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Self-synchronization and Task Fulfilment in Ant Colonies

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Some authors have hypothesized that the observed self-synchronized activity in ant colonies provides some adaptive advantages, and, in particular, it has been suggested that task realization may benefit from this ordered temporal pattern of behaviour (Robinson, 1992, *Ann. Rev. Entomol*, **37**, 637–702; Hatcher *et al*., 1992, Naturwissenschaften, **79**, 32–34). In this paper, we use a model of self-synchronized activity (the fluid neural network) to suggest that with self-synchronized patterns of activity a task may be fulfiled more effectively than with non-synchronized activity, at the same average level of activity per individual.

1. Introduction

Ants, refuting popular fables, do not work untiringly all day long. As Sudd (1967) pointed out, the proportion of time spent in resting can be high, and the study of Herbers (1983) on acts performed by ants of *Leptothorax longispinosus* and *L. ambiguus* species reveals that "(…) ants spent two-thirds of their time apparently doing nothing at all". These behavioural patterns are by no means exceptional; Franks & Bryant (1987) found them in *L. acervorum* and Cole (1986) noted that "(…) Time spent quiescent occupies a large fraction of the total time of an ant (on average 55%)" while studying ants of the species *L. allardycei*. A more refined study by Franks *et al*. (1990) measured even a 72% of time spent resting for workers inside nests of *L. acervorum*. However, not only have patterns of alternate activation been found in individual ants, these patterns also appear *in whole colonies*, *showing synchronized patterns of activity*: surprisingly, Franks & Bryant (1987), by means of video-recording techniques, were able to get a long enough time series of the activity in whole colonies of *L. acervorum* to show, using spectral analysis, that activity was roughly periodic, with periods between 15 and 30 min. This synchronized behaviour has also been found in *L. longispinosus*, *L. ambiguus*, *L. curvispinosus*, *L. allardycei* and *L. muscorum* (see Miramontes, 1992, Chapter 2). Activity patterns are not just synchronized, but *self*-synchronized: no external signal has been found experimentally as a possible cause of colony synchronization (Cole, 1991a).

Self-synchronization, as we already said, has been found in diverse *Leptothorax* species. The work of Cole (1991a) is particularly interesting, since he studies also individual activation dynamics, obtaining data quite relevant for designing individual-based mathematical models of oscillatory behaviour. The method used in Cole (1991a) to collect data from individuals and colonies was based on recording images of whole colonies of *L. allardycei* every 30 s, measuring activity levels by taking the pixel differences between two successive images. The analysis was performed by means of periodograms with peaks in the Fourier components around a period of 27 min per cycle, and autocorrelation functions, whose sinusoidal nature indicates clearly that the time series is periodic, with a mean period of approximately 26 min (see Cole, 1991a for details). The same sort of measures performed over a single isolated ant made evident spontaneous activation and quiescence during long periods of time but no periodic activity. Furthermore, Cole (1991b) was able to show evidence of chaotic activity in individual ants. So, one important conclusion is already at hand, that is, *self-synchronization is a collective property*, since individual patterns of activation are not periodic. Finally, Cole (1991a) discusses the adaptive significance of short-term activity cycles arguing that it is unlikely that these cycles contribute to the efficiency of the colony. They are "(...) the inevitable outcome of interactions within social groups".

However, at least two functional behaviours in ant colonies have been related to self-synchronized activity: task allocation (Robinson, 1992) and mutual exclusion (Hatcher *et al*., 1992).

Mutual exclusion in *L. acervorum* colonies has been proposed as a mechanism for effective exchange of information on task allocation (Hatcher *et al*., 1992). Inside nests of *L. acervorum* nurse workers interact in order to determine which items of brood require attention, with the constraint that no more than a few nurses can tend a brood item (spatial arrangement of brood limits the number of workers that can access brood simultaneously). Assume that nurse workers choose at random which brood item to tend. In this situation, some brood items may be ignored during a too long period of time, long enough to endanger their survival. Assume that the probability of tending a certain brood item is $1/B$ (there are B brood items and A nurse workers), then the probability that no nurse worker tends that brood item is $(1-1/B)^A$. So, the proportion P_{random} of brood tended in any period of time will be

$$P_{random} = 1 - \left(1 - \frac{1}{B}\right)^A.$$

If we had synchronized activity, the situation would be quite different. In this case, all nurses try to tend some brood item, which causes an even distribution due to the spatial access constraint. The proportion $P_{exclusion}$ of brood tended in a period during which each ant is active once (an accounting period) is

$$P_{exclusion} = \begin{cases} A/B & \text{for } A < B, \\ 1 & \text{for } A \geqslant B. \end{cases}$$

Figure 1 makes clear the superior efficiency of mutual exclusion mechanism, that is, self-synchronization plus spatial restrictions in brood access.

Task allocation in ant colonies is an extremely fascinating problem, making evident, perhaps in its very essence, the collective performance of insect societies: each ant in a colony seems to know exactly what to do in order to fulfill *global* colony needs. It seems that self-synchronized behaviour provides a mechanism for information propagation:

> "Sampling behaviour that involves social interactions may be facilitated by synchronous bursts of worker activity, which have been observed in ant colonies (...). The decision of which task to perform would be based on the integration of acquired information, coupled with behavioural

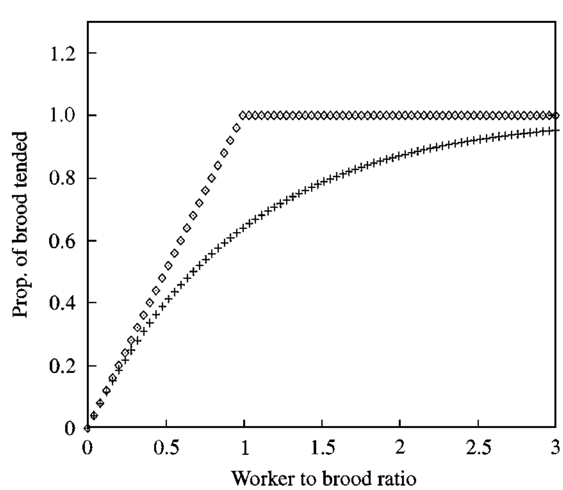

FIG. 1. Proportion of brood tended with respect to worker-to-brood ratio for mutual exclusion and random models. The better efficiency of mutual exclusion is obvious (after Hatcher *et al*., 1992). (◇) mutual exclusion; (+) random.

biases associated with worker, caste, physiological status and prior experience." (Robinson, 1992, p. 652).

So, according to Robinson (1992), self-synchronization facilitates the sampling of any information an individual may need from other individuals. Let us try to clarify this point. Assuming that ants cannot be active all the time (which is what is observed in nature, see above), why would self-synchronized behaviour be a better (simpler) strategy than, say, random (in the sense of "non-synchronized") activity patterns? We will need further assumptions to answer this question: first, the obvious one of locality (an individual is able to get only local information) and second, the quite reasonable (and biologically plausible, see above) assumption that the unique interaction allowed to an *inactive* individual is to be "awaked" by other(s) individual(s); an inactive individual does not carry any information, namely, it is equivalent to a "sleeping" individual. Now, in this context, it would be clear why we should obtain an increase of efficiency with synchronized patterns of activity: it would maximize the number of simultaneously *active* neighbours of an *active* individual. Let us remind ourselves that we are assuming that individuals cannot be active all the time. This reasoning, however clear, must be validated with both theoretical models and experiments, since only by doing so can we explore which assumptions are necessary, and then later go out and see what is the real state of things in real ants. The study of a theoretical model is the main point of this paper.

So, we will explore whether, in general, self-synchronized behaviour induces a more effective way of task performing, in a sense which will be discussed below. In order to test this idea we will proceed by using a mathematical model for temporal oscillations [fluid neural networks (FNNs) Section 2], modified with a mechanism for "task" spreading and "task" fulfilment. FNNs allow us to perform a numerical study to compare the efficiency of a system with self-synchronized activity with the efficiency of a system with non-synchronized (but with the same average activity level per individual and time step). Finally, we will discuss the drawbacks of our approach, the implications of our result and the need for real data concerning the subject of the paper.

2. Fluid Neural Networks

In FNN the standard approach of neural networks is used (Amit, 1989), but a new set of rules defining local movement and individual activation is also introduced. A set of N automata or "neuron-ants" is used. The state of each automaton (say the i-th one) is described through a continuous state variables $S_i(t) \in \mathbf{R}$, at each time step $t \in \mathbf{N}$. Each element can move on an $L \times L$ two-dimensional lattice with periodic boundary conditions.

If $S_j(t)$ is a given automaton (the spatial dependence is omitted for simplicity), the new states are updated following

$$S_i(t+1) = \tanh[g h_i(t)], \tag{1}$$

where g is a gain parameter and $h_i(t)$ can be defined in diverse ways in order to get the desired behaviour. We will obtain oscillations in activity (see below) if the term $h_i(t)$ includes interactions with the eight nearest neighbours:

$$h_i(t) = S_i(t) + \sum_{i \neq j \in B(i)} S_j(t), \tag{2}$$

where $B(i)$ are the nearest automata. To get non-synchronized individuals we do not need interaction with any other automata:

$$h_i(t) = S_i(t). \tag{3}$$

We have seen above that one of the properties observed in isolated ants was spontaneous activation (Cole, 1991b). In FNNs this has been included in the following way: each automaton can be either *active* or *inactive* and, if active, it moves randomly to one of the eight nearest cells (if not space is available, no movement takes place). In our model, a given automaton will be active if $S_i(t) > \theta_{act}$ and inactive otherwise. Once an automaton becomes inactive, it can return to the active state (with a *spontaneous activity level* S_a) with some probability p_a.

The collective behaviour we measure in FNNs is the mean activity of the system. We define an activity for each individual $S_i(t)$, $a_i^t = \Theta[S_i(t) - \theta_{act}]$, so the mean activity at time t

will be

$$\rho_t^+ = \frac{1}{N}\sum_{j=1}^{N} a_j^t = \frac{1}{N}\sum_{j=1}^{N} \Theta[S_j(t) - \theta_{act}], \quad (4)$$

where $\rho_t^+ \in [0, 1]$ and $\Theta[x]$ is such that $\Theta[x] = 1$ if $x \geqslant 0$ and $\Theta[x] = 0$ otherwise. We define also the total density of automata as $\rho = N/L^2$.

In this paper, we have chosen the FNN parameters $N, L, g, \theta_{act}, S_a$ and p_a to get the desired behaviour, that is, self-synchronized activity and non-synchronized activity (see Fig. 2), though in both cases we have imposed the following constraints:

- The number of individuals must be similar to that observed in colonies with synchronized activity (Miramontes, 1992).
- The activity level per individual must be around $\simeq 0.3$, that is, each individual is active for approximately 30% of the time, on average, as observed in species with synchronized activity (Herbers, 1983; Cole, 1986; Franks & Bryant, 1987).
- The density ρ of the system should be around $\simeq 0.2$, as was observed experimentally in Franks *et al.* (1992); see also Solé & Miramontes (1995).

To be more specific, the parameters we use are $N = 120, L = 25, g = 0.1$ and $\theta_{act} = 10^{-16}$. We get synchronized behaviour with $S_a = 0.01$, $p_a = 0.001$ and h_i defined as in eqn. (2), and random behaviour with $S_a = 0.1, p_a = 0.03$ and h_i following eqn. (3). The sort of interactions defined in FNNs (activation among individuals) is currently the subject-matter of experimental research by Cole and collaborators (Cole & Cheshire, 1996) An analysis of FNNs is performed in Delgado (1997) and Delgado & Solé (1997, 1998).

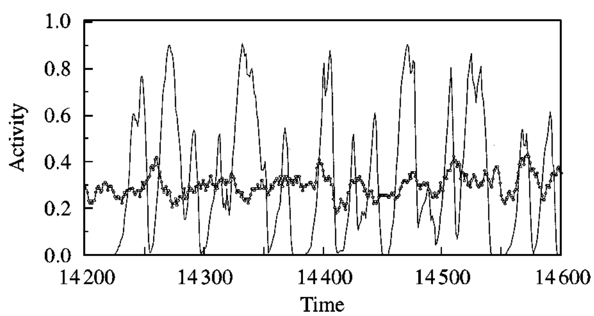

FIG. 2. Evolution in time of ρ_t^+. We get bursts of synchronized behaviour with $S_a = 0.01, p_a = 0.001$ and non-synchronized behaviour with $S_a = 0.1, p_a = 0.03$ (○○○). In both cases the average activity per individual and time step is $\simeq 0.3$, that is, an individual is active for approximately 30% of the time.

3. Task Spreading

Now that we know how individuals get active and inactive (the FNN dynamics), we must define a way for distributing a certain "amount of task" among the individuals of the system. The mechanism we will suggest would be similar to the spread of a large protein source within the nest or to the spread of liquid food via trophalaxis (Hölldobler & Wilson, 1990).

Every individual will be either "working" or "non-working". So there are three possibilities for the state of an individual: active and working, active and non-working, and inactive and non-working. We will omit the fourth possibility, an inactive and working individual; let us recall one of the main points of the discussion in Section 1, that of the biological plausibility of taking an inactive individual as a "sleeping" individual. A non-working individual may become a working individual if it is exposed to an amount s of *stimulus*. This stimulus may come either from the individual lattice coordinates or from working neighbours (see below for details). A working individual has associated a certain amount of stimulus. In fact, we will use the stimulus also as a representation of the "amount of task" to be done, so that once an individual is engaged in a determined task, it has some probability $p(s)$ per unit time of completing the task. Throughout this paper we will use the nonlinear response function

$$p(s) = \frac{1}{(1 + s^2)}$$

so that the greater the task, the less likely the individual will complete the task.

Let us describe in detail our model: assume an $L \times L$ lattice with N individuals distributed on it. Each individual will be characterized by a state $(S_i(t), X_i(t))$ where $S_i(t)$ is the FNN-state of the individual i, $X_i(t)$ is a two-valued variable signalling whether the individual is working ($X_i(t) = 1$) or not ($X_i(t) = 0$). Also, a working ($X_i(t) = 1$) and active ($S_i(t) > \Theta_{act}$) individual may be doing a certain amount of task $c_i(t)$. Each lattice site will be either void or will contain one individual. Besides, it may also contain a certain amount of stimulus.

Initially, our system will be composed of N non-working individuals, with a random initial state. A randomly chosen position of the lattice (the "task origin") will contain a certain amount of total task C_{in} to be performed by individuals, while lattice sites other than the task origin will be initially empty of stimulus.

Our system will evolve in time, as far as $S_i(t)$ is concerned, *exactly* as an FNN (Section 2), so what remains to be defined is the evolution in time of X_i(t) and eventually c_i(t), that is, the task realization process.

1. *Effective realization of the task*. An individual i at time t may be active ($S_i(t) > \theta_{act}$) and working ($X_i(t) = 1$), with a certain quantity of task $c_i(t)$ to be done. At time $t + 1$, this individual may accomplish the task with probability $p(c_i(t))$, in which case the total task remaining in the system will be decreased by an amount $c_i(t)$. If the (active and working) individual i does not get the task done at time $t + 1$, it may become inactive ($S_i(t + 1) \leqslant \theta_{act}$), in which case the amount of task $c_i(t)$ will be stored in the lattice coordinates of the individual i. Inactive individuals do nothing, though they may be activated by the FNN dynamics of the system. The next rule deals with the remaining case, that of active and non-working individuals.

2. *Propagation of the stimulus*: An active and non-working individual may be stimulated by all its active and working nearest neighbours and by the amount of task stored at its lattice position. Each active and working individual, say the j-th, will be able to provide a quantity of stimulus that will depend on the number of active and non-working neighbours, say n_j. A quantity $\sigma_j = \beta c_j(t)/n_j$ will be the stimulus provided by j to each of its n_j non-working active neighbours. Thus, an active and non-working individual, say the k-th, will receive a quantity of stimulus $\sigma_k = \sum_{i(k)}\sigma_i + \alpha\,\Sigma_{x,y}$, where $i(k)$ ranges over the active and working neighbours of the k-th individual

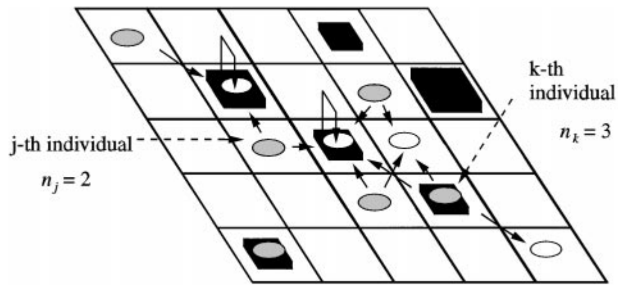

FIG. 3. Graphical representation of stimulus propagation. Active and non-working individuals may be stimulated by the amount of task in their lattice site and by active and working neighbours. These neighbours will share a fraction β of their task with all their active and non-working neighbours, as detailed in the text. Arrows between individuals and from task to individuals indicate sources of stimulus to active but non-working individuals: ⬬ active and working individual; ○ active and non-working individual; ◆ task in Lattice site.

and $\Sigma_{x,y}$ is the amount of task at the lattice coordinates x,y of k (see Fig. 3). When this individual becomes a worker, the quantities σ_i are subtracted from $c_i(t)$ (for all i active and working neighbours of k) and $\Sigma_{x,y}$ will become $(1 - \alpha)\Sigma_{x,y}$. The parameters α and β allow one to control the degree of stimuli received from the task stored in the lattice and the spreading of stimuli from individual to individual, respectively.

To sum up, a certain quantity of initial task C_{in} needs to be done. This quantity of task will be spread over the system, by means of individuals being stimulated by the task in their lattice sites and/or by other individuals carrying some amount of stimulus, which eventually would perform the task. A unique way to do some part of the task is by changing the state from worker to non-worker while being active. In this case, the quantity $c_i(t)$ of the corresponding individual will disappear from the system.

4. Results: Synchronized Activity vs. Non-synchronized Activity

The model detailed in Section 2 and 3 has been used to test whether a system with self-synchronized activity patterns is able to perform an "abstract" task better than a system with random activity patterns, both subject to the constraints mentioned in Section 2. What does "better" mean in this context? It will be equivalent to "faster". Thus, we want to measure how fast a system with certain patterns of activation is able to perform a certain fraction of the initial task C_{in}. We will measure how the total task that remains to be done in the system:

$$C(t) = \frac{1}{C_{in}}\left(\sum_{x,y=1}^{L} \Sigma_{x,y}(t) + \sum_{i=1}^{N} c_i(t)X_i(t)\right) \quad (5)$$

evolves in time with two different patterns of activity: self-synchronized (SS) and non-synchronized (NS). Figure 4 shows that there is no difference in behaviour with a small C_{in}, though a larger initial task makes the SS behaviour more efficient than NS, that is, the SS system gets the task done in less time than the NS system. Now, we define t^*_{SS} as the first time step such that the system with self-synchronized behaviour verifies $C(t) < 0.1$. We define t^*_{NS} in the same way. More systematic calculations have been done computing the difference between t^*_{NS} and t^*_{SS}. As we can see in Fig. 5, the expected value of the difference t^*_{NS}–t^*_{SS}

$$E(C_{in}) = t^*_{NS} - t^*_{SS}$$

grows with C_{in} making clear that the more the "quantity" of task that needs to be done, the more efficient is the SS behaviour.

Robinson (see Section 1 and Robinson, 1992) gave us some clues to ascertain the causes of the superior efficiency of SS behaviour. The key idea is that the spreading of the task is enhanced by the greater number of *simultaneously active* neighbours an individual has, on average, in the SS case. This phenomenon allows the individuals to distribute faster the task, "breaking" it up into smaller pieces, so that it is much more likely that an individual completes its task.

In order to go further into this matter we have performed a numerical study of the behaviour of the model as a function of the β parameter, since this parameter allows one to control the amount of task than an active and working individual is able to share with its active and non-working neighbours. If the above-mentioned hypothesis were correct, a smaller β would induce a slow fragmentation of the initial task C_{in}. Then, the task solving process would depend solely on individuals changing state (from working to non-working) according to the amount of task located at their lattice coordinates. This behaviour would not benefit from the advantage provided by self-synchronization, so that there would be no difference between self-synchronized, and non-synchronized behaviour in what concerns efficiency, as we measure it in this paper. Figure 6 seems to confirm our reasoning. A single run of the model with $\beta = 0$ shows how self-synchronized behaviour does not provide any advantage when

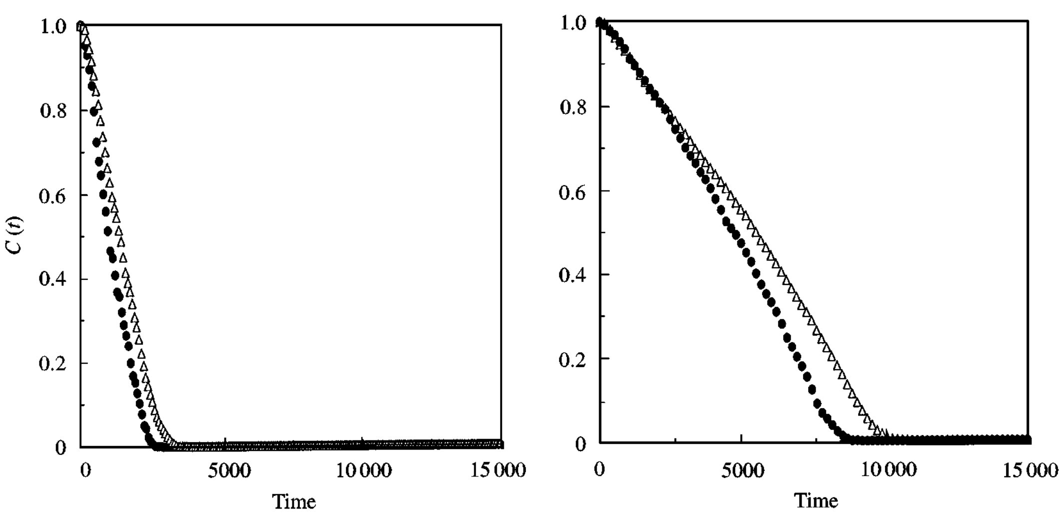

FIG. 4. Single-run simulations to compare $C^{SS}(t)$ and $C^{NS}(t)$. (a) $C^{SS}(t)$ (△△△) and $C^{NS}(t)$ (● ● ●) with $C_{in} = 10\,000$. (b) $C^{SS}(t)$ (△ △ △) and $C^{NS}(t)$ (● ● ●) with $C_{in} = 50\,000$. In both cases, $\alpha = 0.25$ and $\beta = 0.85$; (●) self-synchronized; (△) non-synchronized.

compared with non-synchronized behaviour. Individuals do not share any amount of task with their neighbours, that is, there is no stimulation among individuals, so that active and non-working individuals must find some place in the lattice with some amount of task in order to switch to the working state. We have defined a measure of how fast the self-synchronized system solves the task with respect to the non-synchronized system, as a function of β:

$$D(\beta, t) = C_\beta^{NS}(t) - C_\beta^{SS}(t).$$

Clearly, $D(\beta, 0) = 0$ and $D(\beta, \infty) = 0$ since both systems are able to solve the task. However, we will focus our attention on the intermediate behaviour of $D(\beta, t)$ (as a function of t, for a given β) since the higher the maximum, the more efficient is the self-synchronized behaviour. Figure 7 confirms our suspicion: the maximum of the function $D^*(t) = D(\beta^*, t)$ reaches higher values as β^* grows. Of course, one could raise an objection, since $D(\beta, t)$ measures a difference, so that, in principle, there is not enough information to infer what we stated above. However, Figs 4 and 6 give us the additional information we need to safely deduce that a growing maximum implies an increase of efficiency of the self-synchronized behaviour.

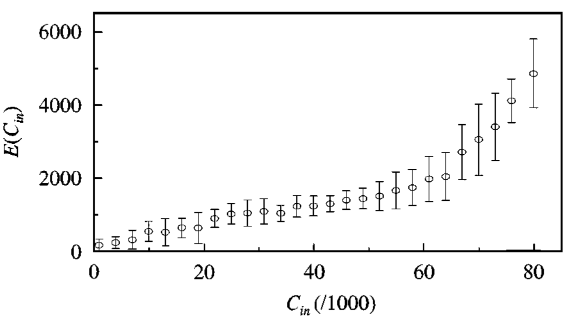

FIG. 5. $E(C_{in})$ (see text) averaged over $M = 25$ samples for each C_{in} with the parameters $\alpha = 0.25$ and $\beta = 0.85$.

These results are quite robust, since modifications of the original model introduced in Sections 2 and 3 do not change them. Let us explore an interesting variant of the model, based on a biologically plausible assumption: each individual has fixed response thresholds to stimuli, so that the lower the threshold the more likely the individual will engage in the task, given exposure. There is an experimental basis that justifies this approach, for example the existence of response thresholds in honey bees has been proved (Bonabeau *et al.*, 1996).

The new model is *exactly the same* as the original one (defined in Sections 2 and 3), but now the change from the non-working state to the working state will be probabilistic. We will assign a *threshold* θ_i to the i-th individual and, given exposure to an amount s of stimulus, the probability of changing the state is defined as

$$P(S_i^{Not\ working} \rightarrow S_i^{Working}) = \frac{s^2}{s^2 + \theta_i^2}. \tag{6}$$

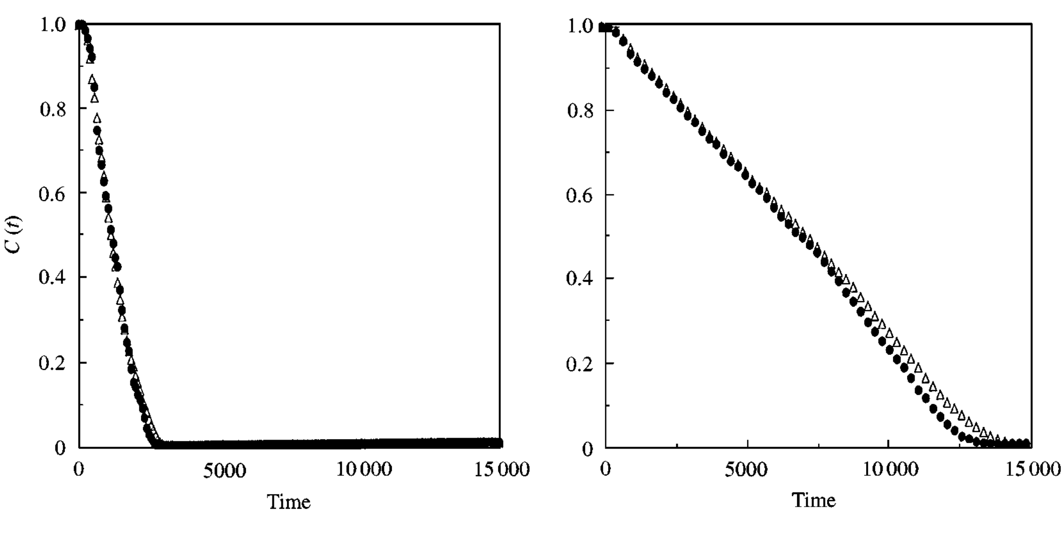

FIG. 6. Single-run simulations to compare $C^{SS}(t)$ and $C^{NS}(t)$. (a) $C^{SS}(t)$ (△△△) and $C^{NS}(t)$ (●●●) with $C_{in} = 10\,000$. (b) $C^{SS}(t)$ (△△△) and $C^{NS}(t)$ (●●●) with $C_{in} = 50\,000$. In both cases, $\alpha = 0.25$ and $\beta = 0$.; (●) self-synchronized; (△) non-synchronized.

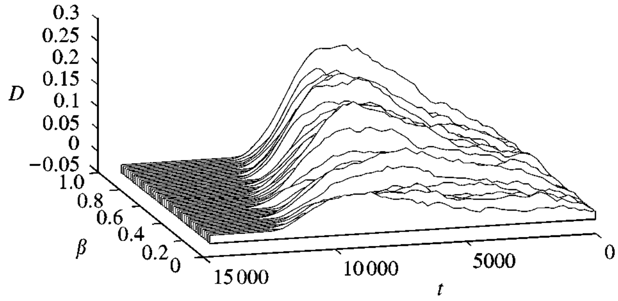

FIG. 7. $D(\beta, t)$ for $0 \leqslant \beta \leqslant 0.85$ and $C_{in} = 50\,000$. As hypothesized in the text, the maximum of $D(\beta, t)$, with β fixed, grows with β, showing clearly that the efficiency of self-synchronized behaviour strongly depends on the ability of individuals to stimulate each other.

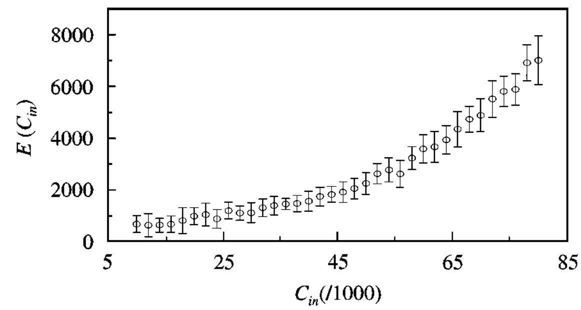

FIG. 8. $E(C_{in})$ averaged over $M = 25$ samples for each C_{in} with the parameters $\alpha = 0.25$ and $\beta = 0.85$. In this case, we used the model with thresholds. The parameters are the same as in Fig. 5 and random thresholds are chosen uniformly from the interval (1, 10).

We have chosen to work with randomly chosen thresholds, reflecting a plausible lack of thresholds uniformity in real ant colonies (Bonabeau *et al.*, 1996). Now, the same measures we performed in the original model can also be performed in this new model, with the same results, as we can see in Fig 8. Again, self-synchronized behaviour is far more efficient than non-synchronized behaviour.

5. Discussion

In this paper, we have introduced a framework with which to study the relation between patterns of activity in social insects and the ability to fulfill some task. We have seen that self-synchronization enhances the efficiency with which the system performs some sort of "abstract" task, though similar to the spread of liquid food via trophalaxis. Our numerical results point out that observations in real colonies, concerning the functional side of synchronized patterns, may reflect a more general relation between task fulfilment and self-synchronization, since, as Robinson (1992) tells us in the quote mentioned above, to ascertain the mechanisms of the spreading out of tasks and/or information inside the colony is important to account for the task allocation abilities of social insects.

The phenomenon is not difficult to understand. The key point is the idea that "if it is not active, it does not work" together with the local transmission of information (stimulus, task, etc.) from individual to individual. If not active permanently, the only way to ensure that an *active* individual will have as many *active* neighbours as possible that can be stimulated, and consequently to get the task as scattered as possible, is having synchronized activity. Besides, individuals are more likely to start tasks immediately on being activated, since the activating neighbours may be work-carrying.

There are other models of self-synchronization (Blanchard & Franks, 1998; Goss & Deneubourg, 1988; Tofts *et al.*, 1992), but it was not clear how to put on top of them a mechanism of task spreading, due to their different mathematical nature (differential equations or probabilistic process algebras). This is the main reason to work with the FNN.

Related work to that introduced in this paper was introduced in Bonabeau *et al.* (1998) where it was suggested that synchronization may enhance foraging efficiency. Finally, some experiments (Franks *et al.*, 1992) and previous work with FNNs (Solé & Miramontes, 1995) clearly suggest a dependence of self-synchronization on colony density. Thus, it would be possibl to do experimental work with real colonies by modifying artificially their density (as in Franks *et al.*, 1992) inducing non-synchronized behaviour. This setting would allow us to compare task fulfiling in colonies with different patterns of temporal activity.

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