



Self-organization or individual complexity: a false dilemma or a true complementarity?

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The collective decisions and patterns discussed in this section are examples of processes based upon behavioral rules of thumb [1] executed by individuals which have only limited access to global information. Most of these behavioral rules can be expressed as relatively simple “if-then” statements which correspond to stimulus-response pairs based upon a change in the internal or motivational state of the individual. These processes involve multiple interactions (the individuals or events are numerous) in the form of positive or negative feedback loops. These interactions modify the characteristics of the system and provide new stimuli for further interactions. In these systems, forms of positive feedback, such as recruitment, often involve specific behaviors by individuals; in contrast, the negative feedback often arises “automatically” as a result of the limits or constraints in the system (e.g. the depletion of building materials or the consumption of food).

The coupling between such feedbacks can lead to some surprisingly non-intuitive dynamics such as the oscillations discussed by Cole and Trampus in this volume. In this case, very simple interactions such as collisions and changes in activity levels are enough to produce organized structures. This contribution suggests that ant colonies might provide useful and interesting models for the study of oscillations in biology [2].

The environment itself plays a key role in the emergence of patterns. The chapter of Theraulaz et al., which concentrates on building, illustrates how a model involving positive feedback in the form of chemiotactic orientation of termites to cement pheromone, coupled with an air flux, can explain the shift from regular pillars to walls [3].

Food recruitment also provides numerous examples of such coupling between positive and negative feedback. Changing patterns of crowding at a food source [4], or variations in the food characteristics due to changes in its exploitation by foragers can lead to foraging dynamics which are far more complicated than the

simple choice of one food source over another. For example, the coupling of food exhaustion due to foraging activity with trail-laying behavior can lead to a homogeneous exploitation of the environment or to foraging trails that rotate systematically around a nest [5] depending upon the dynamics of available food. Similarly, the plasticity in the pattern of recruitment trails may be driven simply by an increase in the number of food sources, without any requirement for changes in the communication system or the individual behavior of the ants. A colony may select only one source if the number of sources is small or if its forager population is large. Alternatively, a colony may exploit all sources equally if the number of food sources is large or if the colony population is small.

In the above examples, collective patterns emerge without any modulation of positive feedbacks. However, in insect societies, random searching of scouts for food or home sites can lead to discoveries and recruitments which can be modulated. The collective decisions may arise as a result of competition between different sources of information flow which are conveyed to nestmates and amplified in a number of different ways. For example, an individual recruiting scout bee or ant may modulate its amount of dancing or trail laying in relation to its perception of the profitability of a particular sugar source [6, 7]. In bees the flow of recruited insects is proportionnal to the number of dancing bees, whereas in ants no such relationship is found between the numbers of recruiting and recruited workers. This seemingly small difference in the recruitment systems is responsible for different properties of collective foraging in honeybees and many ant species. For example, bees are always able to select the most rewarding nectar source even if many weaker food sources have been discovered previously. This is not the case for the ants, which may not be able to break free from a previously selected food source and to switch to a more rewarding source. These different strategies are not primarily due to differences in the sensory or physiological capacities of the individuals involved. They are rather a by-product of small differences between the recruitment "devices" used by the ants or the bees [8].

As discussed above, an individual scout bee or ant may modulate its recruitment behavior in relation to its local perception of food profitability. In addition, other factors unrelated to individual behaviors, such as characteristics of the environment (Detrain et al., this volume) can alter the amplification of recruitment to food sources. Thus, efficient decision making can arise without any modulation of the individual's behavior. In such cases, any constraint which reduces the rate of recruitment (such as the distance between the nest and the food source or the

time spent to discover food) can lead to that food source losing out in its competition with other sources.

The simplicity of the rules involved in the production of a global foraging response appears even more clearly if other colony dynamics, such as changes in the internal demand of workers or larvae, are also taken into account. Such colony dynamics can play a role that is of equal importance to the specifics of the recruitment behaviors. For example, in the case of ants when there is a choice between sources of different quality (e.g. proteins versus sugars), workers will selectively forage to meet colony requirements. In this case, non-foraging workers within the colony can provide important information to foragers by means of trophallactic and behavioral interactions [9–10] (see also Cassill and Tschinkel, this volume). This exchange of information between foragers and domestics is indirect, since it is based on time delays in the unloading of foragers (see also Anderson and Ratnieks, this volume).

With this capacity to produce efficient responses or patterns, it is not surprising to find a large number of such self-organized social systems. Recruitment is used in ants for other purposes such as nest defense [11], exploration [12–14] or trail networks between nests [15]. It is also involved in nest-site selection in honeybees described by Visscher and Camazine in their chapter as well as nest-moving in wasps and ants [16, 17]. The example of social caterpillars discussed by Fitzgerald and Costa, this volume, and [18] also provides a beautiful instance of spatial organization involving recruitment and trails formation. The problem of selection of information can be easily solved by the colony of caterpillars through competition between simple recruitments. Trail recruitment has also been found in very different animals such as mollusks [19], Norway rats [20] and naked mole rats [21].

Besides recruitment, activities such as clustering of workers, brood or food within the nest [22–24] also involve amplification processes. The ability of ants to discriminate between different items (e.g. larval instars) coupled with amplifying processes can explain the spatial organization of these items within the nest. Similarly, mathematical models and intuition suggest that the same basic logic could be extended to task regulation and could be one of the touchstones of social organization [25, 26].

Moreover, self-organization is not limited only to these questions of social organisation but can also be extended to studies on the behavioral specialisation of individuals as well as the emergence of hierarchy and division of labour ([27],

Huang and Robinson, this volume). All these examples address the fundamental question of how the most rewarding site, activity and so on can be selected by a group of individuals or by one individual.

In their approach to social life based on self-organization, all the contributions of this section stress the behavioral simplicity of the individual. This begs the question of how much more diverse and efficient the responses could be with small increases in the complexity of the insects' responses to the stimuli. In the case of trail recruitment, mathematical models show that an increase in individual complexity may not lead to a large increase in collective efficiency [28].

But in other cases in which workers are likely to be sensitive to a great diversity of cues, both from nestmates and the external environment, and to be able to modulate their behavior in response to these cues, we expect to find a greater diversity of colony-level responses. Cooperative defense of *Myrmecocystus* ants is an example that illustrates the alternative: Is complexity of global behavior a by-product of complex individual assessments or the expression of simpler behavioral rules and amplification processes? *Myrmecocystus* tournaments are seen as sites for global harvesting of information and integrative sampling to tally colony strength. Several decision-making processes have been suggested to account for these ritualized fights [29, 30]. On the one hand, the first two models hypothesize behavioral complexity of the individual ant able to census the number of aggressive encounters and the caste of the opponents. The ant "measures", by some analogical counting, the colony size and even gets an image of the opponent colony's caste system. On the other hand, in the third model, recruitment for information storage and processing by individual ants is less demanding. In this case, the mere detection of a supply of unengaged nestmates is in itself sufficient to release recruitment behavior and to result in a raid on the weaker colony. This implies that ants are not engaged in some accurate sampling procedure but are locally reacting to simple behavioral rules.

Odors of nestmates or signals arising from the genetic diversity of a colony are potential sources of diverse cues for individuals. An insect can modulate its response to signals emitted by the conspecifics. This can be achieved in different ways. For example genetic relatedness can favor mutual recognition: cockroaches discriminate their odor from that of other lineages, and alter their gregarious behavior [31]. Some ant species are also able to distinguish their trail from those produced by their nestmates [32]. The ability to learn the characteristics of a pheromonal blend is a means of facilitating mutual recognition in ants

(Lenoir et al., this volume). The degree to which individuals can recognize one another affects the dynamics of the amplification involved in the clustering and leads to a diversity of patterns such as mixed or segregated clusters [33].

Researchers can expect to obtain a great deal of information about insect social life by examining behavioral rules of the individual. Our conviction is that self-organized “scripts” are numerous in group living organisms and that noneu-social species provide important material for exploring the link between self-organization and evolution of sociality. Aggregation is a rather simple social behavior and could be a first step towards more sophisticated social interactions. Most aggregations result from the simple gathering of individuals at the same place. The selection of a valuable site and the spatial organization of the populations are very often by-products of an “amplification-competition” script. The resulting increase in density is a favorable ground for the emergence of new social behaviors such as a cooperative defense or a new function for the cluster such as an information center for food collection (see, for example, Fitzgerald and Costa, this volume).

Put in an evolutionary perspective, an increase in the cooperation among individuals would be difficult to achieve if we assume it to be governed by a plethora of behavioral mechanisms and feedbacks. In this respect, self-organization scripts allow some parsimony in the coding and management of information. Our intuition about the importance of self-organized patterns in social organisms is partially due to our fascination with the impressive structures emerging from simple models of behavior. However, one of the current weaknesses in the approach of self-organization is the few instances in which it can be clearly identified. The paucity of data at both individual and colony levels prevents us from making any general assessment of the contribution of self-organization to the working of biological systems. For this reason, we suggest that more would be achieved at the present time through greater emphasis on experiments enabling us to discriminate between self-organization and other hypotheses on pattern formation and decision making, rather than further speculations and facile computer models [8].

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