Guy Theraulaz

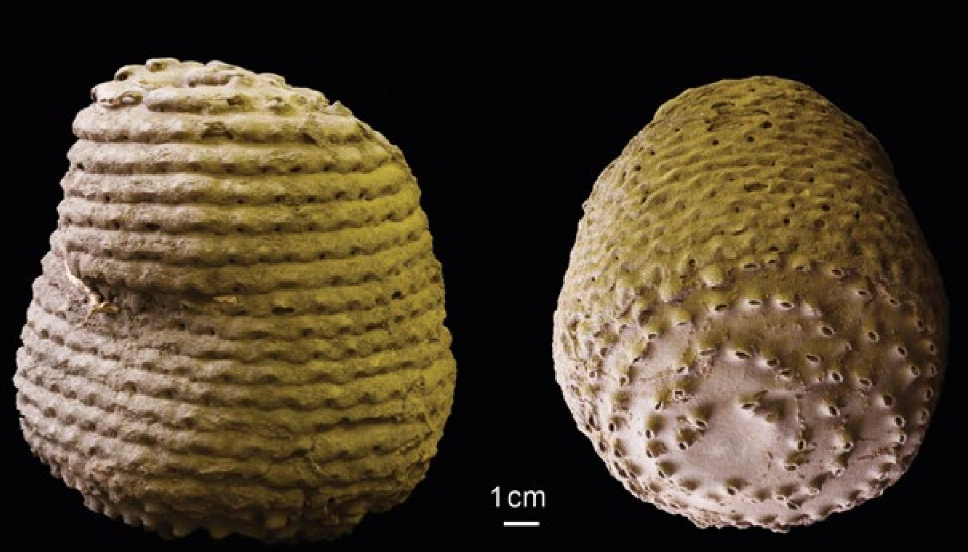
EMBRACING THE CREATIVITY OF STIGMERGY IN SOCIAL INSECTS

In 1959, French biologist Pierre-Paul Grassé coined the term 'stigmergy' to explain the mechanism of spontaneous coordination between agents or actions that leave traces on the environment. Here, **Guy Theraulaz**, a leading researcher in the field of swarm intelligence and a senior fellow at the of the Centre de Recherches sur la Cognition Animale, part of the Centre National de la Recherche Scientifique (CNRS) at Université Paul Sabatier in Toulouse, explains how architects can learn from this type of social interaction among insects.

With the notable exception of man, insect societies are living organisms that build the most diverse and complex forms of architecture.[1] 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 size. The big question is: how do 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 was provided more than 50 years ago by French biologist Pierre-Paul Grassé who introduced the concept of 'stigmergy'.[2]

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 is 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 its 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



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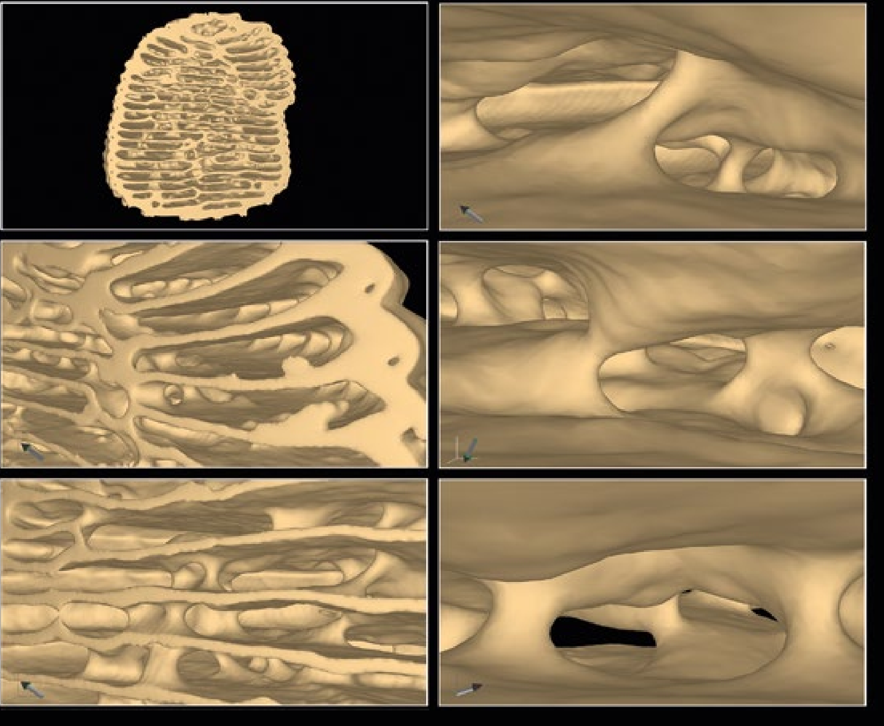
Nests of the African genus of termites *Apicotermes* are constructions made out of clay whose shape resembles that of an old pottery designed and made by skilled craftsmen. This highly complex structure requires the coordination of the building actions of thousands of tiny blind creatures.



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 and delimiting chambers are connected by helicoidal ramps. The architectural complexity is in sharp contrast with the behavioural simplicity of the workers who built it.

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 behavioural 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 blueprint to build their nest. At the Centre de Recherches sur la Cognition Animale, part of the Centre National de la Recherche Scientifique (CNRS) at Université Paul Sabatier in Toulouse, we have spent the last 20 years identifying and characterising the interactions involved in the coordination of nest building in various species of wasps, ants and termites.[3] 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 Moulded Paper Cells

A nice example of stigmergic behaviour is provided by nest building in social wasps. The vast majority of wasps' nests are built with wood pulp and plant fibres that are chewed and cemented together with oral secretions. 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 the building blocks from which the comb is made; and the external envelope that protects the comb. Building activities are driven by the local configuration of cells that are detected by wasps as they move on the surface of the nest.[4] However, not all potential building sites have the same probability of being chosen by wasps; they prefer to add new cells to a corner area where three adjacent walls are already present, rather than start a new row by adding a cell on to the side of an existing row.

Same Rules, Different Patterns

At Toulouse, we have investigated the consequences of applying these local rules, on both the development of combs and the resulting nest architecture, with a simple individual-based model.[5] In this model, wasps are represented by asynchronous agents moving in a three-dimensional discrete hexagonal space, whose building actions are controlled by a stochastic response function to the state of the local environment. Each agent detects only the first 26 neighbouring cells adjacent to the cell it occupies at a given time, and it does not have any representation of the nest architecture to be built. It follows a simple set of construction rules that have been determined by the analysis of experimental data. Some of the configurations trigger a building action, and 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 towards another cell.

As construction rules are stochastic, the probability values associated with each particular configuration of cells, which were estimated from experimental data, could be implemented within the model. The resulting simulations 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, 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.

From Stigmergy to Self-Organisation

Stigmergic interactions are also involved in a large number of other spatial patterns built by social insects such as ants and termites, including networks of pheromone trails, epigeous nest architectures or underground foraging galleries. However, the dynamics and the properties of these emerging patterns are quite different from what has been seen previously in wasps' nest construction. Indeed, in ants and termites, 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 behaviours such as imitation, recruitment and reinforcement processes, and are usually implemented in the form of individual responses to stimuli. In combination with negative feedbacks that

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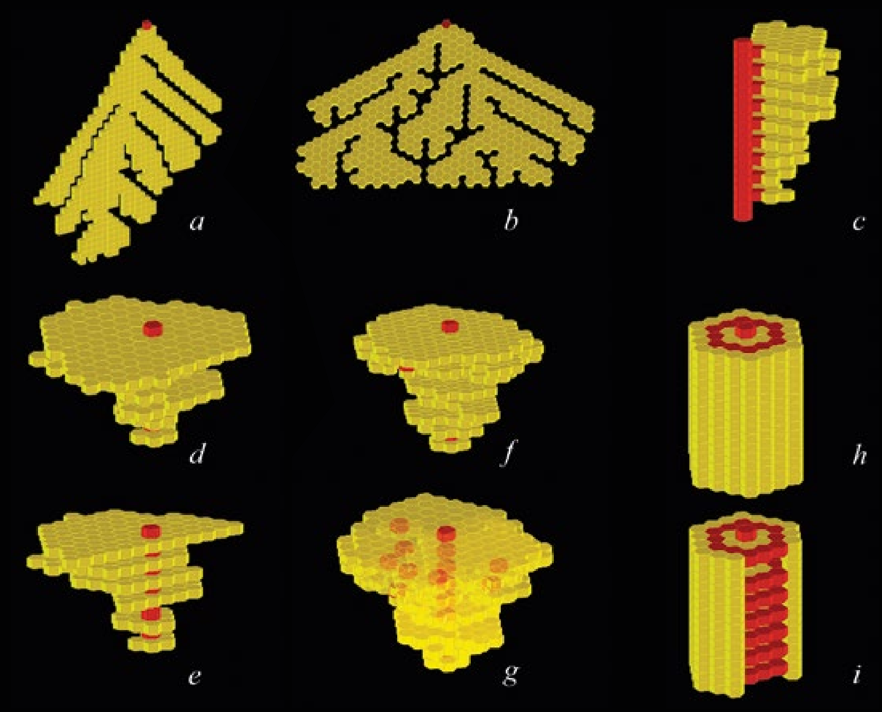
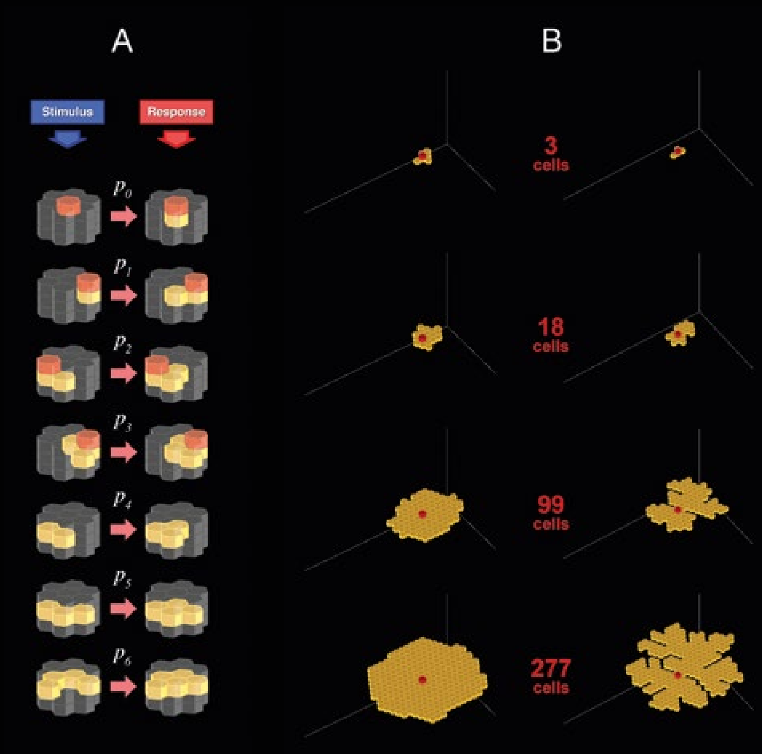
Wasp nest architectures obtained from simulations with a model of stigmergic construction. Although the underlying behavioural principle is quite simple, complex architectures can form, some of which closely match those found in nature.





Computational model of nest construction in wasps. (A) To build a nest, agents use a set of stochastic rules (*p*) 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.

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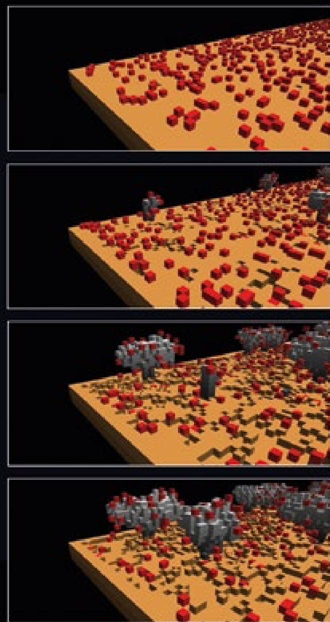
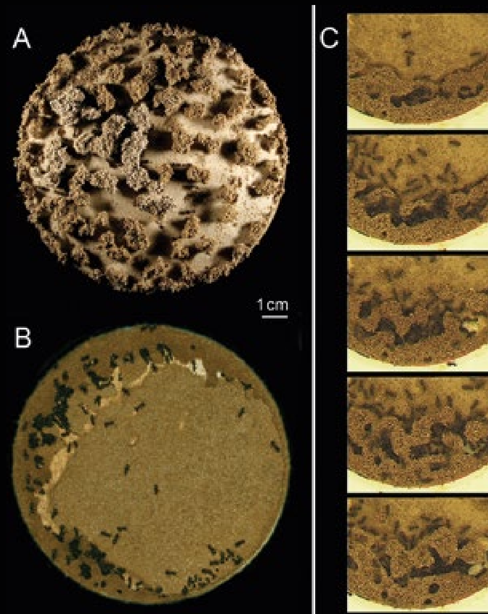
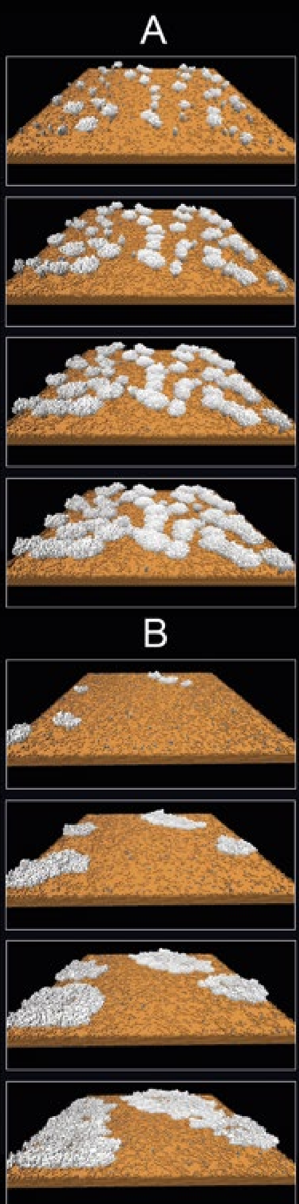
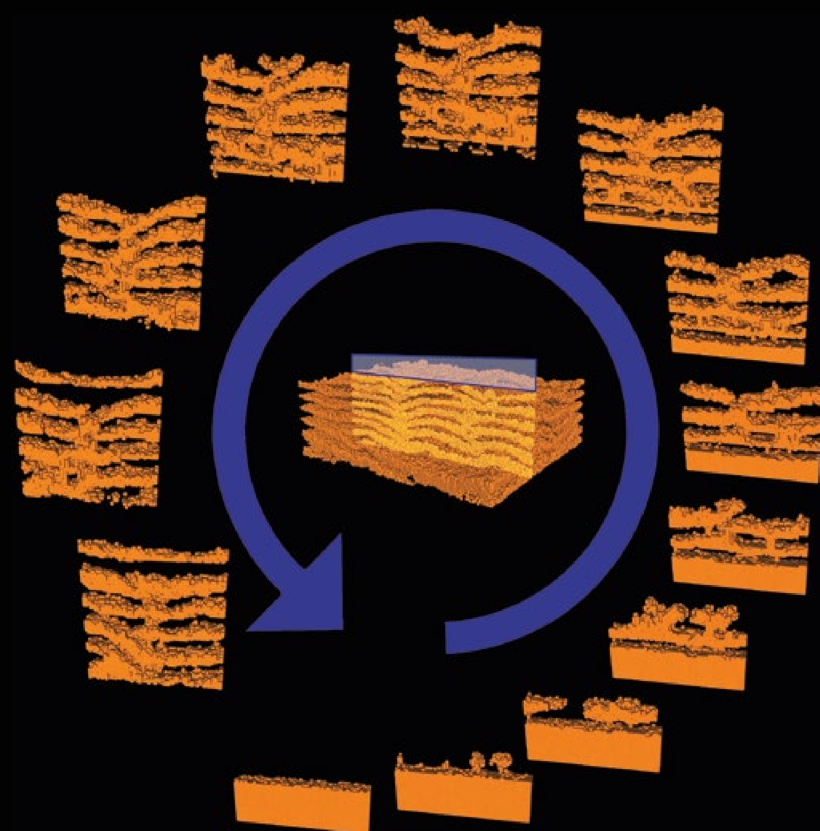
right: 3D agent-based model of ant nest construction. The red blocks are ant agents whose behavioural rules are based on experimental data. They pick up and drop mud pellets (in grey) and their motion is a constrained random walk, meaning that they stay in contact with the outer surface of the architecture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

far right: 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 remodelled: the workers destroy some parts of the nest and at the same time rebuild new structures from the old ones (C).









left: The mean lifetime of the building pheromone has a major impact on the resulting shape of the structure the ants build: 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).

above: Growth and remodelling of ants' 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 shaped connections between successive layers as a consequence of the constant digging activity of the ant agents who remodel the whole nest structure.

may take the form of saturation, exhaustion (pheromone evaporation) or competition, these positive feedbacks are the two basic ingredients of self-organisation in biological systems.[6] A wide range of studies have demonstrated that self-organisation is a major component of many collective behaviours in social insects, but also in many group-living animals as well as human crowds.[7]

Piling Up Mud Balls

Together with emergent properties such as the building of complex and large-scale foraging networks, non-linear interactions cause self-organised systems to bifurcate. Bifurcation is the appearance of new stable solutions when some of a system's parameters change, and this corresponds to a qualitative change in the collective behaviour. In the case of ants' 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*, our experimental results have shown that the deposition of building material in a particular place was reinforced by the pheromone present in the material already deposited in that place. As a consequence, ants tend to accumulate more material in the same place, thus creating a positive feedback. Piling up mud pellets rapidly leads ant workers to build pillars, and once these have reached a critical height, the workers start to add pellets on the sides; they use their body as a kind of template to decide at which height they stop increasing 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 the roofs ants build over the pillars. In the experiments, when temperature was increased there was a transition from a large number of thin pillars topped with capitals of a globular shape, to a small number of larger pillars covered with thin horizontal roofs. To understand the construction dynamics that led to this shape transition, a spatially explicit agent-based model was developed that incorporated the behaviour of ants as characterised in the previous experiments.[8] Here, ant workers were represented by agents whose behavioural rules were modelled according to the probabilities of them performing simple elementary actions depending on the current state of their environment. The model showed that the evaporation rate of the building pheromone is a highly influential parameter on the resulting structures. The functional consequences were quite unexpected, since without changing building rules the shape transition was 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 behaviour: 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. Thus, in social insects, self-organisation enables a real economy of the amount of code that is required at the individual level to produce such amazing nest architectures.

Though extremely simple, stigmergy is thus a powerful mechanism for coordinating the building actions of myriad simple-minded creatures. Traces left and modifications made by groups of insects in the environment may feed back on them and in turn organise their collective behaviour. It is also a simple way of reshaping and optimising the extended phenotype of colonies when they face challenging and variable environmental conditions. ⌀

Notes

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