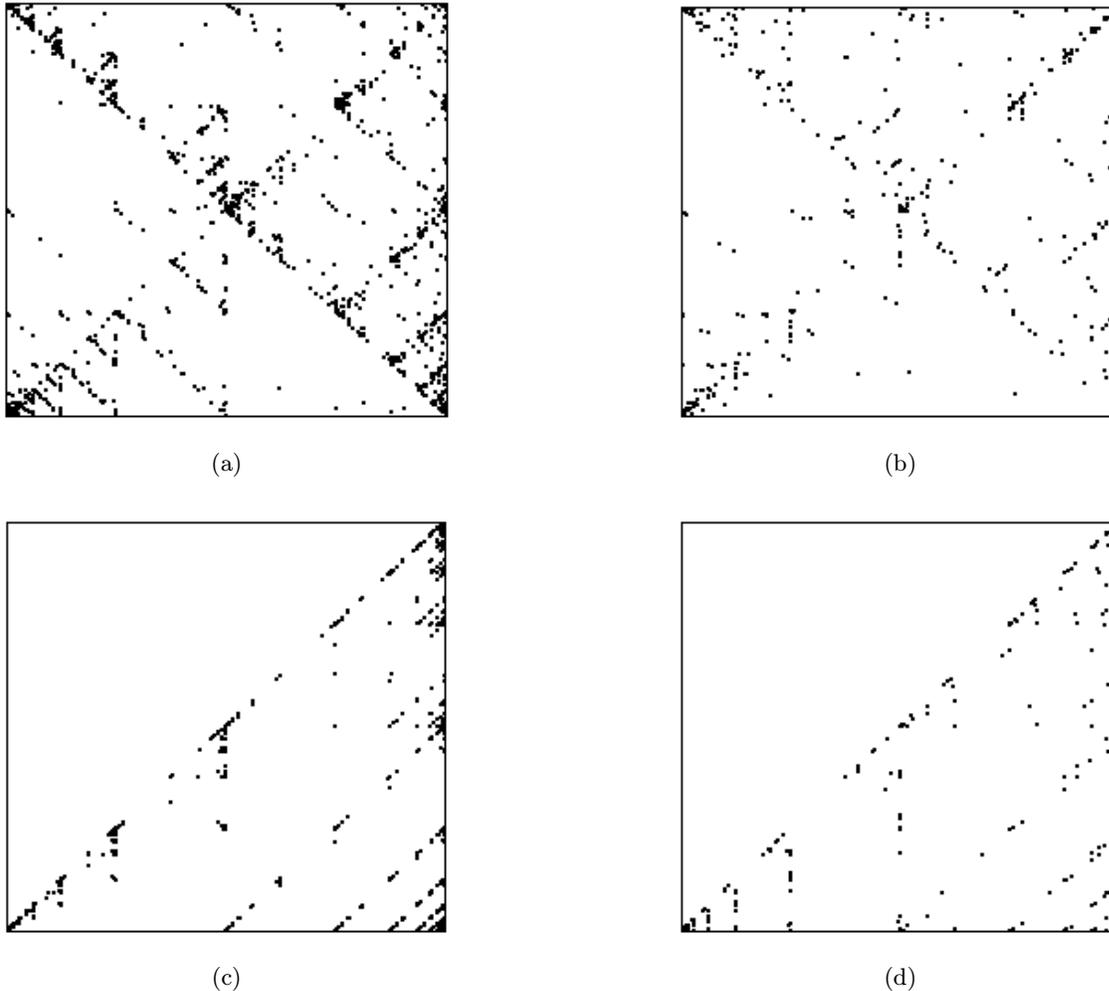


Fig. 6. Iterated Function Analysis (IFS) of the dynamics of temporal activations. (a and b) picture the patterns obtained from one simulated and one real colony respectively. The simulated colony had a density of 0.2 and the pattern is identical to the one obtained from a real colony. The patterns are self-similar with triangle-like structures repeating at different scales. This allows to conclude that the real colony was near a similar density state. The colonies represented in (c) and (d) are simulated and real respectively. The density value of the simulated was 0.1 and since the patterns are very similar, one can conclude that the real colony was perhaps in a low-density state. Still there are faint traces of a self-similar behavior. Finally (e) and (f) represent simulated colonies with densities at 0.6 and 1.0. The IFS analysis works in the following way. The data set is sorted from the minimum to the maximum values and then subdivided into four segments such that each segment contains the same number of points (notice that the segments could be of different lengths). The original unsorted data set is then normalized and coarse-grained into four values, say 1, 2, 3 and 4, representing the quartile to where the data belong. The representation space is a square where the four corners are labeled 1, 3, 2, 4 in a clockwise direction (starting in the lower left corner). Each value of the coarse-grained series is associated with the corner having the same number. A point is plotted half the way between the center of the square and the first point of the series. A second point is plotted half way between the first plotted point and the second point in the series, and so on. The time-series of all the simulated colonies were 2000 steps long. Real colony data as from Franks *et al.* [1990] (Frank's colony 3 is (b) and colony 1 is (c)).

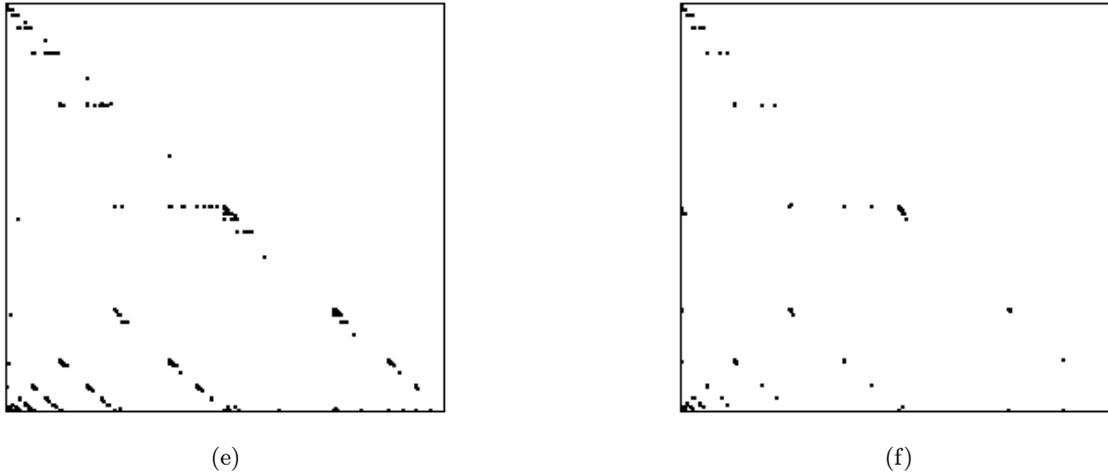


Fig. 6. (Continued)

4. Discussion

A number of models have been presented to attempt the simulation of periodic oscillations in *Leptothorax* [Goss, et al., 1988; Hemerik et al., 1990; Tofts et al., 1992; Solé et al., 1993a]. All of them differ markedly in the assumption of the origin of the cycles and in their degree of biological realism and predictive ability (see [Tofts et al., 1992] for a review of most of them). The dynamics of the model here is in good agreement with the observed phenomena in real ants: (1) Single individuals are chaotic in their spontaneous activations. (2) Activations occur by interactions among the objects and this process is clearly synergetic. (3) There is a transition from chaos into periodic cycles in the global dynamics of the colony as more individuals are allowed to interact. (4) Chaotic activations per object tend to decrease as a function of density. (5) Period length follows an exponential decay for low densities but increases slightly, in a linear way, for higher densities. (6) Spatial distribution of activity seems to follow concentric symmetries over the nest space [Miramontes et al., 1993]. (7) Algorithmic complexity confirms the existence of an order–disorder phase transition in the temporal dynamics at nest densities around 0.2 i.e. the values at which real ants self-organize their nest densities. (8) This *edge of chaos* state is characterized by critical fluctuations that under an IFS representation reveals self-similar patterns that are identical in both real and artificial colonies.

We confirm the hypothesis that coupling of elements reduces the randomness of the activations:

As density is increased the number of chaotic activations per object decreases meaning that the proportion of activations by interactions with another objects increases. This process is nonlinear suggesting that, in this simple model, emergence of coherent collective behavior is synergetic. In fact, the measured time-budget of two interacting automata is greater than the sum of the time-budgets of two isolated objects. In other words, two interacting automata spend more time active than when isolated [Miramontes, 1995]. This phenomenon, completely emergent in the model, is commonly known as social facilitation [Miramontes & DeSouza, 1996].

The social organization of an ant colony may thus be understood as an emergent level of order arising from a synergetic system of elements whose behavior in isolation does not allow one to predict the temporal and spatial patterns of the whole. Individual ants alone or at low density behave chaotically, and only as a result of sufficient interaction does self-organization emerge in the form of global rhythmic activity and spatial patterns. Agreement with experimental data confirm the power of the formalism here used and the legitimacy of interpreting the ants as interacting units that constitute an excitable fluid medium with emergent collective dynamics.

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