Self-Organization in Relation to Several Similar Concepts: Are the Boundaries to Self-Organization Indistinct?

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Abstract. Self-organization is a concept and phenomenon whereby system-level patterns spontaneously arise solely from interactions among subunits of the system. Focusing on self-organization at the organismal level, I ask the question: are the boundaries to self-organization indistinct? After reviewing a number of published definitions of self-organization, I explore the conceptual boundaries among self-organization and two similar concepts, stigmergy and self-assembly. I highlight borderline cases that may blur the distinction among these and suggest that they may indeed be conceptually indistinct and difficult to separate in practice. Consequently, I propose a classification scheme based upon three aspects: whether the stimuli to which individuals respond are quantitative or qualitative, whether positive feedback is involved, and whether interindividual interactions are direct or indirect (stigmergic). In addition, I consider several other issues about self-organization, including (1) could a self-organized system use global information? (2) what is the role of the degree of correlation of activity among individuals? and (3) what is the role of positive feedback?

Introduction

Ernst Mayr, that grand old father of evolutionary biology, claims that "classifications are necessary wherever one has to deal with diversity" (Mayr, 1982: p. 147). In this essay, I consider the diversity around the concept of self-organization—a phenomenon in which system-level patterns spontaneously arise solely from interactions among subunits of the system—and ask the question, are the boundaries to self-organization indistinct? In particular, I focus on the conceptual boundaries among self-organization and two similar concepts, stigmergy and self-assembly. In an ideal, perfectly ordered world, we would possess strict definitions and criteria by which different examples could be categorized unambiguously—this would, for example, provide a rigorous and objective way of identifying the same phenomena and emergent properties occurring in very different systems, such as a purely physical system and a biological one. However, as I discuss, and illustrate with deliberately chosen borderline cases, this does not seem possible with self-organization. Instead, I attempt a classification scheme to deal with this diversity based upon three aspects of the systems: whether the stimuli to which individuals respond are quantitative or qualitative; whether or not positive feedback is involved; and whether interindividual interactions are direct or indirect.

This does not solve the issue, but does serve to highlight the diversity of combinations of key properties that give rise to self-organized behavior in such systems. I also take this opportunity to discuss a few other related issues about self-organization: could a self-organized system use global information? what is the role of the degree of correlation of activity among individuals? and what is the role of positive feedback?

In this essay, I concentrate on self-organization at the organismal level, that is, in systems of (eu)social and gregarious animals. I do this not because I view their self-organization as fundamentally different from self-organization in purely physical and chemical systems (such as sand

Table 1

Various definitions of self-organization (arranged chronologically)

Self-organization is considered to be
1. indicative of a machine that is "determinate and yet able to undergo spontaneous changes of internal organisation" (Ashby, 1947: p. 125)
2. "a set of dynamical mechanisms whereby structures appear at the global level of a system from interactions among its lower level components" (Nicolis and Prigogine, 1977, cited in Bonabeau *et al.,* 1997)
3. "associated with the spontaneous emergence of long-range spatial and/or temporal coherence among the variables of the (organized) system" (Nicolis, 1986: p. 7)
4. "the spontaneous emergence of coherence or structure without externally applied coercion or control" (Ho and Saunders, 1986: p. 233)
5. "a system is self-organizing if it acquires a spatial, temporal or functional structure without specific interference from the outside. By 'specific' we mean that the structure or functioning is not impressed on the system, but that the system is acted upon from the outside in a nonspecific fashion" (Haken, 1988: p. 11)
6. "the ability of systems comprising many units and subject to constraints, to organize themselves in various spatial, temporal or spatiotemporal activities. These emerging properties are pertinent to the system as a whole and cannot be seen in units which comprise the system" (Babloyantz, 1991: p. ix)
7. "the creation of macroscopical patterns by the action of forces distributed in a much more homogeneous way than the structures that arise. Hence, this kind of transformation implies a spontaneous breaking of symmetry" (Beloussov, 1993)
8. "the spontaneous emergence of nonequilibrium structural organization on a macroscopic level due to collective interactions between a large number of simple, usually microscopic, objects" (Coveney and Highfield, 1995: p. 432)
9. "a process where the organization (constraint, redundancy) of a system spontaneously increases, i.e. without this increase being controlled by the environment or an encompassing or otherwise external system" (Heylighen, 1997)
10. "a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern" (Camazine *et al.,* 2001: p. 8)

dunes and the Beloussov-Zhabotinsky reaction)—although animals do have the added potential to vary the individual-level rules they employ, and thus may represent another level of complexity of individual-level behavior and collective-level patterns—but because study of organismal self-organization is relatively new and lags behind the decades of progress made in these other fields. Before we proceed with the above issues, it is crucial to consider the question of what precisely is self-organization.

What Is Self-Organization?

Consider the collective movement of a school of fish. The school snakes through the water like a single entity, turning in unison, waves of activity flashing across the shoal. This group-level behavior is not encoded within each individual, nor is there a leader or small group of individuals directing the movement of the school. It is a process whereby individual fish react to movements of their immediate neighbors, and, as a result of such local interactions, the group-level pattern of activity emerges spontaneously (Reynolds, 1987; Huth and Wissel, 1992; Camazine *et al.,* 2001; Parrish *et al.,* 2002)—in short, the school is self-organized.

Self-organization, or at least use of the term self-organizing system, dates back to at least 1947 (Ashby, 1947). However, the general concept stems much further back in history, at least since Aristotle's *Metaphysica.* It is perhaps surprising then that rigorous study of self-organization has its roots in physics and chemistry (but often inspired by

biological systems), yet only relatively recently have biologists taken up the challenge to understand biological self-organization, at least at the organismal level (Bonabeau *et al.,* 1997, 1999; Camazine *et al.,* 2001; Anderson, 2002).

What precisely, however, is self-organization, and do we have an adequate definition of it? Table 1 lists 10 definitions of self-organization from the literature (mostly from physics). Summarizing across all these definitions, what picture emerges? A key aspect is the creation of a macroscopic, group-level "pattern." Such a pattern may consist of a spatio-temporal physical structure or behavior. And this pattern is "emergent" (another term difficult to define satisfactorily); that is, it cannot be deduced from even a full knowledge of the lower-level components and the nature of the interactions among them—the stock phrase is that "the whole is more than the sum of its parts" (Aristotle, *Metaphysica,* 10f-1045a). This emergence implies that there is some nonadditive, nonlinear interaction involved, and thereby implicates the role of positive feedback (but see later). What is crucial too is that there are multiple lower-level components and hence multiple interactions, or possibly even a single individual but many repeated interactions (phase transitions often occur such that the emergent patterns arise only above a certain critical number or density of interactions or components). Also, Table 1 shows that the authors of the definitions consider that the group-level properties must arise solely from within the system, not generated from interference or other external guiding forces, such

as templates (Camazine *et al.,* 2001; Anderson, 2002). This is not to say, however, that the environment has no role to play. Self-organized systems often exhibit what is termed multistability, so that the system may sometimes switch between different semi-stable patterns, but without any changes in the lower-level behavioral characteristics (Ünsal, 1993). Importantly, the system may switch because of intrinsic factors, such as random fluctuations within the system, or extrinsic factors, such as small changes in the environment with which the system interacts (Deneubourg *et al.,* 1989; Camazine *et al.,* 2001).

To sum up, self-organization supposedly contains a number of "key ingredients": (1) positive feedback as one of the forces driving change in the system (usually nonstabilizing change, that is, change in the same direction as a perturbation; see later); (2) negative feedback as a stabilizing force (that is, driving change in the opposing direction to a perturbation); (3) stochasticity and randomness generating diversity upon which the feedback works, and (4) multiple interactions (Bonabeau *et al.,* 1997, 1999; Camazine *et al.,* 2001).

The "characteristics" or signatures of self-organization include, but are not restricted to, (1) creation of emergent group-level spatiotemporal structures or behaviors, and (2) multistability and symmetry breaking, such that even only small changes in individual behavior can lead to large changes in collective behavior (even multistationarity), and small changes in the environment, without changes in individual behavior, can lead to different collective states (Ünsal, 1993; Bonabeau *et al.,* 1997; Camazine *et al.,* 2001).

If I have labored the above points, it is because a comparison between self-organization and similar mechanisms requires an understanding of what self-organization is perceived to be even if we lack a satisfactory all-encompassing definition. As background for the comparison, two points should be considered.

Could a self-organized system use global information?

Could a self-organized system in fact use some global information? The following example, albeit simple and debatable, is instructive (I must acknowledge J. L. Deneubourg for his insights and discussion of this example). Bumblebees, *Bombus* spp., actively regulate the climate in their nests. When nest air temperature becomes too high, bees fan their wings to draw in and circulate fresh air, thereby cooling the nest (O'Donnell and Foster, 2001; Weidenmüller, 2001; Weidenmüller *et al.,* 2002). If the temperature becomes too low, they may commence brood incubation, releasing heat from their shivering muscles. At certain temperatures the two behaviors may co-occur (Vogt, 1986; O'Donnell and Foster, 2001).

Each bee appears to have her own temperature threshold, and when the temperature exceeds that threshold she may or

may not start to fan (Weidenmüller, 2001; C. Anderson *et al.,* unpubl. ms.). Thus, in this sense, bees make individual decisions on the basis of the air temperature around them, and hence the decision is local. However, the air is reasonably homogeneously mixed, and so in another sense is the equivalent of a *global* signal, the same temperature experienced by all the bees. I would argue that the dynamics of nest air temperature is the global pattern, determined by which bees and how many are fanning or incubating over time. This is, of course, a simple temporal pattern. (There is a strong analogy here with the Beloussov-Zhabotinsky reaction [*e.g.,* Goodwin, 1994; Ball, 1999]; if the reactants for this autocatalytic process are left to develop in a petri dish, wonderful spiral and circular patterns arise. However, if homogeneously mixed, the solution oscillates between red and blue. The mixing of air would seem to be constraining the complexity of the temperature dynamics in a similar manner. Might it generally be true that the degree of "locality" of interactions somehow determines the spatial scale of a self-organized pattern—more local meaning a finer pattern—in the same way that diffusion rate has such a crucial role in other pattern formation processes, such as reaction-diffusion?)

The temperature profile is generated by the action of individuals interacting with each other indirectly through the medium of the air. Moreover, the air acts as a sort of filter, screening off the individual level to produce only the net effect of all individuals fanning and incubating. Overall, I would argue that this is a system with local decisions: bees do not need to know what every other bee is doing and they do not interact directly, but they do affect others *indirectly* by their actions upon the stimulus. Because bees' decisions to fan are probabilistic, we cannot deduce the precise dynamics from knowledge of a bee's proximate rule. To my mind, this could be considered an example of quantitative stigmergy (see below) with a homogeneously mixed stimulus and without positive feedback.

What is the role of the degree of correlation of activity among individuals?

I suggest—merely as a working hypothesis that could be tested—that there must be a critical window of correlation of activity among individuals in order for self-organization to occur. That is, above some upper threshold and below some lower threshold, self-organization breaks down, and the emergent properties no longer exist.

By correlation of activity I mean a combination of the strength and likelihood that the behavior, location, movement, etc., of individual A affects and so causes a similar change in those properties of individual B. This is best illustrated by a simple example. Imagine a reasonably polarized school of fish. Each fish reacts to some predator or to the movements of a few of its nearest neighbors. Fish

react solely in terms of a change of heading, either in order to swim away from a predator or to avoid crashing into neighbors. Finally, consider a parameter $0 \leq r \leq 1$, which determines the degree of correlation of activity among individuals: if fish i moves, Prob(i's neighbors move) $= r$. (The parallel with a product moment correlation coefficient should thus be clear.) Thus, if r is high, movement of one individual causes a change in most or all of its neighbors, and if r is very low, the movements of fish A cause little or no change in the school. I hypothesize that there are two thresholds, r_1 and r_u (where $0 \leq r_1 < r_u \leq 1$), that define the range within which self-organization exists.

My reasoning is thus: suppose that $r = 1$ (as if each fish were connected to its neighbors by a rigid rod). Any fish that turns causes a change in its neighbors, and therefore their neighbors, and so on across the school. A group-level pattern, polarity (or more precisely, the exact initial configuration), is maintained as the school moves. However, the pattern is not self-organized; the behavior is not emergent, it is simply additive—tell me how fish A will turn and I can predict precisely the behavior of non-neighbor fish Z. (There is of course the problem that different fish—for example, those trying to flee predators coming from different directions—could conflict with each other.) Such a rigidly constrained system would not have sufficient "slack" to allow group-level adaptive behavior, such as the fountain effect, hourglass, or other anti-predator strategies that are observed in real fish schools (Partridge, 1982; Camazine *et al.,* 2001). Consider the other extreme, $r = 0$: each fish has no effect upon its neighbors, and no spatiotemporal structure could exist. Overall, it is tempting to consider $1 - r$ as similar to λ, Langton's (1986) parameter associated with behavioral complexity in dynamic systems and in particular "the edge of chaos." This is the region at which these systems act as complex adaptive systems (Lewin, 1993; Bonabeau, 1998), and therefore are more likely to be selected for.

The above example is highly simplified; in particular, the crucial region of parameter space is likely to be a function of a number of other factors too. For instance, is there also a crucial range of the number of neighbors each individual interacts with? (An alternative way to express this is to ask whether there is a crucial range of "average system connectedness," *sensu* Moritz and Southwick [1992].) For example, Huth and Wissel's (1992) simulation of fish schools demonstrates that tight, coherent schooling behavior requires that each fish interacts with more than two neighbors. As hinted earlier, the locality of those interactions (*i.e.,* whether immediate neighbors or individuals farther away in the school) may also play a crucial role. Finally, the strength of response (and hence feedback) may have crucial limits. These working hypotheses should be testable.

Quantitative *versus* Qualitative Stigmergy

I suggest that the definitions of self-organization (Table 1) could encompass two other similar pattern-formation mechanisms found in biological systems: qualitative stigmergy and self-assembly. Stigmergy, a term first coined by termite researcher Pierre Paul Grassé (1895–1985), is a "class of mechanisms that mediate animal-animal interactions" through work in progress (Theraulaz and Bonabeau, 1999). The work (for example, a half-built pillar in a termite mound) acts as a stimulus to respond, that is, do more work by adding further material to the pillar. Importantly, the result of this stimulus-response sequence is that it alters the stimulus for subsequent individuals. (Note that these are *indirect* interactions among individuals.) In some cases, the stimulus varies in a *quantitative* manner, altering the probability of eliciting the same response from other individuals (thus, the bumblebees would qualify here). Termite mound construction is one such example because workers add pheromone-containing saliva to the soil pellets they place on the growing structure. The local pheromone concentration affects where subsequent individuals will place their pellets—new individuals tend to place their pellets in an area where there is already a high pheromone concentration (Deneubourg, 1977), thus creating a positive feedback (probably absent from the bumblebee case). The response, to place or not to place a pellet, is always the same, and it is the intensity of a single stimulus, the pheromone concentration, that determines whether an individual will respond or not. This mechanism is termed quantitative stigmergy, is characterized by positive feedback and phase transitions (a.k.a. instabilities and mulistationarity; Solé and Goodwin, 2000; Camazine *et al.,* 2001), and is considered to be "an ingredient of self-organization [that] mediates interactions among workers" (Camazine *et al.,* 2001: p. 58).

The second mechanism, qualitative stigmergy, is similar to quantitative stigmergy in that it involves a series of stimulus-responses. In this situation, however, the stimuli differ from each other *qualitatively* and may elicit different responses. Qualitative stimuli include the shape of a structure. A proposed example, nest construction in *Polistes* wasps, is shown in Figure 1 (Bonabeau *et al.,* 1999; Theraulaz and Bonabeau, 1999; Camazine *et al.,* 2001). Builders add new cells to the margin of the nest, and in this particular case there are 12 places, 12 stimulating configurations (S_i's), where they can build a new cell. However, there are different classes of stimuli here that will require a slightly different building procedure. That is, there are 7 locations (S_1's) where there is already a single wall present and individuals must construct 5 new walls to complete a new hexagonal cell; there are 4 locations (S_2's) with 2 walls already present, thus requiring 4 new walls. Finally, there is a single location (S_3) with 3 adjacent walls, thus requiring just 3 new walls. It is clear, at least from a human perspec-
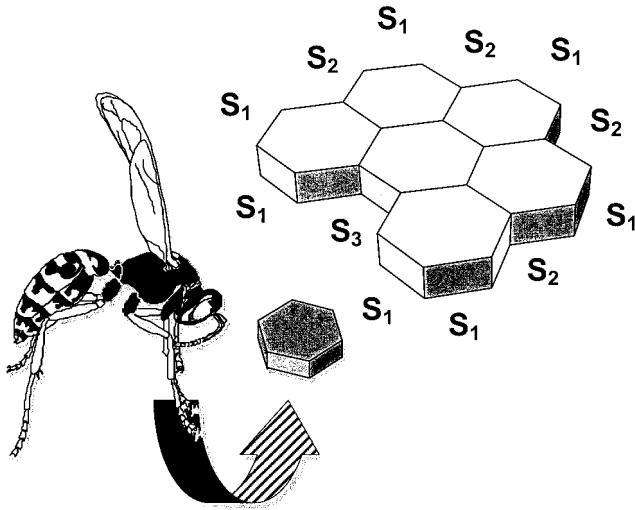
Figure 1. In qualitative stigmergy, an individual responds to qualitatively different stimuli, which involve qualitatively different responses. Thus, to create a new hexagonal cell on the margin of this comb, the *Polistes* wasp must respond by adding 5 new walls (at one of the locations indicated by stimuli, S_1's), 4 new walls (at the S_2's) or just 3 walls (at S_3). Qualitative stigmergy is not considered to be a self-organized process. Figure drawing by Guy Theraulaz, used with permission.

tive (Karsai, 1999), that different stimuli (S_i) elicit qualitatively different responses (R_i) from the builders. Qualitative stigmergy (reviewed in Bonabeau *et al.,* 1999; Camazine *et al.,* 2001), although similar in many ways to quantitative stigmergy, is not characterized by positive feedback and is not considered an ingredient of self-organization (Camazine *et al.,* 2001).

Although these two mechanisms are conceptually very different, I question how easy it is in practice to distinguish between them. Is the boundary between them indistinct? For instance, in *Polistes* nest construction, the probability of constructing a new cell in a certain location is dependent upon the number of adjacent walls (3 walls: probability = 0.55; 2 walls = 0.05; 1 wall = 0; from Camazine *et al.,* 2001: 425; see also Bonabeau *et al.,* 1999). (This is excepting the very earliest stages of construction when only a few cells are present; Downing and Jeanne, 1990; Karsai and Theraulaz, 1995.) These are interpreted as three qualitatively different configurations, but how can we be sure that they do not represent a nonlinear relationship to a quantitative variable? Would we still categorize the response as qualitative if the construction probabilities were directly proportional to the number of adjacent walls (or data resembled fig. 3 of Karsai and Pénzes, 1993)? Karsai and Pénzes (2000) recently suggested that age of cells (a quantitative variable) might be a better explanatory variable of *Polistes* nest construction than the number of adjacent walls (a qualitative variable). Thus, their study, and earlier works (Pénzes and Karsai, 1993; Karsai and Penzés, 1993; Karsai, 1999), interprets the same phenomenon, nest construction in

social wasps, solely from a quantitative stigmergic viewpoint. Viewing the qualitative *versus* quantitative question from the other direction, in the formation of an ant cemetery, the number of corpses in a pile is believed to be a *quantitative* variable, and self-organization plays a role (G. Theraulaz *et al.,* unpubl. ms.). But what if an ant regards a group of two or more ants as a processed "pile," and perceives a single dead ant as something qualitatively different—perhaps as an unprocessed ant that just happened to die on that spot?

My point is that for us—animals sometimes several orders of magnitude larger than the organisms we study—it may be difficult to decide what represents qualitatively or quantitatively different configurations and responses. What appears to be a randomly deposited soil pellet to our eyes may represent a particular qualitative configuration to a termite. A confounding problem is that behavioral data are often noisy. Furthermore, nature probably has few pure self-organization systems; that is, situations that involve no other pattern-formation mechanism. Given these problems, such issues may be difficult to tease out without detailed, tedious, and time-consuming observations and experiments. We must invest some thought into considering what key features and critical tests will allow us to distinguish between qualitative and quantitative stimuli and responses.

Qualitative Stigmergy *versus* Self-Assembly

In this section, I propose that the distinction between qualitative stigmergy and self-assemblages may not be clear-cut. Self-assemblages are "physical structures formed by individuals linking themselves to one another" (Anderson *et al.,* 2002). In insect societies, various examples of self-assemblages exist. For instance, an army ant bivouac is an adaptive structure composed of many workers linked together and is therefore a self-assemblage. Other examples include living ant-bridges (*Oecophylla* and *Eciton*), bee-curtains (see below), and floating ant-rafts that allow colonies to survive nest flooding (*Solenopsis*). Self-assemblages are reviewed in Anderson *et al.* (2002) and are a product of the process of self-assembly (see Sendova-Franks and Franks, 1999).

The way that self-assemblages form involves a new individual moving over the surface of the growing structure and attaching itself. As the individual moves over the surface, it is likely to encounter different stimulating configurations of individuals already part of the structure. Once it attaches itself, it has created a modified structure that probably affects the attachment of subsequent individuals (Fig. 2). Qualitative stigmergy and self-assembly have many common features: movement of an individual over a structure; individuals that presumably encounter different stimulating configurations; qualitatively different responses (attaching at the end of the chain is a different response than
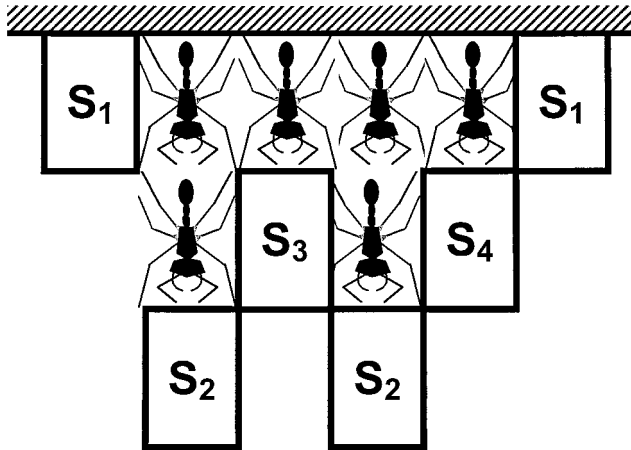
Figure 2. An individual must make a choice when joining a self-assemblage. In this highly stylized view of the beginnings of an army ant bivouac (hanging from an attachment point, hatched section), there are four qualitatively different attachment positions, or stimuli (S_1–S_4). If these different stimuli are associated with different probabilities of joining at this site, then there is a very strong similarity with qualitative stigmergy.

attaching oneself in a "hole" on the surface); and responses that produce a new and probably qualitatively different structure.

In qualitative stigmergy, individuals place new material, in this case wood pulp, onto a structure, the nest, creating a new, qualitatively different structure. The distinction between the material being placed, pulp, and the individuals doing the placing, the worker wasps, is clear. However, in self-assemblages there is not this clear distinction; in a sense, self-assemblages involve individuals that are both the workers, while searching for an attachment site, and the material, once they have attached. In my opinion, this difference between qualitative stigmergy and self-assemblages is unimportant because the same feedbacks seem to be operating in both mechanisms. Are they regarded as distinct merely because qualitative stigmergy involves inanimate stimulating structures whereas self-assemblages involve animate ones?

Self-Assembly *versus* Self-Organization

The way that self-assemblages form, self-assembly, is a mechanism in which the global pattern, in this case a physical structure such as a chain of ants, presumably depends entirely upon local and probably simple interactions among neighboring individuals, without reference to the global pattern. Compare this to the definitions of self-organization (Table 1 and earlier section) and a strong similarity between self-assembly and self-organization is evident (but see Sendova-Franks and Franks, 1999). For instance, it is extremely unlikely that an army ant joining a bivouac has any sense of the global structure it is joining. For one thing,

workers of some army ants species are totally blind—for example, *Eciton burchelli,* which produces what perhaps are the most striking and impressive bivouacs—and rely on local pheromone trails and other chemical and tactile signals rather than visual cues (Franks, 1989; Gotwald, 1995). It is, of course, possible that in some self-assemblages a signal or cue such as total pheromone concentration might correlate with the number of individuals composing the current structure and could give a new individual some information about the global pattern. However, my feeling is that this is probably not the case in most situations, and that—as in self-organization—local information and local interactions are the major mechanisms involved.

What Is the Role of Positive Feedback?

If the above similarity were not enough, another major aspect of self-organization that may link and perhaps blur the distinction between self-organization and self-assembly is positive feedback. Positive feedback is considered a key ingredient but not a crucial component of self-organization: "*most* self-organizing systems use positive feedback" [my italics] (Camazine *et al.,* 2001: p. 15). In this section, I argue first that positive feedback could occur in self-assemblage formation; and second, that some examples of biological self-organization may contain little or no positive feedback. I propose that these are further reasons why self-organization and self-assembly may be conceptually indistinct.

Could self-assemblages involve positive feedback?

Positive feedback is a mechanism that promotes change in a system; moreover, it drives change in the same direction as a perturbation. For instance, in many ant species, a scout ant that has found a source of food lays down a pheromone trail as it returns to the nest. This provides a source of information for other individuals, allowing them to follow the trail and find the food. In turn, as new recruits reach the food and return to the nest, each laying a trail, the trail gets progressively stronger, making it more likely that other recruits will both follow the trail and reinforce it with additional pheromone (*e.g.,* Hölldobler and Wilson, 1990). (Incidentally, the pheromone trails here are another example of quantitative stigmergy.) Thus, from a small "perturbation" such as a single pheromone trail across the ground, a strong trail can develop (Camazine *et al.,* 2001; Deneubourg *et al.,* 2002; Detrain and Deneubourg, 2002).

I argue that positive feedback could be involved in self-assemblage formation. Imagine several chains of *Eciton* ants hanging from a rock, as in Figure 2. A new ant wanders over the chains and attaches itself at some position. If it is more likely to attach itself to the end of the longest chain—the lowest available attachment position—then this creates a positive feedback mechanism: longer chains attract more ants, and so grow faster and longer, thus attracting more

Table 2

A classification scheme of the different examples on the basis of three variables: (1) whether interindividual interactions are direct or indirect (stigmergic), (2) whether or not positive feedback is involved, and (3) whether the stimuli to which individuals respond are quantitative or qualitative. All examples are discussed in the text

Nature of stimulus	Positive feedback involved?	Nature of interindividual interactions	Example
Quantitative	Yes	Direct	(A) Self-organization: fish schools
		Indirect	(B) Self-organization involving quantitative stigmergy: termite nest construction
	No	Direct	(C) Honeybee swarm thermoregulation
		Indirect	(D) Bumblebee thermoregulation
Qualitative	Yes	Direct	(E) Self-assembly: defense posturing in *Apis dorsata*
		Indirect	(F) Not possible?
	No	Direct	(G) Self-assembly: *Eciton* chain formation?
		Indirect	(H) Qualitative stigmergy: *Polistes* nest construction

ants, and so on. In Figure 2, this would mean that the individual responds with greater probability to qualitative stimulus S_2 than S_1, S_3, or S_4.

Positive feedback mechanisms are certainly involved in relation to the probability that an individual will join a growing structure. For example, in weaver ants (*Oecophylla*), which form chains between branches, the probability of joining a group is positively correlated with the size of the group (Lioni *et al.,* 2001). This is presumably adaptive for the colony in that it helps form a collective choice so that there is just a single quick-growing cluster rather than several competing and slow-growing clusters. For this section, however, the key issue is whether positive feedback could operate *within* the structure, that is, once a new individual is wandering over the surface of (and perhaps in) the growing structure. I feel that such positive feedback could occur in self-assemblages, which could further blur the distinction between self-assemblages and self-organization.

Do some examples of self-organization lack positive feedback?

Although a "key ingredient," positive feedback is not part of the self-organization definitions (Table 1). Consequently, in some examples of self-organization the positive feedbacks, if they do occur, are not obvious. Self-organized thermoregulation in honeybee (*Apis mellifera*) swarms is one such example. Bees move between the surface and core of the swarm cluster in an attempt to regulate their own temperature. Overall, there is an adaptive global pattern: the temperature profile of the cluster, which buffers changes in ambient conditions (Heinrich, 1981; Watmough and Camazine, 1995; Sumpter and Broomhead, 2000). Similarly, in two species of Asian bees, *A. dorsata* and *A. florea,* individuals link together to form a living curtain, a self-assemblage, over the comb (Michener, 1974; Anderson *et al.,* 2002). Individuals actively regulate their temperature, and

that of the comb below, by altering their interindividual spacing. When temperature rises they push against their neighbors, increasing the interneighbor distance, thereby allowing air to move more freely through the curtain and cool the nest. Cooling may also be enhanced by individuals fanning their wings and thus increasing airflow (Morse and Laigo, 1969; Michener, 1974; see also Anderson and Franks, 2001). In contrast, at cold ambient temperatures, individuals pull against their neighbors to reduce airflow and increase temperatures. Like these Asian species, honeybee swarms also fan their wings for cooling and move closer together for warming.

Why does the honeybee case class as self-organization (*e.g.,* Camazine *et al.,* 2001) and a self-assemblage (Anderson *et al.,* 2002), but the bees forming a living curtain in an *A. dorsata* colony only class as a self-assemblage (Anderson *et al.,* 2002)? Both seem to utilize very similar mechanisms.

Conclusions

In considering all the previous examples, I have primarily focused on three aspects: (1) whether the stimuli to which individuals respond are quantitative or qualitative, (2) whether positive feedback is involved, and (3) whether interindividual interactions are direct or indirect (stigmergic). From these three binary variables, there are eight possible combinations (Table 2).

It is likely that many researchers would view fish schools (case A) and termite nest construction (case B)—both examples with quantitative stimuli and positive feedback—as self-organized (Bonabeau *et al.,* 1997; Camazine *et al.,* 2001). Honeybee swarm thermoregulation (case C), however, lacking the "key ingredient" of positive feedback, has merely the "flavor" of self-organization, yet is still considered self-organized (Camazine *et al.,* 2001: esp. p. 58). I have proposed that nest thermoregulation in bumblebees (case D) has this same flavor of self-organization yet involves global information.

It has been previously suggested that qualitative stigmergy (case H) is not a self-organized process (Bonabeau *et al.,* 1997, 1999; Camazine *et al.,* 2001). However, I would like to suggest that, by itself, the criterion of qualitative stimuli may be insufficient grounds for declaring that a system is not self-organized. Might a self-organized system involve qualitative stimuli, positive feedback, and direct interindividual interactions? Consider defensive posturing in the giant Asian honeybee, *Apis dorsata* (case E), the species mentioned earlier that forms a living curtain of bees over the comb. When attacked, the outermost bees of this self-assemblage perform a jerky abdominal shaking, behavior that spreads across the surface as a wave (Kastberger and Biswas, 1998; see also Kastberger *et al.,* 1998), sometimes even as spirals, as observed in many other "excitable media" such as heart tissue during cardiac arrhythmia (*e.g.,* Davidenko *et al.,* 1992; Goodwin, 1994; Ball, 1999). A responding bee performs a single wing stroke (of 80–160 ms duration), an abdominal thrust (an additional 200–250 ms), and remains still for a period (200 ms) (Kastberger and Biswas, 1998). A bee performing this sequence of behaviors stimulates its neighbors to "jerk," which in turn affects their neighbors, and so on. Thus, this behavior spreads across the surface in a positively reinforced manner coupled with a crucial refractory period (remain still for 200 ms). (Such refractory periods are vital for traveling waves of activity—as in nerve cells, the Beloussov-Zhabotinsky reaction, activity cycles in ants, etc.—because they prevent backpropagation; that is, the wave travels forward only [*e.g.,* Goodwin, 1994; Ball, 1999].) A bee can be classified as defense posturing or not, and thus the stimulus is most likely qualitative. Lastly, interactions are clearly direct, neighbor to neighbor. What is observed, however, at the global level—traveling and spiraling waves—is generated entirely from within the system and emergent. At least from the definitions in Table 1, it would classify as self-organized.

I cannot envision a situation in which both positive feedback and indirect interactions could be realized with a qualitative stimulus (case F). I will, therefore, *tentatively* suggest that this scenario is not possible, but would welcome suggestions from readers. Finally, with my conceptual scenario of self-assemblage formation (described earlier), I suggest that a situation with direct interactions, qualitative stimuli, and no positive feedback is possible (case G) and would probably qualify as self-organized under the definitions of Table 1. However, as Anderson *et al.* (2002) stress, we are very ignorant about the proximate mechanism involved in self-assemblage formation.

Where does this leave us? I have endeavored to show that the distinction between a number of mechanisms—principally self-organization, qualitative stigmergy, and self-assembly—may, in certain cases, be indistinct. This is not necessarily a problem, as borderline cases can be very illuminating (Anderson and Franks, 2001); only by attempting to push the limits of a concept are we likely to find where the boundaries truly lie. The identification of key variables—direct *versus* indirect interindividual interactions, positive feedback, and quantitative *versus* qualitative stimuli—helps to distinguish among these indistinct cases and also highlights the observed diversity of functional organization (Table 2). It does not, however, solve the problem of what precisely is, and is not, self-organization. I believe that we are unlikely to suceed in formulating a single, well-defined, and satisfactory definition of self-organization. (The concept of "complexity" is similar: you know it when you see it, but there is no consensus on its definition.) Rather than worry about semantics, we should focus on studying these fascinating phenomena, in particular, striving to identify their underlying proximate mechanisms.

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