Spatial patterns in ant colonies


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The origins of large-scale spatial patterns in biology have been an important source of theoretical speculation since the pioneering work by Turing (1952) on the chemical basis of morphogenesis. Knowing how these patterns emerge and their functional role is important to our understanding of the evolution of biocomplexity and the role played by self-organization. However, so far, conclusive evidence for local activation–long-range inhibition mechanisms in real biological systems has been elusive. Here a well-defined experimental and theoretical analysis of the pattern formation dynamics exhibited by clustering behavior in ant colonies is presented. These experiments and a simple mathematical model show that these colonies do indeed use this type of mechanism. All microscopic variables have been measured and provide the first evidence, to our knowledge, for this type of self-organized behavior in complex biological systems, supporting early conjectures about its role in the organization of insect societies.

Many biological systems display large-scale features involving some characteristic scale that is much larger than the size of its individual components (1). These structures are observed in a broad range of systems and scales, from animal coats (2), shell patterns (3, 4), and neural structures (5) to the spatial distribution of individuals in ecosystems (6). In many cases, they reflect functionality and adaptation and in all of them, they provide clues for the underlying rules that generate them. In most cases, it is clear that the information available to individual units is gathered from a local neighborhood much smaller than the resulting structures, suggesting some type of amplification mechanism that relies on collective behavior.

The first theoretical explanation of these types of structures was suggested in 1952 by Alan Turing (1, 7, 8). The basic mechanism at work involves local amplification of fluctuations (activation) and long-range inhibition and actually falls within a general class of mechanisms (9–12). These mechanisms have been identified in physical (13) and chemical (14) systems, in ecosystems (2, 6, 10, 15–18) and morphogenesis (2–5, 11, 19–26). In the slime mold (27, 28), the evidence is also strong. Critics have argued that a proof requires the identification and measurement of the microscopic mechanisms at work, and this is obviously a rather difficult task in biology.

In this context, it was early suggested that social insects might actually use these types of mechanisms to build their nests (29, 30) and produce a wide variety of spatiotemporal structures (31–34). Here we use social insects and their behavioral patterns of organization as our reference system. We follow a standard approach, using a well-defined and controlled experimental setup in which the whole set of parameters can be measured and therefore all of the microscopic rules can be identified. We show that the formation of cemeteries in ants (35–38) falls within the family of local activation–long range inhibition (LALI) processes originally suggested by Gierer and Meinhardt (9), the inhibition resulting from the depletion of the substrate. In experiments carried out with the ant Messor sancta, we confirm the presence of self-organization dynamics as responsible for the regular structures generated by the clustering process, and a mathematical model is presented, consistently reproducing the experimental observations.

Methods

Colony Collection and Ant Maintenance. Experiments were carried out with colonies of the ant M. sancta. Ants were collected in southwestern France, near Narbonne, and then reared in the laboratory at 25°C with 12 h light/12 h dark. Colonies were housed in several glass test tubes placed in 27 × 27-cm plastic boxes whose sides were coated with Fluon to prevent ants from escaping. Ants were provided with water in the form of moist cotton, fed ad libitum with a mixture of seeds and twice a week with bits of crickets.

Experiments. The experimental arena is a circular structure (of two possible diameters, Ø = 25 or 50 cm) below which the nest box is located. The ants can access the arena by climbing on a wood rod placed in a hole at the center of the arena and randomly walk to the periphery. The experimental setup was designed to reduce the problem to a one-dimensional system with periodic boundary conditions: because the ants exhibit strong thigmotaxis (a tendency to follow the inner walls), their paths can be considered to be confined to one dimension. Corpses are initially homogeneously distributed along the periphery, close to the inner wall (Fig. 1a). Two different initial numbers of corpses are used in both arena sizes: 100/200 and 200/400 for the small and large arena, corresponding to 127 and 265 corpses m⁻¹, respectively. The average size of the corpses is 3 mm, the initial mean distance between them being 4.9 and 0.9 mm for the small and high density, respectively. The duration of the experiments was set to 24 h for the small arena and 48 hr with the large arena. Fifteen replications were performed for each density with the small arena and 25 replications with the large arena. Another set of 10 experiments was performed with the large arena and a small initial number of corpses corresponding to 13 corpses m⁻¹ to test the existence of a critical density of corpses. The duration of these experiments was set to 24 hr. The floor of the arena was washed with diluted alcohol and hexane before each experiment.

Recording and Data Analysis. The experiments were videotaped by means of a Sony (Tokyo) DCR-VX1000E high-definition camera allowing the regular sampling of the aggregation process. The two images were recorded every 10 min. A video analysis was then performed with a specially designed software that calculated the position and the size of the piles at each time interval. Two neighboring corpses are considered to belong to the same pile when the distance between them is less than 1.5

Abbreviation: LALI, local activation–long range inhibition.

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Results

Clustering Behavior: Collective and Individual Levels. After having reached the arena, workers pick up corpses and drop them to form piles. After a few hours, several clusters are formed. Over time, some clusters grow and others disappear, leading to an apparent steady state with a stable number of clusters over the duration of the experiment (Fig. 1 b–d). The sigmoidal growth of surviving clusters, an illustration of which is given in Fig. 2, suggests that cluster formation is autocatalytic. The number of clusters initially grows to reach a maximum after about 3 hr and then decreases and stabilizes.

The above results suggest a LALI mechanism: because the addition of corpses to a cluster is more likely as the cluster increases in size, cluster growth is locally self-enhancing and is inhibited by the depletion of corpses in the cluster’s neighborhood. This type of LALI model, coined “activator-substrate” (9), has been suggested in the formation of certain seashell patterns (4). To confirm this conjecture, the underlying microscopic rules have to be identified. Observation of the ants’ behavior shows that workers pick up or drop corpses with a probability that depends on the local density (c) of corpses. Picking up and dropping probabilities and their functional form have been estimated from experimental data (Fig. 3 a and b). Unladen ants pick up corpses with a probability that decreases with cluster size, whereas corpse-carrying ants drop corpses with a probability that increases with cluster size. The latter ants are also characterized by a spontaneous dropping probability that has been estimated from experimental data (Fig. 3 c). Trajectory measurements show that the ants move randomly along the arena’s periphery (one-dimensional random walk) and allow the identification of two additional microscopic characteristics: individual velocity and mean free path. The mean velocity of ants is 

\[ \nu = 1.6 \pm 0.7 \text{ cm s}^{-1} \] (n = 25), and for such parameter range, random walk can be shown to be only little influenced by the velocity distribution. Further discussion will therefore assume a constant velocity of walking at the average velocity value. Ants are also characterized by a constant probability per unit of time of making a U-turn during their walk (0.10 s⁻¹), and the corresponding mean free path (l = 15.8 cm) is significantly smaller than the size of the arena’s periphery (78.5 and 157.1 cm for the arena sizes used in the experiments).

Model Description. These estimates of microscopic behavioral parameters and the response functions have been used to build a macroscopic mathematical model that falls within the activator-substrate class of LALI models, which thus confirmed our previous assumptions. The model involves two variables: 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. \( \rho \) is the density of noncarrying ants. At any given time, their proportion in experiments is large (\( \rho/(\rho + \rho) = 0.94 \pm 0.07 \)), estimated over 135 observations; mean density \( \rho \pm SD = 20.0 \pm 7.0 \text{ m}^{-1} \). Because of the diffusion process resulting from the random walk of noncarrying ants, \( \rho \) is assumed to remain uniform and constant over time in the model. Ants’ behavior can then be approximated by the following reaction–diffusion equations:

\[
\frac{\partial c}{\partial t} = \Omega(c, a) \tag{1}
\]

where \( \Omega(c, a) \) is a function of the density of corpses and the density of corpse-carrying ants. This function can be expressed in the form of a reaction–diffusion equation with variable coefficients. The reaction term \( \Omega(c, a) \) accounts for the production and consumption of corpses and corpse-carrying ants. The diffusion term \( \Delta c \) accounts for the spatial spreading of corpses and corpse-carrying ants. The boundary conditions for this system are

\[
\begin{align*}
\frac{\partial c}{\partial x} & = 0 \\
\frac{\partial a}{\partial x} & = 0
\end{align*}
\]
detect corpses (dedicated experimental measurements lead to a
value \( \nu c_1 \). The picking rate per noncarrying ants (III) results
from the presence of noncarrying ants picking available corpses.
It decreases when \( \phi_1 \) increases. Therefore, according to III,
cluster size acts as a negative feedback on the picking rate,
because \( \phi_1 \) is a local indicator of cluster size. As a result of II and
III, clusters form, and their growth inhibits the further growth
of other clusters. A standard stability analysis, where a perturbation
around the unique homogeneous steady state \( (c_s, a_s) \) is intro-
duced \( c = c_s + \delta c e^{i\omega t+\lambda x}, a = a_s + \delta a e^{i\omega t+\lambda x} \),
leads to the characteristic equation:

\[
\omega^2 + (-\Gamma + \Phi + D\lambda^2)\omega - \Gamma D\lambda^2 = 0,
\]

where

\[
\Gamma = \frac{\sin(\Delta\lambda)}{\lambda} \left( \frac{\alpha_1 c_1 a_s}{(a_2 + c_s)^3} + \frac{\alpha_3 \rho c_4}{(a_4 + c_s)^3} \right) - \frac{\alpha_3 \rho}{(a_4 + c_s)},
\]

\[
\Phi = \frac{\alpha_1 c_1}{(a_2 + c_s)}.
\]

Solving Eq. 4 for \( \omega \) yields the rate of growth \( \omega(\lambda) \) of the
perturbation for a given wave number \( \lambda \). Here \( \omega(\lambda) \) exhibits
a finite range of unstable modes that includes the marginally stable
mode \( \omega(0) = 0 \) (Fig. 4). This is a well-known property of systems
involving a conservation law. Furthermore, as is usual with such
models, the most unstable wave number, that is the one for which
\( \omega(\lambda) \) is maximum, is proportional to corpse density. In other
words the analysis predicts (i) that in the vicinity of the homo-
geneous state, doubling corpse density should lead to twice as
many piles; this situation may change over time as the system
relaxes away from the homogeneous state as other unstable wave
numbers may become amplified; (ii) that doubling the arena’s
diameter while keeping the density constant should lead to twice
as many piles; (iii) that a critical density of corpses exists \( (c_c =
46 \text{ corpses m}^{-1}) \) below which no aggregation occurs.

\[
\frac{\partial a}{\partial t} = -\Omega(c, a) + \frac{\partial^2 a}{\partial x^2},
\]

where \( \Omega(c, a) \) is the sum of three terms:

\[
\Omega(c, a) = v \left[ k_{d1} a + \frac{\alpha_1 \rho c_1}{a_2 + c_s} + \frac{\alpha_3 \rho c_4}{a_4 + c_s} \right] .
\]

In Eq. 3, \( v \) is the linear velocity of the ants, part I represents
spontaneous dropping (with \( k_{d1} \) the spontaneous dropping rate
per laden ants), and parts II and III represent density-dependent
dropping and picking, respectively. I and II are proportional
to the density of corpse-carrying ants \( (a) \), and III is proportional
to noncarrying ants \( (\rho) \). \( \alpha_1, \alpha_2, \alpha_3, \) and \( \alpha_4 \) are empirical constants.
\( \phi_1 \) is a nonlocal term that introduces a short-range interaction
between workers and corpses:

\[
\phi_1 = \frac{1}{2\Delta} \int_{x-\Delta}^{x+\Delta} c(z) dz,
\]

where \( \Delta \) is a small radius of perception within which workers can
detect corpses (dedicated experimental measurements lead to a
characteristic radius of 0.5 cm < \( \Delta < 1.0 \text{ cm} \) ). The dropping rate

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Comparison of the Model’s Predictions with Experimental Results. As shown in Fig. 5, the dynamics of the average number of piles with time and the time at which the maximum number of piles is reached given by the model are in close agreement with the experiments in the four conditions studied. In particular, predictions of the stability analysis are confirmed in the initial phase (up to maximum pile number): (i) doubling the density leads to a doubling of the number of piles; (ii) doubling the arena’s diameter, whereas keeping the same density also leads to twice as many piles; (iii) in experiments performed with an initial density of corpses (13 corpses m−1) below, no stable clusters were observed. In situations where several piles coexist after 24 or 48 hr (far from the homogenous state), although no strict regularity may be noticed, a critical distance exists between two consecutive piles below which only one of them can “survive” in the long term as shown in Fig. 6. After 24 hr, with the small arena and whatever the initial density of corpses, the presence of two consecutive piles within 20 cm of each other is very unlikely. In any case, the distance between piles is never less than 10 cm. The most frequent distribution, with piles located on opposite sides of the arena, is observed in 50% of the cases. The corresponding theoretical distribution is not significantly different from the experimental one, and both distributions differ significantly from a random distribution (Fig. 6).

Discussion

The observation of cemetery formation in ant colonies suggests a LALI mechanism based on individual worker behavior. It is a peculiar example of such mechanisms in that it involves animal behavior and not physical and chemical morphogens. All of the behavioral parameters of the corresponding model were quantified in dedicated experiments. When loaded with the experimental parameter values, the model not only leads to the formation of patterns that reproduce the properties of cemetery formation, but also predicts how the pattern is affected by such experimental characteristics as corpse density and arena size. Experiments aimed at testing the model’s predictions show that the predictions are indeed satisfied. This is a strong indication that the formation of cemeteries in ants is an example of LALI morphogenesis, which makes it one of the first convincing documented biological examples and certainly the first involving higher organisms. Our work should encourage researchers to look for such mechanisms in other collective behavioral patterns such as network formation, nest construction, or herd patterns, where it could be easier to identify the underlying activation and inhibition mechanisms than in other systems.

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