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Embracing the creativity of stigmergy in social insects

Deciphering construction rules in swarms

With the notable exception of Man, insect societies are living organisms that build the most diverse and complex forms of architectureⁱ (see Figures 1 & 2). The nests built by ants, wasps, bees and termites play a crucial role in the growth and survival of colonies. The amazing evolution of construction techniques used by social insects has provided a whole set of innovations in terms of architectural designs that proved to be efficient to solve problems as various as controlling nest temperature, ensuring gas exchanges with the outside environment or adapting nest architecture to growing colony sizeⁱⁱ. The big question is: how these efficient designs emerge from the combination of millions of local building actions performed by individual workers? The explanation for these phenomena lies in the interactions between these workers and it has been provided more than fifty years ago by French biologist Pierre-Paul Grassé, who has introduced the concept of *stigmergy*ⁱⁱⁱ.

Stigmergy in a nutshell

There is no master architect, nor even a supervisor in these colonies. Grassé has shown that the key information required to ensure the coordination of building actions performed by insects was provided by their previously achieved work: the architecture itself. Grassé coined the term stigmergy from the Greek words *stigma*, meaning « sting » and *ergon* meaning « work » to describe this form of indirect communication. For instance, each time an ant or a termite worker executes a building action, in response to a local stimulus, such as adding or removing a piece of material from the existing nest structure, it modifies the stimulus that has triggered his action. The new stimulus will then influence other specific actions from that worker or potentially from any other workers in the colony. The stimulus itself can be a particular pattern of matter sometimes soaked with chemical signals called pheromones. Coordination is simply achieved through judiciously chosen stimulating patterns of matter. And the architecture provides enough information and constraints to ensure the coordination and regulation of building actions. The whole chain of stimuli and behavioral responses leads to an almost perfect collective construction that may give the impression that the whole colony is following a well-defined plan. Thus,

individual insects do not need any representation or any blueprint to build their nest. My colleagues and I have spent the last twenty years identifying and characterizing the interactions involved in the coordination of nest building in various species of wasps^{iv}, ants^v and termites^{vi}. This work has led us to identify similar building principles behind the impressive diversity of insect nest architectures and to build distributed construction models that implement these principles.

Assembling molded paper cells

A nice example of stigmergic behavior is provided by nest building in social wasps. The vast majority of wasp nests are built with wood pulp and plant fibers that are chewed and cemented together with oral secretions (see figure 3). The resulting paper is then shaped by the wasps to build the various parts of the nest: the pedicel, which is a stalk-like structure connecting the comb to the substrate, the cells that are building blocks from which a comb is made of, or the external envelope that protect the combs. Building activities are driven by the local configuration of cells that are detected by wasps as they move on the surface of the nest^{vii}. To decide where to build a new cell, wasps use the information provided by the local arrangement of cells on the outer circumference of a comb (see figure 4). However, potential building sites do not have the same probability to be chosen by wasps when they start to build a new cell. Wasps prefer to add new cells to a corner area where three adjacent walls are already present, while the probability to start a new row, by adding a cell on the side of an existing row, is very low.

Same rules, different patterns

We have investigated the consequences of applying these local rules on the development of combs and on the resulting nest architecture with a simple individual-based model^{viii}. In this model, wasps are represented by asynchronous agents moving in a three-dimensional discrete hexagonal space, and whose building actions are controlled by a stochastic response function to the state of the local environment. Each agent only detects the first twenty-six neighboring cells that are adjacent to the cell it occupies at a given time, and it does not have any representation of the nest architecture to be built. Each agent follows a simple set of construction rules that have been determined by the analysis of experimental data (see figure 5). Some of these configurations trigger a building action, and as a consequence, a new cell is added to the comb at the particular

place that was occupied by the agent. In all the other cases, no particular building action takes place and the agent just moves toward another place. As construction rules are stochastic, we can implement in the model the probability values associated with each particular configuration of cells that have been estimated from experimental data. The simulations of the model reproduced the growth dynamics and the shape of the natural nests showing that the complexity of these architectures does not require sophisticated construction rules. Moreover the exploration of the morphospace has revealed that a whole variety of nest architectures that closely match those found in nature can be built with simple stigmergic algorithms (see Figure 6).

From stigmergy to self-organization

Stigmergic interactions are also involved in a large number of spatial patterns built by social insects, such as networks of pheromone trails, epigeous nest architectures or underground foraging galleries in ants and termites. However the dynamics and the properties of these emerging patterns are quite different from what has been seen previously in wasps' nests construction. Indeed, in that case, stigmergic interactions between individuals promote positive feedbacks that create the patterns and act for their subsistence against negative feedbacks that tend to eliminate them. In social insects, these positive feedbacks may result from several kinds of behaviors such as imitation, recruitment, reinforcement processes and are usually implemented under the form of individual responses to stimuli^{ix}. In combination with negative feedbacks that may take the form of saturation, exhaustion (i.e. pheromone evaporation) or competition, these positive feedbacks are the two basic ingredients of *self-organization* in biological systems^x. A wide range of studies demonstrated that self-organization was a major component of a wide range of collective behaviors in social insects but also in many group-living animals and human crowds^{xi}.

Piling up mud balls

Together with the emergent properties, non-linear interactions lead self-organized systems to bifurcations. A bifurcation is the appearance of new stable solutions when some of the system's parameters change. This corresponds to a qualitative change in the collective behavior. In the case of ant nest construction, a pheromone added to the building material by the workers is a key parameter that controls the shape transitions in the nest structure. In the garden ant *Lasius niger*, we have shown that the pheromone stimulates the deposition of building material. As a

consequence, ants tend to accumulate more material at the same place, thus creating a positive feedback. Piling up mud pellets rapidly leads ant workers to build pillars. Then, once pillars have reached a critical height, workers start to add pellets on their sides; and they use their body as a kind of template to decide at which height they stop to increase the size of the pillar and start to build a roof.

Environmentally induced phenotypic plasticity

The air temperature in the surrounding environment has a dramatic consequence on the shape of roofs built by ants over the pillars. When temperature increases, we got a transition from a large number of thin pillars topped with capitals with a globular shape, to a small number of larger pillars covered with thin horizontal roofs (see figure 7). To understand the construction dynamics that leads to this shape transition, we developed a spatially explicit agent-based model in which we have incorporated the behavior of ants characterized in the experiments^{xii}. In the model, ant workers are represented by agents whose behavioral rules are modeled according to probabilities to perform simple elementary actions depending on the current state of the environment around the agent (see figure 8). The model showed that the evaporation rate of the building pheromone is a highly influential parameter on the resulting structures (see figure 9). The functional consequences are quite unexpected since without changing building rules a shape transition is got for free, simply driven by the evaporation rate of the building pheromone. So when temperature increases, ants build shelters that are much more appropriate for their protection. And this feat is not encoded in their own behavior: it is a genuine product of the interplay between the construction process and the chemical properties of the building pheromone. Further explorations of the model also revealed that the building rules identified in ants are able to generate some unexpected complex structures such as helicoidal ramps (see Figure 10). Thus in social insects, self-organization enables a real economy of the amount of code that is required at the individual level to get these amazing nest architectures.

While being extremely simple, stigmergy is a powerful mechanism for coordinating the building actions of myriads of simple-minded creatures. Traces left and modifications made by groups of insects in the environment may feed back on them and organize in turn their collective behavior. It is also a powerful mechanism for reshaping and optimizing the extended phenotype^{xiii} of colonies when they face challenging and variable environmental conditions.

Figure captions

Figure 1. Nests of the African genus of termites *Apicotermes* are constructions made out of clay whose shape resembles that of an old pottery designed and made by skilled craftsmen^{xiv}. This is one of the most complex structures ever built in the animal kingdom by a group of animals and it requires the coordination of building actions of thousands of tiny blind creatures.

Figure 2. A virtual tour inside an *Apicotermes* nest reveals beautiful spiral staircases and the sophisticated harmony of its architecture. Here computer tomography shows that the inner architecture resembles a parking garage in which regularly spaced floors delimiting chambers are connected by helicoidal ramps. This architectural complexity is even much more remarkable because of the sharp contrast that exists with the behavioral simplicity of the workers that have built it.

Figure 3. Some examples of nest architectures built by social wasps. (A) *Agelaia testacea*. (B) *Parachartergus fraternus*. (C) *Vespa crabro*. (D) *Chartergus chartarius* (a portion of the envelope has been removed to show the organization of combs).

Figure 4. Stigmergic construction in the paper wasp *Polistes dominulus*. Colored blotting paper is used as building material to visualize the successive construction steps and identify the configurations of cells that trigger a building action.

Figure 5. A computational model of nest construction in wasps performing random walks in a 3D discrete space, having access to local space and time information and acting on a pure stimulus-response basis. (A) To build a nest, agents use a set of stochastic rules (p_i) defined as the association of a particular stimulating configuration and a brick to be deposited. (B) Small differences in the execution of rules give rise to important morphological changes of the resulting architectures. With the experimentally-measured probabilities, these rules lead to the construction of a round shape comb similar to *Polistes dominulus* nests; with different probability values, indented combs are built similar to the nest of *Parapolybia varia*, a species living in south-east Asia.

Figure 6. Wasp nest architectures obtained from simulations with a model of stigmergic construction. Although the underlying behavioral principle is quite simple, complex architectures can form, some of which closely match those found in nature.

Figure 7. When the air temperature increases, a shape transition occurs from regularly spaced pillars and walls (A) to large roofs supported by a small number of pillars (B). The architecture is permanently remodeled: the workers destroy some parts of the nest and in the same time they rebuild new structures from the old ones (C).

Figure 8. 3D agent-based model of ant nest construction. The red blocks are ant agents whose behavioral rules are based on experimental data. They pick up and drop mud pellets (in grey) and their motion is a constrained random walk, meaning that they stay in contact with the outer surface of the architecture they built.

Figure 9. The mean lifetime of the building pheromone has a major impact on the resulting shape built by ants: regularly spaced pillars and walls when it is long corresponding to a small evaporation rate (A) or large roofs when lifetime is short corresponding to a strong evaporation rate (B).

Figure 10. Growth and remodeling of ant nest architecture. With a large amount of building material, ant agents build a laminar structure: roofs are built through the progressive merging of the growing capitals and new pillars are built over the successive floors. The cross sections show the construction of helicoidal shape connections between successive layers as a consequence of the constant digging activity of the ant agents that remodel the whole nest structure.

Short biography

Guy Theraulaz is a senior fellow at the Centre National de la Recherche Scientifique in Toulouse, France. He is a leading researcher in the field of swarm intelligence, primarily studying social insects but also distributed algorithms, e.g. for collective robotics, directly inspired by nature. His research focuses on the understanding of a broad spectrum of collective behaviors in animal and human societies.

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