Emergent Behavior in Insect Societies: Global Oscillations, Chaos and Computation

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Achilles: Familiar to me? what do you mean? I have never looked at an ant colony on anything but the ant level

Anteater: Maybe not, but ant colonies are no different from brains in many respects ...

Gödel, Escher, Bach; Douglas Hofstadter

Abstract: Insect societies are formed by a huge number of individuals in interaction. Ant behavior is simple and, apparently, predictable, but recent results suggest that low-dimensional chaotic dynamics would be implicated at the individual level dynamics. In this paper, we explore several recent experimental results concerning global properties of ant societies, with the individuals defined as chaotic automata.

1 Introduction

Metamorphosis and flight were two revolutions in the evolutionary history of insects, together with the appearance of complex societies [1]. The social structure can be understood as a higher-level behavior of a set of simple and predictable organisms. Such units (say ants) are the basic structure of a “social mind” (the ant colony). The organization is maintained by interactions among many individuals, and two well known examples of such emergent structures are trail formation and nest building. Such behavior appears also in other systems in which some kind of computation is performed [2–4].

The analogies between ant colonies and brains are certainly not trivial. Both neurons and ants (Figs. 1a,b) have several common properties:

a. The behavior of single elements (ants or neurons) give us no information about how the colony or brain works: new phenomena arise when such elements are connected (in some way).

b. Global computational properties are observed as the outcome of the interaction of these structures and the environment.

c. When some number of elements are removed, the system is still able to show normal levels of performance [5–7].

The connection between the two structures has been pointed out several times in the past. In a 1969 book, Rémy Chauvin wrote: “We must also add that electronic engineers have now constructed circuits in which the different parts are joined to each other by
2 Neural Network Models

The study of real social insects and their tasks is not a static phenomenon (mathematics, etc) and this interaction is not a state of a given ant [6]. Some reasons are:

a. Ant colonies are formed by units) which can be classified into specific activity pattern. Ants can be active or inactive [6].
b. Under normal (stationary) conditions, the total number of tasks remains more or less the same.
c. Perturbation experiments (involving given classes) are external events that excite the internal state of the colony and are not purely linear.
d. The given task distribution in the colony is not organized in a process emergent from local interactions.

The ant colony will be formed into one of \( m \) given categories. The state vector is given by \( S_i = (S_i^1, \ldots, S_i^k) \), where there are \( m = 2^k \) possible states. The local interactions of the \( p \)-th local field.

\[
S_i^p(t + 1) = \Phi(S_i^p(t), \tilde{a}_i^p(t))
\]

as in standard neural network models, where the interaction between the actual categories: if \( S_i \) and \( a_i \) are given, respectively, then the interaction is defined as

The couplings are then defined as a function of the given individual shows a category of interest.

Several choices of \( \Phi \) are possible. We may define the interaction function can also be defined in the form:

\[
H(A_i, a_i) = \sum_{j=1}^{m} R_{ij} a_j
\]

and the corresponding stability

\[
\{S_i^p, A_i^p\}
\]
2 Neural Network Model

The study of real social insects [12] shows that the distribution of individuals among tasks is not a static phenomena. Ants interact at several levels (directly, through chemicals, etc) and this interaction can imply a change in the actual category (the internal state of a given ant) [6]. Some general points are well established:

a. Ant colonies are formed by a finite (usually large) set of individuals (i.e. simple units) which can be classified into some natural categories, by depending on the specific activity pattern. At a given moment (or over a time interval) each individual can be active or inactive [6,7].

b. Under normal (stationary) conditions, it can be shown that a given mean distribution of tasks remains more or less invariant. This special distribution is related to the fitness of the colony as a whole [13].

c. Perturbation experiments where the states of a given number of individuals (of some given classes) are externally changed shows that several categories responded non-linearly to these perturbations, in a way which suggests the existence of a complex process of parallel interaction [6].

c. The given task distribution of the ant colony is the result of a self-organization process emergent from local interactions.

The ant colony will be formally defined by a set of N individuals which are engaged into one of m given categories. The state of the i-th ant will be defined through the vector state $S_i = \{S_i^1, ..., S_i^m\}$, where $S_i^j = \pm 1$ with $i, j = 1, ..., N$. With this state definition, there are $m = 2^k$ possible states available to each individual i.e. $m$ possible “categories”. A matrix structure is defined between these categories, i.e. $\Omega_{ij}$ with $i, j = 1, ..., m$. We consider a Boolean interaction rule: the $p$-th component of $S_i$ will change under the effect of the $p$-th local field:

$$S_i^p(t+1) = \Phi \left( \sum_{j=1}^{N} A_{ij}^p S_j^p(t) \right) \quad \forall \ p = 1, ..., k$$  \hspace{1cm} (1)

as in standard neural networks [5]. Here $\{A_{ij}^p\}$ represents the interaction strength associated with the $p$-th component. The couplings are defined by taking into account the actual categories: if $S_i$ and $S_j$ are individuals pertaining to the $g$ and $h$ categories respectively, then the interaction strength will be $A_{ij}^p = \Omega_{gh}$.

The couplings are then determined in a simple way from the current states. As a given individual shows a category change, the corresponding couplings also change.

Several choices of $\Phi$ are possible; we take in our model $\Phi(z) = \text{sign}(z)$. An energy function can also be defined in the usual way:

$$H(\{A_{ij}^p\}, \{S_i^p\}) = -\frac{1}{2} \sum_{p=1}^{k} \sum_{i,j=1}^{N} A_{ij}^p S_i^p S_j^p .$$  \hspace{1cm} (2)

and the corresponding stability condition is described by the inequality

$$\{S_i^p A_{ij}^p > 0\} \quad \forall i = 1, ..., N \quad ; \forall p = 1, ..., k$$
we have \( h_{i}(+1) = \alpha N_1 - \beta N_2 \), the function will be:

\[
H = -\frac{1}{2} \sum_{i,j} J_{ij} S_i S_j
\]

\[
= -\frac{1}{2} \sum_{S_i = +1} S_i h_i + \sum_{S_i = -1} S_i h_i
\]

with \( C_{11} = C_{22} = \alpha \) and \( C_{12} = C_{21} = \beta \).

Using this new definition we look for a space defined by \((n_1, \ldots, n_m)\). A similar space is defined by representing a two-dimensional plane in which \( H \) is calculated using the colony size \((n_1, n_2 \leq N/2)\) and we measure the local interaction of the other categories.

If we only use a sample of size \( n \) and averaging over \( x \) samples and averaging, we obtain an attractor at \( n_0 = (20, 20, \ldots) \). The surface is observed at \( (20, 20) \). The map is robust with respect of local interaction because of the existence of cooperation as a linear sum of isolated maps.

The previous problem deals with the way in which the map can be interpreted, which is the task of attractor theory. The attractor theory seems to be a promising approach to understanding the dynamics of active workers having different behaviors.

### 3 Periodic Oscillations

Ant colonies are able to show regular ring periodic oscillations of activity levels [6]. Ant colonies show short-time periodic oscillations, and studies [6,10,11] have revealed the periodic nature of these oscillations.

One of the results of Cole's experiments [6] was that five samples give \( D_f < 0.5 \). When the results were averaged over five samples, the new value became \( D_f > 0.5 \), linked with periodic oscillations.

This result, obtained from experimental results, is in fact the first experimental evidence for periodic oscillations. Chaos would serve as a new explanation for the behavior observed in ant colonies.
we have $h_i(-1) = \alpha N_1 - \beta N_2$, $h_j(-1) = \beta N_1 - \alpha N_2$. Finally, the corresponding energy function will be:

$$H = -\frac{1}{2} \sum_{i,j} J_{ij} S_i S_j = -\frac{1}{2} \sum_i S_i \left( \sum_j J_{ij} S_j \right) = -\frac{1}{2} \sum_i S_i h_i$$

$$= -\frac{1}{2} \left[ \sum_{S_i = \pm 1} S_i h_i + \sum_{S_j = -1} S_j h_j \right] = -\frac{1}{2} (\alpha N_1^2 + \alpha N_2^2 - 2\beta N_1 N_2) = -\frac{1}{2} \sum_{k=1}^{2} \sum_{i=1}^{2} C_{kl} N_k N_l$$

with $C_{11} = C_{22} = \alpha$ and $C_{12} = C_{21} = -\beta$.

Using this new definition we can describe the energy function in the $m$-dimensional space defined by $(n_1, ..., n_m)$. An image of the energy surface (see Fig.2) can be obtained by representing a two-dimensional section given by the surface $H(n_1, n_2; R(n_k > 1))$ in which $H$ is calculated using the pairs of points $(n_1, n_2)$ linked with the two first categories (here $1 \leq n_1, n_2 \leq N/2$) and where the other $N' = N - n_1 - n_2$ individuals are randomly selected from the other categories.

If we only use a sample of such combinations, a rugged surface is obtained; using ten samples and averaging, we obtain a smooth surface. In our example (see ref [7]) we have an attractor at $n_0 = (20, 20, ..., 20)$. The bottom of the energy landscape at our section surface is observed at $(20, 20)$. It can be shown that the colony movement towards $n_0$ is robust with respect of local interactions. As a consequence of our previous results, we can understand how the task distribution can move in phase space after perturbation experiments. The nonlinear character of interactions causes changes in several tasks because of the existence of cooperative phenomena. These changes cannot be explained as a linear sum of isolated events.

The previous problem deals with the existence of a stable point attractor. Such an attractor can be interpreted, in adaptative terms, as the best distribution of workers and steady state seems to be a typical situation. However, oscillations and chaos in the numbers of active workers have been recently described [10,11,14]. In the next section, we will analyze such situation by using a cellular automaton (CA) model.

3 Periodic Oscillations with Chaotic Elements

Ant colonies are able to show a very unexpected kind of dynamical behavior: global oscillations of activity levels [10]. This means that, under some conditions, some ant colonies show short-time periodic changes in the numbers of active workers. Recent studies [6,10,11] have revealed the existence of nonlinear dynamics through local interactions.

One of the results of Cole's experiments was that single ants behave as chaotic elements. He measured the fractal dimension $D_f$ of single ant dynamics and an estimation over five samples gave $<D_f> \approx 2.43$, corresponding to that of a strange attractor. When global dynamics was analysed, the value over the same number of samples was $<D_f> \approx 3.09$, linked with periodic motion.

This result, obtained from studies in laboratory colonies of Leptothorax allardyceii is in fact the first experimental evidence of chaotic dynamics in animal behavioral processes. Chaos would serve as a source of unpredictability and flexibility in search and
Fig. 3. Individual oscillations (From Cole [10])

Fig. 4. Global coherent oscillations (From Cole [10])

predator avoidance. For a neural system with simple organization, low dimensional deterministic chaos represents the simplest way in which a nonlinear selforganized system can show randomness. In fact, the same mechanisms and structures implicated in other phenomena in which steady states are required, can generate chaos when some bifurcation parameter is changed above a given threshold. External inputs (or their absence) can be the source of such bifurcations.

Let $\mathcal{X}(n, t) = \{S_1(t), ..., S_n(t)\}$ be the global state of a colony of $n$ individuals (all microscopic states). Here $S_i(t) \in \mathbb{R}$ is the activity state of the $i$-th individual. A given ant is called active if $S_i(t) > \theta$ and inactive otherwise. Here $\theta$ is a threshold below which the ant becomes unactive (here we take $\theta = 0$. In order to compare our results with experimental data, we study the number of active elements, $0 \leq n_a(t) \leq n$.

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

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as \( S_k(r; t) \rightarrow S_k(r'; t + 1) \). If the ant is inactive or all nearest points are occupied, no movement takes place.

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

\[
S_k(r; t + 1) = tanh \left[ g \sum_{q \in C(r)} J_{km} S_m(q; t) \right]
\] (5).

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 nontrivial assumption is also introduced: self-interaction of individuals is present. In Cole's experiments, isolated ants were studied on a two-dimensional domain. In macroscopic terms, the previous observed behavioral patterns are in fact a kind of excitatory medium [15,16]. Each activation event gives birth to a wave of excitation throughout the colony. In mathematical terms, this situation resembles that of an excitatory neural tissue [16]. Let \( a(x, t) \) the activity level at a given spatial position \( x \). The evolution of the activity can in fact be approximated by:

\[
\frac{\partial a}{\partial t} = -\gamma a + \epsilon \int \int_{\mathbb{R}^2} e^{(\frac{a(x, t)}{e})} tanh(ga) \, dx \, dy + R(a - \theta)
\] (6)

with \( \delta, \epsilon, \gamma > 0 \) being some given constants and \( R \) a threshold-dependent function including random pulses (activations). Under some conditions, this model will be able to develop oscillations of activity, but using this approach makes difficult a careful comparison with the previous experimental results, in particular those results dealing with the number of individuals in interaction.

As a microscopic model, we consider here the dynamics of individual ants as defined by a so-called mobile cellular automaton (MCA) [15,17], being each ant described as a nonlinear dynamical system.

4 Strange Attractors, Oscillations and Spatial Structure

The chaotic dynamics of activation in the observed ant colonies strongly suggest the existence of a low-dimensional chaotic mechanism in the nervous activity of individual ants. Such a mechanism will act at the level of activation phenomena, and will be modelled here by using a continuous chaotic system. Here we will use the following neural model (Ermentrout, 1984):

\[
\frac{dx}{dt} = y - \mu z \ ; \ \frac{dy}{dt} = z - \nu x \ ; \ \frac{dz}{dt} = q z^2 - \gamma x.
\] (7)

The stability analysis of the rest equilibrium point \( x_0 = (0, 0, 0) \) shows that this point is stable if \( \mu, \nu, \gamma > 0 \) and \( \mu \nu - \gamma > 0 \) (Routh criterion). If \( \gamma = \mu \nu \), the eigenvalues are \( \lambda_1 = -\mu \) and \( \lambda_{2,3} = \pm i \sqrt{\nu} \) and for \( |\gamma - \mu \nu| \) small, a limit cycle can emerge through Hopf bifurcation. Using \( \mu = 1, q = 2 \) and \( \nu = 2 \), the first bifurcation occurs for \( \gamma_c = 2 \) and this limit cycle becomes unstable for \( \gamma \approx 3.09 \), the first period-doubling bifurcation. For \( \gamma > 3.45 \), chaotic attractors are present, as shown in Fig. 5.

Here we take \( z(t) \) as the "control variable" which determines the activation sequence of individuals: an inactive individual will become active if \( z(t) - \theta > 0 \), where \( \theta \) is a
Fig. 5. Strange attractors obtained from eq. (7) for $\gamma = 3.50$. Two reconstructions have been used: (a) $z(t) - z(t + \tau)$ with $\tau = 40$ and (b) same as before with $z(t)$.

Fig. 6. Nonlinear dynamics of a single individual. We show: (for $\gamma = 3.50$ and $\theta = 2.0$) (a) $z(t)$ (from eq.7) and (b) activation state; here $s_i = 1$ if activated and $S_i = 0$ otherwise.

given threshold. In Fig. 6, an example of the $z(t)$-dynamics is shown together with the activation state ($1 = $active, $0 = $inactive) for a single ant.

Now we consider the behavior of a set of $n$ interacting individuals. The interaction matrix (following the previous approach) is defined for active-inactive ants:
in which: \( J_{11} \): active-active coupling (now self-interaction is considered), \( J_{22} \): 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 with \( J_{11} = 0 \) seem 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 value). 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, however, be changed by depending on these cross-interactions.

Now, using our set of automata under the previously described dynamics (eq.5), we find that, by increasing the number of individuals, periodic oscillations are present as shown in Fig.7. Increasing the colony density (i.e. \( \rho = N/L^2 \)) with \( L=7 \), we can see that the global pattern of activation is periodic for enough high densities, as observed in experimental colonies [10,14]. The density is clearly related to the existence of percolation of activity. The computation of the Fourier spectrum shows the emergence of a well defined dominant peak as \( \rho \) is increased. In particular, we can analyse the effect
Fig. 8. Colony activity versus self-interaction $J_{11}$ and density (number of individuals). The arrow shows the appearance of global constant activation levels.

Fig. 9. Spatiotemporal distribution of activity. Top: no local interaction between individuals. Bottom: local interaction with nearest lattice points.

of several parameters on the periodicity and numbers of active elements. In Fig. 8 the activity level (the number of active ants at each point averaged over 500 time steps) is shown as a function of the self-interaction and the number of individuals. As we can see, higher $J_{11}$ values give higher activity levels with saturation beyond some threshold (see arrows). Still more interesting, the effect of density is also clear from Fig. 8b. In both
cases, we can see that the activity and as a consequence the use of energy resources is strongly dependent on both parameters.

Here we can speculate about the possible adaptive meaning of these oscillations: the colony can operate at a nonstationary state (as in some physiological systems) being able to minimize the use of energy (enough to guarantee brood care and colony survival). As the number of active units increases, the energy is increasingly used, and such situation can move to a full-time activated colony. The increasing levels of activity could be able to trigger colony fission, as observed in experimental colonies. Finally, this activity pattern is reflected in the spatial distribution of activity. A recent study using this model with random activation [15,18] has shown that activity is distributed in concentric patterns (Fig. 9) if self-interaction is present. This result also explains the self-organizing pattern of the brood observed inside the ant nests, also distributed as concentric rings [19]. Once more, the introduction of local interactions in a spatially distributed system results in new emergent phenomena [20,21].

5 Discussion

Emergent behavior is shown to be present in insect societies. These emergent properties are the outcome of synergetic processes obtained from the nonlinear interactions. In our study, global oscillations are present as the macroscopic pattern of spontaneous activation. The individual behavior was described through a chaotic attractor; using a neural-like interaction, the global pattern of activity acts as an order parameter which "enslaves" the individual behavior of ants. When isolated, these individuals are again random-like units. Such individual states can be used as an adaptation as shown by Deneubourg [22-24]. Low dimensional chaos can provide the (deterministic) source for such probabilistic behavior [22]. Oscillations are able to synchronize the ant colony as a single macroscopic unit. The spatial patterns of activity can be the source of order, and again the observed brood distribution inside the ant nests is here obtained from the emergent behavior.

It is well known that several properties of insect societies can be explained on a genetic basis [1,13]. Are then nonlinear phenomena and synergetics necessary in our understanding of evolution or social behavior? Genetic constraints are, we believe, only part of the story. In our examples, the local structure of interactions (which would be encoded at the genetic level) gives birth to higher-order phenomena (which are not). In this context, the emergence of a social structure as the ant colony can be seen (to some extent) as the result of a search in the "space of emergent properties". A full understanding of these systems needs a complementary approach from both levels of observation.

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