

# The formation of spatial patterns in social insects: from simple behaviours to complex structures

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Many of the collective activities performed by social insects result in the formation of complex spatio-temporal patterns. Without centralized control, workers are able to work together and collectively tackle tasks far beyond the abilities of any one individual. The resulting patterns produced by a colony are not explicitly coded at the individual level, but rather emerge from nonlinear interactions between individuals or between individuals and their environment. We present a few selected examples to illustrate some of the basic mechanisms used by social insects, such as templates, stigmergy and self-organization. These mechanisms can be used in combination to organize pattern formation at the colony level.

**Keywords:** self-organization; template; stigmergy;  
pattern formation; morphogenesis; social insects

## 1. Introduction

Many of the collective activities performed by social insects result in the formation of complex spatio-temporal patterns (Wilson 1971; von Frisch 1975; Hansell 1984; Hölldobler & Wilson 1990; Camazine *et al.* 2001). Some of these patterns spread over large-scale surfaces and there may be several orders of magnitude difference between the size of an individual and the size of the structure built by a colony; we can find, for instance, a whole range of species of ants and termites that build huge nests and large-scale networks of chemical trails or underground galleries. In the ant *Formica lugubris*, super-colonies that contain more than 20 million individuals are spread over several thousand square metres. These super-colonies build tens of kilometres of trail networks that are several million times the size of an individual ant (Cherix 1980). Among the most impressive nest structures are those produced by African termites

One contribution of 18 to a Theme 'Self-organization: the quest for the origin and evolution of structure'.

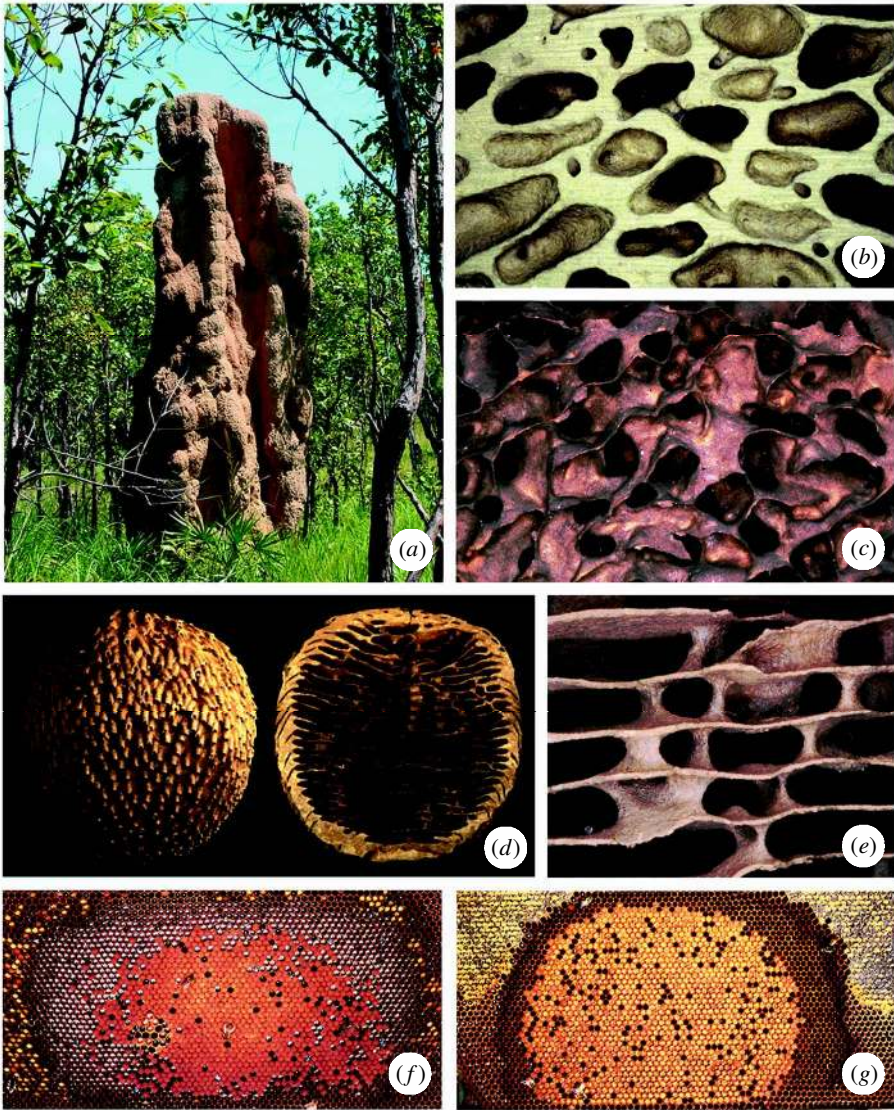


Figure 1. A selection of characteristic spatial patterns built by social insects. (a) A termite mound built by *Nasutitermes triodiae* (northern territory of Australia). (b) A cross-section of *Cubitermes* spp. nest showing its alveolar structure (Ivory Coast, Africa). (c) A cross-section of a *Lasius fuliginosus* nest showing its sponge-like structure (France). (d) An external view and a cross-section of an *Apicotermes lamani* nest (Gabon, Africa). (e) A close-up view of helicoidal ramps connecting successive floors inside an *Apicotermes lamani* nest (Gabon, Africa). (f), (g) Two frames showing the characteristic pattern of a centrally located brood surrounded by a band of pollen and a peripheral region of honey in a bee hive (*Apis mellifera*). (Copyright Scott Camazine & Guy Theraulaz.)

of the subfamily Macrotermitinae: the fungus growers (see figure 1*a*). A mature nest of a *Macrotermes* species usually reaches 6 or 7 m high, while individuals are at most a few millimetres long (Howse 1970; Collins 1979; Grassé 1984); in this case the ratio (nest size/individual size) may reach  $10^4$ – $10^5$ . Not only is the characteristic scale of the patterns typically much larger than the size of the individuals but the patterns themselves can also be highly complex. Many species of ants and termites build architectures comprised of a variety of delicate and highly regular structures. For instance, *Apicotermes* termites build subterranean oval nests about 20 cm high, in which we can find stacked horizontal chambers connected by helix-shaped vertical passages that are used as spiral staircases (Desneux 1956). The outer surface of the nest is covered with a set of regularly spaced pores that open towards corridors circulating inside the internal wall of the nest (see figure 1*d, e*). In ants a large number of species, such as *Lasius fuliginosus*, build sponge-like nest structures with a complex network of galleries interconnecting chambers (see figure 1*c*). Finally, the patterns built by social insects are more than the simple repetition of the same basic module; even if some basic elements are repeatedly present, they are organized in superstructures. For instance, a beehive is not just an array of hexagonal cells (see figure 1*f, g*); cells are organized into combs, and each comb is organized into three distinct concentric regions, with a central area where the brood is located, surrounded by a ring of cells that are filled with pollen, and finally a large peripheral region of cells where honey is stored (Camazine *et al.* 1990; Camazine 1991).

These observations raise the key questions of how a collection of insects can coordinate their working to build patterns of such astonishing size and complexity. A first point of note is the large number of individual actions required to build all these structures. As an example, one hundred million individual actions are necessary to fill one cubic metre with brushwood and pine needles used to build the large mounds of the European red wood ant *Formica polyctena* (van Damme 1998). A second point is the dynamic aspect of the patterns, which are not frozen structures; instead their shape changes with time, often because of conflicting actions arising between insects (Bouillon 1958). For instance, we can frequently observe an ant or a termite worker breaking up what has just been built by another individual. Despite this randomness at the individual level, collective structures which fulfil numerous functional and adaptive requirements (protection against predators, substrate of social life and reproductive activities, thermal regulation, etc.) are produced. Finally, we should not seek the origin of nest complexity in the ability of individual insects to process a large quantity of information, but rather in the multitude of stimulus responses resulting from the relatively simple behaviours of interacting individuals. In the last 20 years there has been a large amount of work suggesting that a social-insect colony is a decentralized system comprised of cooperative, autonomous units that are distributed in the environment, exhibit simple probabilistic stimulus-response behaviour, and only have access to local information (Deneubourg & Goss 1989; Bonabeau *et al.* 1997; Theraulaz *et al.* 1998; Camazine *et al.* 2001). Without centralized control, workers are able to work together and collectively tackle tasks far beyond the abilities of any one individual. The resulting patterns produced by a colony are not explicitly coded at the individual level, but rather they emerge from myriads of simple nonlinear interactions between individuals or between individuals and their environment.

Insects are equipped with a sensory-motor system (including chemoreceptors, mechanoreceptors, thermoreceptors, hygroreceptors, etc.) that enables them to respond to stimuli. Although such signals are not equivalent to signs, which could have symbolic value—these signals are simply attractive or repulsive, activating or inhibiting—they affect behaviour in a way that depends on their intensity and on the context in which they are released. A large variety of patterns built by social insects result from the variety of stimuli that surround insects. These stimuli include not only environmental cues but also direct and indirect interactions among nestmates, which often involve pheromones. The stimuli that initially trigger building behaviour may be quite simple and limited in number but, as pattern formation proceeds, these stimuli become more complex and more numerous, thereby inducing new types of behaviour. Pattern formation can then be seen as a morphogenetic process during which past construction sets the stage for new building actions (Franks *et al.* 1992). This principle can be coupled with demographic effects: as the nest gets bigger, the greater the variety of signals and cues it is likely to encompass (the probability of finding heterogeneities also increases when the colony expands its territory). This may in part explain why the most populous termite societies have the most complex nests (Grassé 1984).

The aim of this paper is to review some of the basic mechanisms used by social insects to build the above-mentioned patterns, to introduce biological examples where these mechanisms have been clearly demonstrated and modelled and, finally, to examine the way in which several pattern-formation mechanisms might be combined with each other.

## 2. Template-based patterns

A first mechanism widely used by social insects to organize and coordinate their building activities relies on templates: the blueprint of the nest 'already exists' in the environment in the form of physical or chemical heterogeneities. Many ant species, including *Acantholepsis custodiens* (Brian 1983), *F. polyctena* (Chauvin 1958, 1959; Gallais-Hamonn & Chauvin 1972; Ceusters 1986) and *Messor ebenius* (Thomé 1972), make use of temperature and humidity gradients to build their nests and spatially distribute eggs, larvae and pupae. More generally, the behaviour of most insects is influenced by heterogeneities in the environment: they tend to walk, build, store or lay eggs along such heterogeneities. Heterogeneities are any perceptible deviations from a uniform distribution or constant quantity: this includes irregular soil levels, obstacles, gradients and predictably varying quantities such as temperature or light intensity. For instance, the shapes of the *Formica* mounds are modified by temperature and light (Lange 1959; Ceusters 1980). When the surface of the mound is warmed up with an infrared light the nest becomes flat but, when the light is moved away from the nest, the mound adopts a hemispheric shape. This is an indirect consequence of an innate tendency of the ants to run away from direct sunlight and the increase of their running speed with temperature. The environment might also influence the shape of the resulting structure by changing the physical properties of the construction material. For instance, in *L. niger* ants a change in humidity conditions results in a change in the shape of the craters built at the nest's surface, from a chimney-like shape after a rainfall to that of a flattened disc when the excavated material is dry. Although the transporting and unloading behaviours remain

unchanged whatever the humidity conditions, the cohesion of the building material strongly changes with humidity. When this variation is combined with the ants' unloading behaviour, it leads directly to the observed variety in crater shapes.

Sometimes, an individual can directly provide a template, as illustrated by the example of the construction of the royal chamber in termites (*Macrotermes subhyalinus*): the queen of *M. subhyalinus* emits a pheromone that diffuses and creates a pheromonal template in the form of a decreasing gradient around her. It has been shown experimentally that a concentration window, or a threshold, exists that controls the workers' building activities: a worker deposits a soil pellet if the pheromone concentration lies within this window or exceeds the threshold (Bruinsma 1979; Bonabeau *et al.* 1998). Otherwise, they do not deposit any pellets and they may even destroy existing walls. If we place a freshly killed physogastric queen in various positions, walls are built at a more or less constant distance from the queen's body, following its contours, while a wax dummy of the queen does not stimulate construction. In this description, we have omitted for simplicity tactile stimuli and other pheromones, such as cement and trail pheromones, that facilitate the recruitment, coordination and orientation of individual workers, and that determine the detailed shape of the reconstructed chamber: the major organizing role is played by the queen's building pheromone, which creates a chemical template. With this mechanism, the termite workers are able to build at any moment an adjusted chamber that fits the size of the queen. When the queen gets bigger the concentration thresholds move towards the periphery and a new chamber is built instead of the old one.

There also exists another type of template, which is not directly present in the environment. Instead, the template can be within the insects themselves in the form of a probability of performing an action. The construction of domes in *Formica* ants and the formation of craters near the entrance hole of *Messor* ants' nests are examples of structures that result from the use of internal templates (Gallais-Hamonne & Chauvin 1972; Chrétien 1996; van Damme 1998). Both structures result from the stacking of pine needles or soil particles that are transported by workers, each ant being characterized by an increasing probability to drop the object she carries as a function of the distance from the nest entrance. Crater formation in the ant *M. barbarus* has been studied in detail under experimental conditions (Chrétien 1996). Workers were given access to sand through a little hole placed at the centre of an arena. When an ant comes out of the hole with a sand pellet, she moves in a centrifugal way until she drops the load, and then she goes back in a more or less straight line to the digging site. There is no evidence in favour of any spatial or directional fidelity. Each ant chooses randomly and uniformly its direction of walking once she comes out of the hole. After three days, the workers have built a crater similar to the one shown in figure 2*a*. Analysis of individual behaviours reveals that the probability that an ant will drop a pellet increases as the distance of walking increases. The dropping rate shown in figure 2*b* was estimated by the natural logarithm of the proportion of ants still carrying a pellet since coming out of the hole. Note that a linear fitting would have meant that the dropping rate remains constant with the distance covered by the ants. The resulting distribution would have been characterized by an exponential decay, which is not the case here. It is a modulation of the dropping rate as a function of the distance from the nest entry that gives rise to the internal template. The crater-like structure shown in figure 2*c* has been

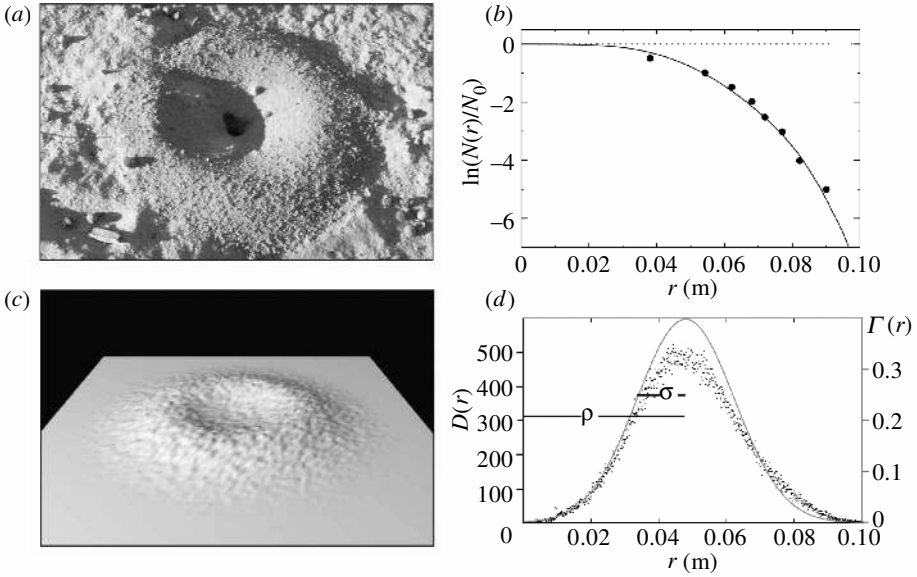


Figure 2. The morphogenesis of a crater around the nest entrance of the ant *M. barbarus*. (a) An example of a crater found around a natural nest. (b) The natural logarithm of the proportion of ants still carrying a pellet as a function of the distance covered ( $r$ ) from the nest entrance in the experiment (black dots) and the theoretical fitting (continuous line). (c) The resulting structure obtained in the simulation after  $N_0 = 160\,000$  droppings. (d) A cross-section of the Gaussian template  $\Gamma(r)$  shown as a solid line. The longitudinal space has been divided into 1000 cells ( $c_i$ ) and  $D(r)$  is the number of droppings that occurred in the simulation in each cell. Hence, in (b),  $N(r)/N_0 = 1 - \sum_{c_0}^{c_r} D(c_i)/N_0$ . Parameters  $\sigma = 1.44$  cm and  $\rho = 4.8$  cm that control, respectively, the width of the Gaussian template and its distance from the nest entrance have been fitted to the experimental data.

obtained with an individual-based model aimed at simulating the behaviour of ants relying on an internal template that is very close to the one used by *M. barbarus*. In the simulation, loaded ants move on a surface and asynchronously leave a central point representing the nest entrance. At each time-step  $t$ , each loaded ant has a probability  $P_t$  of dropping its pellet, which depends on  $r$ , the distance she covered from the hole, in the following way:

$$dP_t = \Gamma(r_t) dt, \quad \text{where } \Gamma(r) = \frac{1}{\sqrt{2\pi}} \exp \left[ -\frac{(r - \rho)^2}{2\sigma^2} \right]$$

is a Gaussian ring materializing the internal template and  $\rho$  and  $\sigma$  are parameters that control the width of the Gaussian and its distance from the nest entrance (see figure 2d).

The use of templates appears to be a very efficient way to organize the building actions of an insect colony and make use of the information directly available in the environment. In the above example, the pre-existing template was not changed by the resulting activity of the insects. However, this is far from being a general situation and we will discuss this issue in § 4. When a template is used to build a structure, insects do not need to communicate with each other. A more sophisticated

coordination between insects can be obtained when interactions take place between individuals, as we shall see in the next section.

### 3. Stigmergy and self-organized patterns

A second mechanism used by social insects to coordinate their actions and build complex spatial patterns is stigmergy. It refers to a class of mechanisms that mediate indirect interactions between animals. Stigmergy (from the Greek *stigma*, sting, and *ergon*, work) was initially introduced by the French ethologist Grassé to explain indirect task coordination and regulation in the context of nest reconstruction in termites of the genus *Bellicositermes natalensis* (see Grassé (1959) and, for a historical review of the concept of stigmergy, Theraulaz & Bonabeau (1999)). Grassé showed that the regulation of the building activity does not depend on the workers themselves but is mainly achieved by local configurations of mud encountered on the nest: a stimulating configuration triggers a response, a building action, by a termite worker, transforming the configuration into another configuration that may trigger in turn another action performed by the same termite or any other worker in the colony. Stigmergy is an elegant and stimulating concept to understand the coordination and regulation of collective activities. It explains how individual builders can act independently on a structure without the need for direct interactions or sophisticated communications. The basic principle of stigmergy is extremely simple: traces left and modifications made by individuals in their environment may feed back on them. The colony records its activity in part in the physical environment and uses this record to organize its collective behaviour. Various forms of storage are used by social insects: gradients of pheromones, material structures (impregnated, or not, by chemical compounds) or spatial distribution of colony elements. One crucial problem is then to understand how all these stimuli are organized in space and time to generate robust and coherent patterns. Indeed, colonies of a given species produce qualitatively similar patterns, be they nest architectures or networks of foraging trails and galleries. One way to achieve this coordination is through self-organization (Deneubourg & Goss 1989; Bonabeau *et al.* 1997). Self-organization denotes a set of dynamical mechanisms whereby structures are created from an initially homogeneous, structureless substrate through the nonlinear amplification of random fluctuations (Nicolis & Prigogine 1977, 1989). The rules specifying the interactions among the system's constituent units are executed on the basis of purely local information, without reference to the global pattern, which is an emergent property of the system rather than a property imposed upon the system by an external ordering influence.

One example of a self-organized pattern that results from stigmergic behaviour is the formation of cemeteries by ants (Haskins & Haskins 1974; Howard & Tschinkel 1976; Ataya & Lenoir 1984; Gordon 1983). Numerous species of ant get the corpses out of the nest and aggregate them near the nest entrance. The morphogenesis of the resulting spatial structures has been studied in great detail under experimental conditions (Theraulaz *et al.* 2002). When dead bodies are randomly distributed on the surface of an arena, the workers form clusters within a few hours (see figure 3). Over time, some clusters will continue to grow, while others will disappear, leading to a steady state with a stable number of clusters over the duration of the experiment. It has been shown that workers pick up or drop corpses with a probability that depends on the local density of corpses they can detect in their range of perception. Ants pick

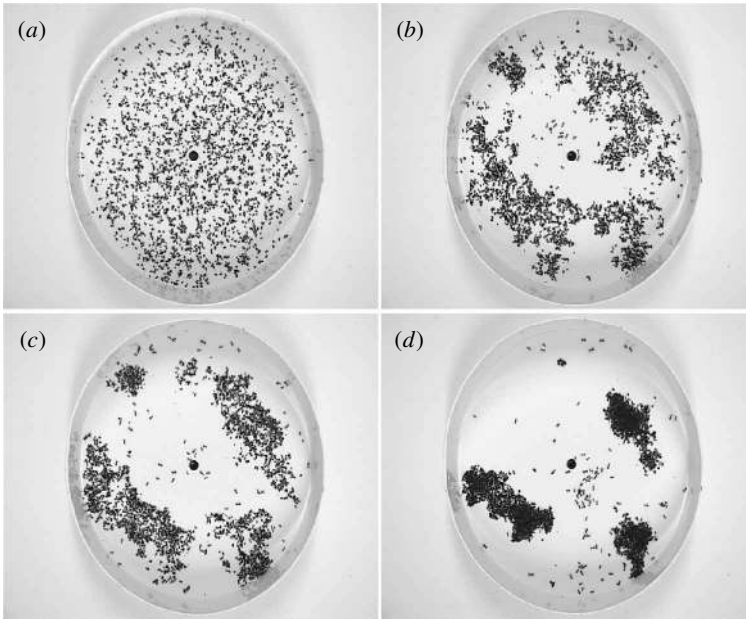


Figure 3. An example of corpse-aggregation dynamics in the ant *M. sancta* observed for an arena of  $\varnothing = 30$  cm and with 1500 corpses. (a) The initial state, (b) after 3 h, (c) 6 h and (d) 36 h.

up corpses with a probability that decreases with cluster size, while corpse-carrying ants drop corpses with a probability that increases with cluster size (see figure 4). This creates a positive feedback mechanism, since the accumulation of corpses at a particular place reinforces the dropping behaviour while at the same time cluster size acts as a negative feedback on the picking rate. Negative feedback also results from the depletion of corpses trapped by the self-enhancing process, which prevents the formation of other clusters in the neighbourhood of a cluster already in place. The size and final number of clusters depend on the initial density of corpses. Doubling the corpses' density leads to a doubling of the number of clusters. Moreover, if the density of corpses is too small, no stable aggregation occurs, because the amplification mechanism cannot work. The system undergoes a bifurcation at a critical density: no cluster emerges below it, but clusters can emerge above it.

The following set of differential equations describes the evolution of the density of corpse-carrying ants  $a(x, t)$  and the density of corpses  $c(x, t)$ , where  $x$  and  $t$  stand for space and time, respectively,

$$\frac{\partial c}{\partial t} = v \left[ k_d a + \frac{\alpha_1 a \phi_c}{\alpha_2 + \phi_c} - \frac{\alpha_3 \rho c}{\alpha_4 + \phi_c} \right], \quad (3.1)$$

$$\frac{\partial a}{\partial t} = -v \left[ k_d a + \frac{\alpha_1 a \phi_c}{\alpha_2 + \phi_c} - \frac{\alpha_3 \rho c}{\alpha_4 + \phi_c} \right] + D \nabla^2 a, \quad (3.2)$$

$v$  is the linear velocity of the ants,  $k_d$  is the spontaneous dropping rate per laden ant, and the second and third terms represent the density-dependent dropping and picking rates respectively;  $\rho$  is the density of non-carrying ants, which remains uniform and constant over time in the model;  $\alpha_1$ ,  $\alpha_2$ ,  $\alpha_3$  and  $\alpha_4$  are empirical constants and  $D \nabla^2 a$  accounts for the diffusion of ants on the surface, with  $D$  being the constant diffusion



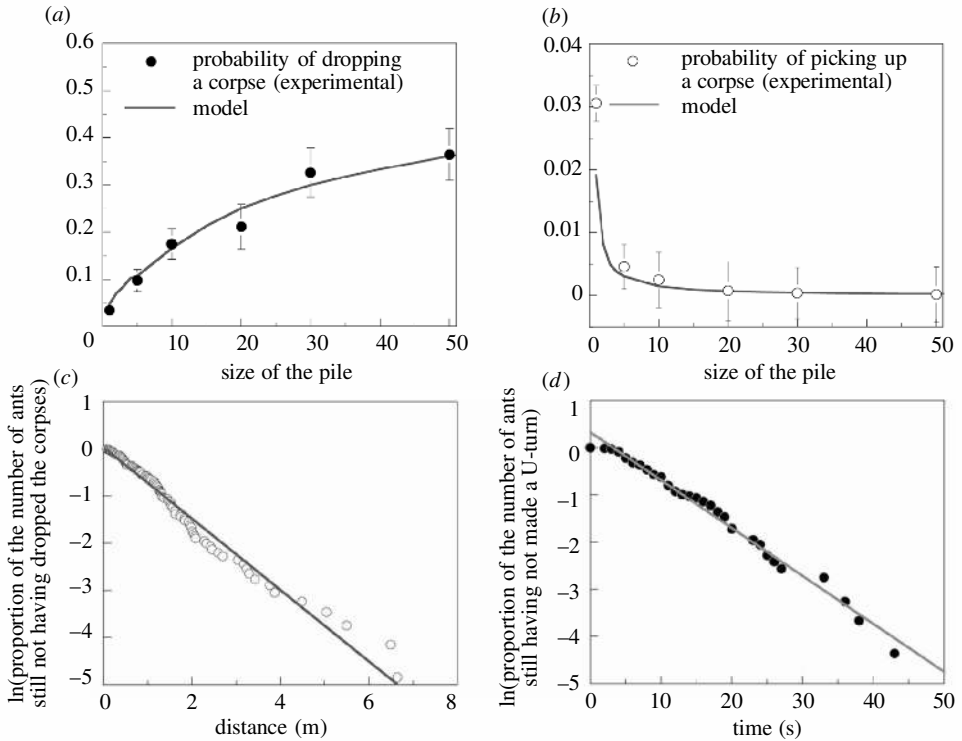


Figure 4. Individual behavioural rules involved in corpse clustering in the ant *Messor sancta*. Density-dependent probabilities of (a) dropping and (b) picking a corpse, as estimated from experiments and theoretical fittings of the dropping and picking rates (continuous line). The theoretical fitting was obtained using equations (3.1) and (3.2) (see text). A pile of corpses is introduced in the theoretical set-up to reproduce the experimental procedure. The fraction of corpse-carrying ants crossing the pile and dropping their load gives the rate of dropping for this pile. This fraction is computed for different pile sizes. The comparison between this theoretical fraction and the corresponding experimental one provides an estimate of the parameters of the dropping functions  $\alpha_1$  and  $\alpha_2$ . The same procedure is used to adjust the picking rate ( $\alpha_3$  and  $\alpha_4$ ), for which the fraction of laden ants leaving the cluster was measured. Adjusted values of the parameters  $\alpha_1 = 31.75 \text{ m}^{-1}$ ,  $\alpha_2 = 1000 \text{ m}^{-1}$ ,  $\alpha_3 = 3.125 \text{ m}^{-1}$  and  $\alpha_4 = 50 \text{ m}^{-1}$  were obtained with  $k_d = 0.75 \text{ m}^{-1}$ ,  $\rho = 40/\pi\varnothing \text{ m}^{-1}$ ,  $\Delta = 1 \text{ cm}$ ,  $v = 1.6 \times 10^{-2} \text{ m s}^{-1}$ ,  $l = 15.8 \times 10^{-2} \text{ m}$  (mean free path) and  $D = v(l/2) = 1.3 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}$ . (c) Spontaneous probability of dropping a corpse estimated by the natural logarithm of the proportion of ants ( $N = 127$ ) still carrying a corpse as a function of the distance covered since they had picked it up. The relationship is best described by the natural log of the proportion of ants that did not yet drop the corpse they carried  $= 0.026 - k_d x$  with  $k_d = 0.75 \text{ m}^{-1}$  ( $r^2 = 0.975$ ;  $x$  is the distance in metres). (d) Probability of making a U-turn per unit of time, estimated by the natural logarithm of the proportion of ants ( $N = 78$ ) still not having made a U-turn as a function of time since a previous U-turn. This relationship is best described by the linear regression  $y = 0.324 - P_{\text{U-turn}} t$  with  $P_{\text{U-turn}} = 0.101 \text{ s}^{-1}$  ( $r^2 = 0.987$ ;  $t$  is the time in seconds). The corresponding mean free path, which is the mean distance covered by an ant before she makes a U-turn, is  $l = 15.8 \times 10^{-2} \text{ m}$ .

coefficient.  $\phi_c$  is a non-local term which introduces a short-range interaction between workers and corpses,

$$\phi_c = S^{-1} \int_{r-\Delta}^{r+\Delta} c(\bar{r}') \, d\bar{r}',$$

where  $S$  is a small area of perception within which workers can detect corpses (dedicated experimental measurements lead to a characteristic radius of perception  $\Delta \approx 1.0$  cm). The dropping rate per laden ant increases with  $\phi_c$ , while the picking rate per non-carrying ant decreases when  $\phi_c$  increases.

Figure 5 shows the results of Monte Carlo simulations of the corpse-aggregation model on a two-dimensional circular arena and for increasing densities of corpses. At low density, the aggregation process leads to the formation of clusters (figure 5*a*), while, at high density, a sponge-like structure with several chambers surrounded by walls is produced (figure 5*c*). In this latter case, the resulting pattern is very similar to some of the nest structures shown in figure 1*b, c*. When little holes appear at some places characterized by a low density of corpses or no corpse at all, there is a high probability that these places will be cleaned even more and the corpses located on the edges of these holes will be removed. This result shows that the same behavioural rules at the individual level can thus lead to the production of different structures under different initial conditions. There exists some empirical evidence showing that the rules used by ants to aggregate the corpses should be involved in other pattern-formation activities such as nest building (Franks *et al.* 1992), brood or seed sorting (Franks & Sendova-Franks 1992; Deneubourg *et al.* 1991) and the formation of leaf caches (Hart & Ratnieks 2000). Instead of removing corpses, ants remove and aggregate soil pellets or larvae. While these different activities certainly rely on different physiological implementations, the logical mechanisms of amplification that lead to the formation of piles and clusters are very similar.

This example illustrates three important properties or signatures of the self-organized dynamics associated with stigmergic behaviour.

(i) The emergence of spatio-temporal structures in an initially homogeneous medium, that is, a random spatial distribution of corpses. The basic mechanism that leads to the emergence of these structures is positive feedback (the snowball effect); once the structures are created, they are stabilized through negative feedback that prevents the amplification from reaching infinity. Negative feedback comes from the depletion of corpses and competition among neighbouring clusters. In social insects, positive feedback may result from several kinds of behaviours such as imitation or allelomimesis, recruitment and reinforcement processes, and is usually implemented in the form of individual responses to stimulations (Deneubourg & Goss 1989). Negative feedback, however, usually comes from the environment: for instance, recruitment to a food source is a positive feedback that relies on trail laying and trail following in ants (Beckers *et al.* 1990; Deneubourg *et al.* 1990; Goss *et al.* 1989; Pasteels *et al.* 1987) or dances in bees (Camazine & Sneyd 1991; Seeley *et al.* 1991), which are individual behaviours, and this positive feedback is limited by food-source exhaustion or food hoarding in the nest. Negative feedback may also result from a competition between positive feedbacks that inhibit one another.

(ii) The possible coexistence of several stable states (multi-stability): structures emerge through the nonlinear amplification of fluctuations, and any such fluctuations can be amplified, so that the system converges to one among several possible

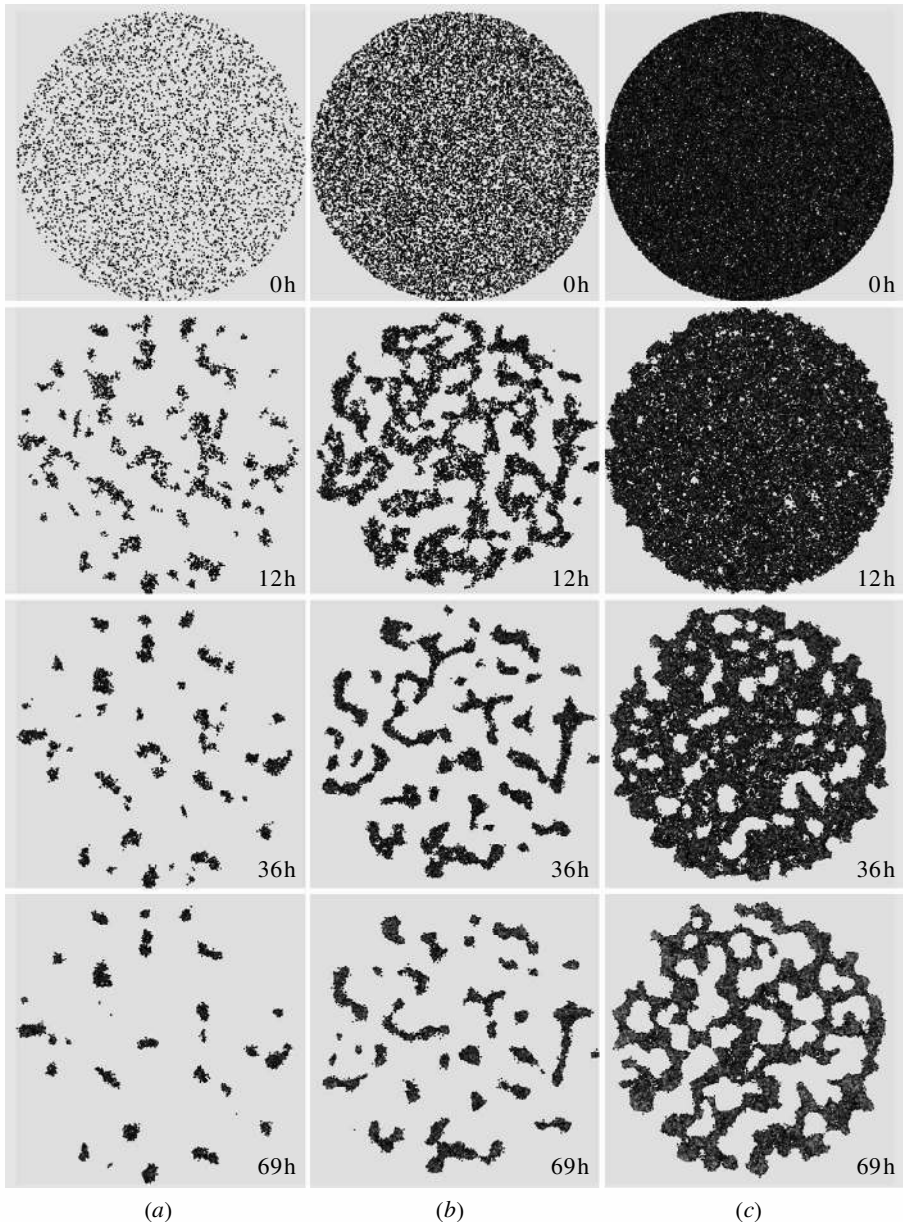


Figure 5. Transition from piles to walls observed in Monte Carlo simulations of the clustering process in a 50 cm diameter arena when corpse density increases. From left to right, the initial number of corpses is (a) 5000, (b) 20000 and (c) 80000. From top to bottom, the resulting patterns obtained in the simulation after 0 h, 12 h, 36 h and 69 h are shown. The ratio of number of workers/number of corpses (= 0.01) was kept constant in the simulations which were performed with the following parameter values:  $l = 7 \times 10^{-2}$  m,  $v = 2 \times 10^{-2}$  m s $^{-1}$ ,  $\Delta = 1$  cm,  $\alpha_1 = 25.87$  m $^{-1}$ ,  $\alpha_2 = 500$  m $^{-1}$ ,  $\alpha_3 = 10$  m $^{-1}$ ,  $\alpha_4 = 75$  m $^{-1}$  and  $k_d = 0.2$  m $^{-1}$ .

stable states, depending on the initial conditions. Random fluctuations often result from the random component in individual behaviours (see, for example, Deneubourg *et al.* 1983). In such cases, not only do structures emerge despite randomness, but randomness is also a crucial ingredient, since it enables the destabilization of homogeneous states.

(iii) The existence of parameter-driven bifurcations, where the behaviour of a self-organized system changes dramatically. In the case of corpse clustering in ants, one critical parameter that controls the bifurcation is the density of corpses. In some other cases, such as recruitment behaviour in ants, a critical parameter is the number of individuals required for establishing a pheromone trail toward a food source (Pasteels *et al.* 1987). Owing to diffusion and evaporation, pheromone trails may not be able to persist if their renewal rates are insufficient, that is, if there are not enough individuals to lay the pheromone. A critical number of workers is also required in termites during nest building. Grassé (1959) observed that, below a critical density, termite workers are unable to build a regular network of pillars and walls.

The idea that pattern formation in a biological system should result from a competition between local-amplification processes inducing a positive feedback and long-range inhibition processes inducing a negative feedback was suggested at the beginning of the 1970s by Gierer & Meinhardt (1972). Using mathematical models, they were able to show how these mechanisms could be related to the kinds of processes known to take place during real biological patterning and development. This work was following Turing's original discovery that the interaction of two substances with different diffusion rates can produce pattern formation out of an initially uniform mixture of these components (Turing 1952). It is particularly striking that similar mechanisms are found to govern pattern formation at different scales in biology and physics (see, in particular, Ball 1998; Meinhardt 1982). Indeed the formation of cemeteries by ants is a clear example of local activation and long-range inhibition morphogenesis; but there is also a large amount of experimental and theoretical evidence showing that several other collective patterns such as building behaviour in termites (Deneubourg 1977) or gallery-network formation in ants (Rasse 1999; Rasse & Deneubourg 2001; Buhl *et al.* 2002) should result from the same kind of processes involving local amplification and spatial competition between the resulting structures.

#### **4. Patterns resulting from the interplay between template and self-organization**

In the previous section, we saw how the 'attractivity' of dead bodies, implemented in the form of density-dependent probabilities to pick-up and drop corpses, can lead to the formation of clusters and sponge-like structures depending on corpse density. Self-organization lies in this 'attractivity', which induces a snowball effect: the larger a cluster, the more likely it is to attract even more items. As is often the case in biology, several pattern-formation mechanisms may interact with each other and self-organization can also be combined with a template mechanism in the process of clustering. An example of such a combination is provided by the construction of nest walls by the ant *L. tuberointerruptus* (Franks *et al.* 1992; Franks & Deneubourg 1997). These ants nest within flat crevices in rocks and construct a simple perimeter

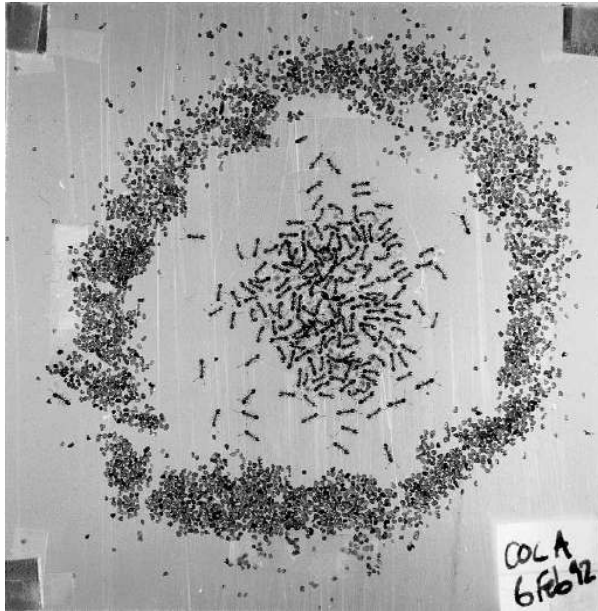


Figure 6. A *Leptothorax tuberointerruptus* nest in the laboratory. The ants have been given a 1 mm deep cavity between 40 mm  $\times$  40 mm glass plates. They have built a dense wall from sieved sand. Each grain of sand is roughly 0.5 mm in diameter. The worker ants, each approximately 2.5 mm in length, are densely clustered around the central queen, the largest individual present, and the white brood. There is a corridor between the dense-brood/adult-ant cluster and the inside of the wall. The entrance to the nest is at '7 o'clock'. Photograph courtesy of Nigel Franks.

wall encircling the colony. Construction behaviour in these *Leptothorax* ants can easily be studied in the laboratory, where colonies containing a single queen, up to 500 workers and a similar number of brood items nest between two microscope slides held 1 mm apart by a cardboard pillar at each corner (see figure 6). When building material is provided in the form of grains of carborundum the colony will encircle itself with a dense cohesive wall with a single narrow entrance. The circular wall is constructed at a given distance from the brood, which serves as a chemical and physical template. In the same way the size of the royal chamber was adjusted to the queen size in termites; the template mechanism allows the size of the nest to be regulated as a function of brood size. But in parallel with the template there is an additional stigmergic self-organized mechanism: grains attract grains, so deposition behaviour is influenced by two factors: the local density of grains and the distance from the brood. The probability of depositing a grain is highest when both the distance from the brood is appropriate and the local density of grains is large; it is lowest when the brood is either too close or too far away, and when the local density of grains is small. When the distance from the brood does not lie within the appropriate range, deposition can, nevertheless, be observed if grains are present; conversely, if the distance from the brood is appropriate, deposition can take place even if the number of grains is small. It is interesting to note that the brood, which has been compactly aggregated by the workers and plays the role of template in the wall construction, is itself resulting from a self-organized clustering.

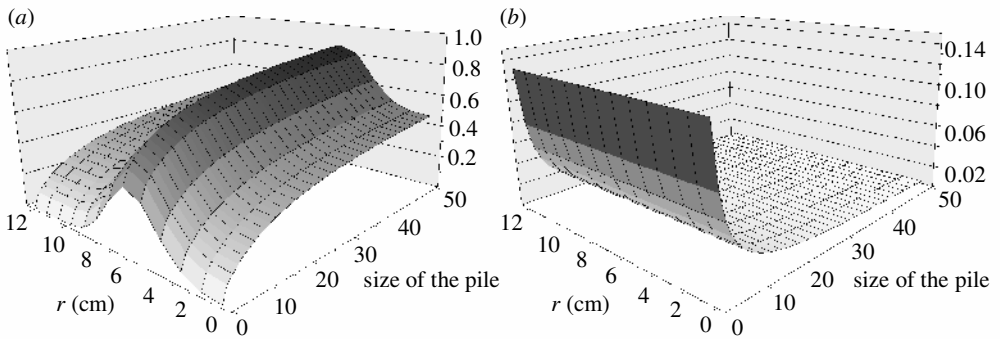


Figure 7. Individual behavioural rules used in the model of the construction of nest walls by the ant *L. tuberointerruptus*. Probabilities of (a) dropping and (b) picking up an item depend both on the local density of items and on their distance from the nest entrance.

This double mechanism may be sufficient to explain nest construction and regulation as a function of colony size (Franks & Deneubourg 1997). This pattern formation can be described by the coupling of the two models presented in §§ 2 and 3. In order to make comparisons as easy as possible, all parameter values were kept identical to those used in the preceding sections for both mechanisms, namely the template and the self-organized process. We consider that, instead of clustering corpses, ants aggregate sand grains, and their behaviour depends both on a chemical template defined by a Gaussian similar to the one used in § 2, and their perception of the local density of grains they encounter in the course of their displacement. Figure 7 shows the combined effect of these mechanisms on the density-dependent probabilities of dropping and picking up an object. The resulting structure shown in figure 8 is a mix between a purely template-driven pattern and a self-organized one. Items begin to accumulate loosely on the ring shape defined by the template. Then a reallocation of the items occurs at particular locations, as a consequence of reinforcement and competition processes. With a small concentration of items (5000 items), piles eventually emerge leading to a crenel profile of the resulting structure (figure 8*a*). When the concentration of items is higher (20 000 items), a more or less continuous wall is built, through which pathways may be managed similar to the natural nest structure.

A similar combination of templates and self-organization has also been found in termites, where pillar building results from a self-organized process, but the arches joining the pillars are mainly produced with template mechanisms. The combination of mechanisms can even be slightly more complex when it involves a modification of the physics of the system. In some cases, fluxes or gradients can appear as a result of the building actions of individuals, and these fluxes or gradients have in turn an effect on individual behaviours (Howse 1966; Bruinsma 1979). For instance, in termites, in the presence of a pheromone trail, the same mechanism that leads to the emergence of pillars when there are no pheromones produces galleries along the trail (Bruinsma 1979; Bonabeau *et al.* 1998). The trail pheromone diffuses away from the centre of the trail, thereby creating a chemical template, very similar to the queen's chemical template, along which walls are built in a self-reinforcing way. What is remarkable is that the template generated by the trail is no longer a pre-existing heterogeneity imposed upon the colony by the environment or by the queen: the template

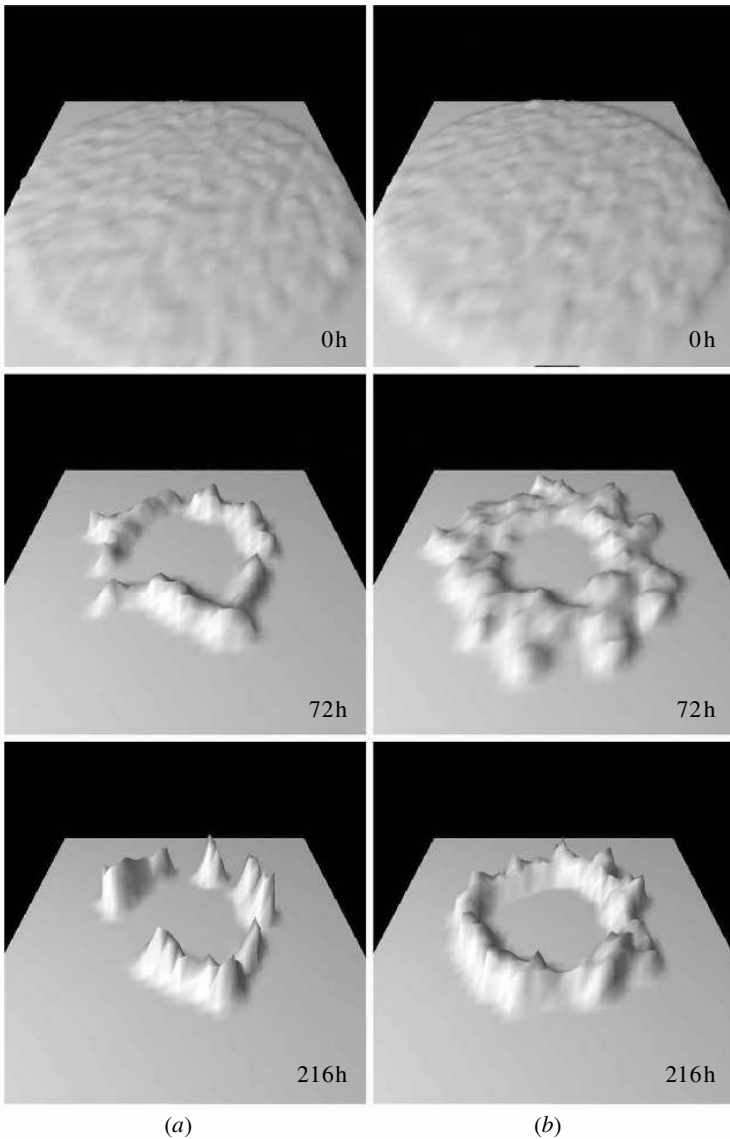


Figure 8. Monte Carlo simulations showing the evolution of the structure resulting from the interplay of a Gaussian-ring template and a self-organized process for two different initial densities of items: (a) with 5000 items; (b) with 20 000 items. From top to bottom, the resulting patterns obtained in the simulation after 0, 72 and 216 h are shown. The initial distribution of items on the surface is random and uniform, and the movement of ants is a random walk. Parameter values used in the model are the same as those in figures 2 and 5. The ratio of number of workers/number of corpses ( $= 0.02$ ) was kept constant in the simulations.

results from the colony's activities. Indeed, a trail network emerges because of the trail-laying–trail-following behaviour of individual termites. The pillars that emerge from the building actions of individuals create a spatial heterogeneity which modifies both fluxes of termites and of pheromone. This provides us with a clear picture of

a powerful complexity-generating mechanism: a first structure can emerge from a homogeneous medium through self-organization (for example, pillars in termites); once it has emerged, this structure is a heterogeneity that serves as a template that channels individuals' actions; these actions create in turn new stimuli that trigger new building actions, either based on self-organization or templates or both; and so forth.

## 5. Conclusions

The few examples we have discussed show that the morphogenesis of spatial patterns in social insects might be explained by the combination of a small number of simple mechanisms and the interplay of simple individual behaviours with varying external as well as internal conditions. Self-organization and templates are examples of simple rules of thumb based on a limited individual cognitive ability and a limited access to global information. Most of these behavioural rules are responses to stimuli or simple modifications of the internal state of insects. Among the mechanisms involved in pattern formation, self-organized processes have received increasing attention over the last 15 years and there now exists a growing literature in which numerous examples involving these processes have been discussed (Camazine *et al.* 2001). Experimental and theoretical studies have shown that self-organization was involved in the formation of trail networks and foraging patterns in numerous species of ants (Aron *et al.* 1990; Deneubourg *et al.* 1989, 1990; Franks *et al.* 1991); in the collective choice of a food source in ant and bee colonies (Beckers *et al.* 1990; Seeley *et al.* 1991; Camazine & Sneyd 1991); in chain formation in ants and bees (Lioni *et al.* 2001); in thermoregulation in bees; in rhythmical patterns and bursts of synchronized activity in ants; in various aspects of division of labour inside a colony (Deneubourg *et al.* 1987; Theraulaz *et al.* 1998; Gautrais *et al.* 2002); and in many aspects of building activities including the development of the characteristic pattern on the combs of honey-bee colonies (Belic *et al.* 1986; Skarka *et al.* 1990; Camazine *et al.* 1990; Camazine 1991; Franks *et al.* 1992; Deneubourg & Franks 1995). The importance of self-organizing processes far exceeds the field of social insects studies, since they have been identified in a wide range of biological phenomena, from the organization of microtubules and molecular motors in the eukaryotic cell (Nédélec *et al.* 1997; Surrey *et al.* 2001) to the pattern formation in social amoeba (Keller & Segel 1970, 1971) and bacterial colonies (Ben-Jacob *et al.* 2000), and the collective behaviours of fish schools (Parrish & Edelstein-Keshet 1999; Stöcker 1999; Couzin *et al.* 2002), herding mammals (Gueron *et al.* 1996) and even human systems (Helbing *et al.* 1997*a, b*).

The recent developments in the understanding of the underlying mechanisms of pattern formation and collective behaviours in social insects do not only have consequences in the study of animal cognition and morphogenesis in biology. They also provide powerful tools to transfer knowledge about social insects to the field of intelligent-system design, as has been recently outlined (Bonabeau *et al.* 1999; Bonabeau & Theraulaz 2000). As a matter of fact, a social-insect colony is undoubtedly a decentralized problem-solving system, comprised of many relatively simple interacting entities. The daily problems solved by a colony (e.g. finding food, building or extending a nest, efficiently dividing labour among individuals, responding to external challenges, spreading alarm, etc.) have counterparts in engineering and



computer science. Among the most important features of social insects is that they can solve these problems in a very flexible and robust way: flexibility allows them to adapt to changing environments, while robustness endows the colony with the ability to function even though some individuals may fail to perform their task. Finally, social insects have limited cognitive abilities: it is therefore simple to design agents, including robotic agents, that mimic their behaviour at some level of description. In short, the swarm intelligence of social insects can help in the design of artificial distributed problem-solving devices that self-organize to solve problems such as optimization algorithms. These techniques of swarm intelligence have been applied successfully to a variety of scientific and engineering problems. For example, optimization and control algorithms, inspired by models of cooperative food retrieval in ants, have been unexpectedly successful, and have become known in recent years as Ant-Based-Optimization (Dorigo *et al.* 1996; Dorigo & Gambardella 1997) and Ant-Based-Routing (Schoonderwoerd *et al.* 1997; Di Caro & Dorigo 1998; Heusse *et al.* 1998). In addition to achieving a good performance over a wide spectrum of 'static' problems, such techniques tend to exhibit some degree of flexibility and robustness in a dynamic environment and have been successfully applied to the routing problem in communication networks.

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