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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,

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

38

39 **Assembling molded paper cells**

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

52

53 **Same rules, different patterns**

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

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

71 72 **From stigmergy to self-organization**

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

87 88 **Piling up mud balls**

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

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

100

101 **Environmentally induced phenotypic plasticity**

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

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

126

127 **Figure captions**

128
129 **Figure 1.** Nests of the African genus of termites *Apicotermes* are constructions made out of clay
130 whose shape resembles that of an old pottery designed and made by skilled craftsmen^{xiv}. This is
131 one of the most complex structures ever built in the animal kingdom by a group of animals and it
132 requires the coordination of building actions of thousands of tiny blind creatures.

133
134 **Figure 2.** A virtual tour inside an *Apicotermes* nest reveals beautiful spiral staircases and the
135 sophisticated harmony of its architecture. Here computer tomography shows that the inner
136 architecture resembles a parking garage in which regularly spaced floors delimiting chambers are
137 connected by helicoidal ramps. This architectural complexity is even much more remarkable
138 because of the sharp contrast that exists with the behavioral simplicity of the workers that have
139 built it.

140
141 **Figure 3.** Some examples of nest architectures built by social wasps. (A) *Agelaiia testacea*. (B)
142 *Parachartergus fraternus*. (C) *Vespa crabro*. (D) *Chartergus chartarius* (a portion of the
143 envelope has been removed to show the organization of combs).

144
145 **Figure 4.** Stigmergic construction in the paper wasp *Polistes dominulus*. Colored blotting paper
146 is used as building material to visualize the successive construction steps and identify the
147 configurations of cells that trigger a building action.

148
149 **Figure 5.** A computational model of nest construction in wasps performing random walks in a
150 3D discrete space, having access to local space and time information and acting on a pure
151 stimulus-response basis. (A) To build a nest, agents use a set of stochastic rules (p_i) defined as the
152 association of a particular stimulating configuration and a brick to be deposited. (B) Small
153 differences in the execution of rules give rise to important morphological changes of the resulting
154 architectures. With the experimentally-measured probabilities, these rules lead to the construction
155 of a round shape comb similar to *Polistes dominulus* nests; with different probability values,
156 indented combs are built similar to the nest of *Parapolybia varia*, a species living in south-east
157 Asia.

158

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

162
163 **Figure 7.** When the air temperature increases, a shape transition occurs from regularly spaced
164 pillars and walls (A) to large roofs supported by a small number of pillars (B). The architecture is
165 permanently remodeled: the workers destroy some parts of the nest and in the same time they
166 rebuild new structures from the old ones (C).

167
168 **Figure 8.** 3D agent-based model of ant nest construction. The red blocks are ant agents whose
169 behavioral rules are based on experimental data. They pick up and drop mud pellets (in grey) and
170 their motion is a constrained random walk, meaning that they stay in contact with the outer
171 surface of the architecture they built.

172
173 **Figure 9.** The mean lifetime of the building pheromone has a major impact on the resulting shape
174 built by ants: regularly spaced pillars and walls when it is long corresponding to a small
175 evaporation rate (A) or large roofs when lifetime is short corresponding to a strong evaporation
176 rate (B).

177
178 **Figure 10.** Growth and remodeling of ant nest architecture. With a large amount of building
179 material, ant agents build a laminar structure: roofs are built through the progressive merging of
180 the growing capitals and new pillars are built over the successive floors. The cross sections show
181 the construction of helicoidal shape connections between successive layers as a consequence of
182 the constant digging activity of the ant agents that remodel the whole nest structure.

183 184 **Short biography**

185
186 Guy Theraulaz is a senior fellow at the Centre National de la Recherche Scientifique in Toulouse,
187 France. He is a leading researcher in the field of swarm intelligence, primarily studying social
188 insects but also distributed algorithms, e.g. for collective robotics, directly inspired by nature. His
189 research focuses on the understanding of a broad spectrum of collective behaviors in animal and
190 human societies.

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