

Self-organizing Systems

Introductory article

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Self-organizing systems are physical and biological systems in which pattern and structure at the global level arises solely from interactions among the lower-level components of the system. The rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern.

WHAT IS SELF-ORGANIZATION?

Self-organization is a process whereby pattern at the global level of a system emerges solely from interactions among the lower-level components of the system. The rules specifying the interactions among the system's components are executed using only local information, without reference to the global pattern. Examples of self-organization include a wide range of pattern formation processes in both physical and biological systems: sand grains assembling into rippled dunes, chemical reactants forming swirling spiral patterns, the patterns on sea shells, or fish swimming in coordinated schools (Figure 1). 'Pattern' is used here in a broad sense to refer not only to a particular arrangement of objects in space, but also to structure and organization in time. An example is the remarkable synchronous flashing that sometimes develops among aggregations of thousands of fireflies in southeast Asia. In neurobiology, self-organization contributes to temporal structure and anatomical organization in systems ranging from central pattern generators in simple invertebrates to cognition in humans.

In self-organizing systems, pattern and organization develop through interactions internal to the system, that is, without the intervention of external influences, such as a 'leader' who directs or oversees the process. The pattern is an emergent property of the system itself, rather than a property imposed upon the system by an external supervisory influence.

EMERGENT PROPERTIES IN A SELF-ORGANIZING SYSTEM

The term 'emergence' refers to a process by which a system of interacting elements acquires qualitatively new pattern and structure that cannot be understood simply as the superposition of the individual contributions. Although the term may suggest that something mysteriously or magically materializes within the system, this is not the case. The human mind is generally poor at predicting the properties of systems that consist of multiple components with complex, dynamic interactions. Thus, even if one has a full knowledge of the system's elements and their mode of interaction, the collective properties of a self-organizing system often seem to arise unexpectedly.

HOW DOES A SELF-ORGANIZING SYSTEM WORK?

An example may make this abstract description of self-organization and emergent properties clearer. Striped and mottled patterns are found throughout nature – on a zebra's coat, on a fish's skin, and in the ocular dominance columns of the brain (Figure 2). Experimental and theoretical work suggests that these patterns develop from a few simple rules that are continually iterated among the components of the system. Suppose, for example, that each pigment cell on a zebra's coat could either produce a dark pigment or not, depending on a certain chemical activation above or below a certain threshold level. Further suppose that the cells in the skin produced both a chemical activator and an antagonistic inhibitor (called 'morphogens'), which both diffused through the skin. The rules regulating the state of each cell – either 'on' (producing pigment) or 'off' (not producing pigment) – depend on the relative strengths of the activation and inhibition,

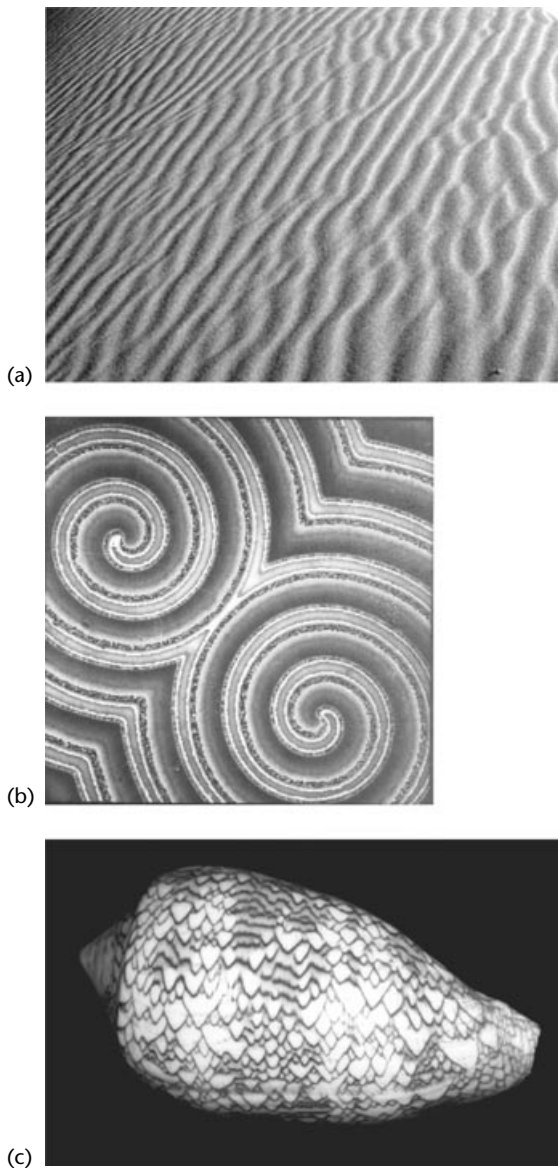


Figure 1. Examples of self-organized pattern formation in physical, chemical, and biological systems. (a) Sand dune stripes. (b) Belusov-Zhabotinsky chemical reaction (image courtesy of Stefan C. Müller). (c) A cone shell from Ceylon.

their diffusion rates, the initial distribution of the cells, and their thresholds for pigment production.

In 1952, Alan Turing first suggested the general scheme for this mechanism of self-organized pattern formation. In 1972, A. Gierer and H. Meinhardt developed a model as shown in Figure 3. Their system has a series of sites that are the source of a short-range activator, which has two functions: to promote its own productions (autocatalysis), and to cause an increase in the production of an

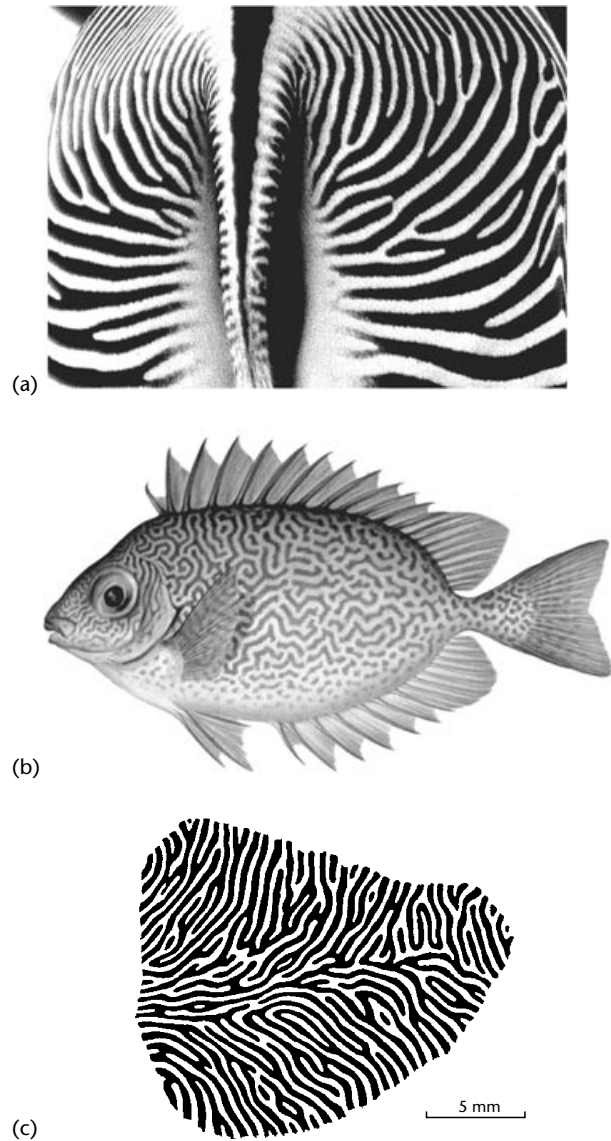


Figure 2. Striped and mottled patterns found in biological systems. (a) Alternating stripes on a zebra's coat (*Equus grevii*). (b) Mottled pattern of pigments on the skin of a vermiculated rabbitfish (*Siganus vermiculatus*). (c) Ocular dominance stripes in the visual cortex of a macaque monkey. Regions receiving inputs from one eye are shown in black, and regions receiving inputs from the other eye are shown in white. Adapted from: Hubel DH and Wiesel TN (1977) Functional architecture of the macaque monkey visual cortex. *Proceedings of the Royal Society, Series B* **198**: 1–59.

antagonist, the inhibitor. Since the inhibitor diffuses rapidly into the surroundings, the result is a local increase in the activation and a long-range antagonistic effect that restricts the self-enhancing reaction and keeps it localized.

SIMULATION OF SELF-ORGANIZING SYSTEMS

Because of the difficulty of predicting the behavior of these systems, computer simulations are a useful means of performing 'thought experiments' and for better understanding how these systems work. One method of modeling these systems is by the use of nonlinear differential equations. Another method is to simulate the system by means of cellular automata.

A cellular automaton is a simulation that is discrete in time, space, and state. Typically, the components (cells) of the system are arranged on

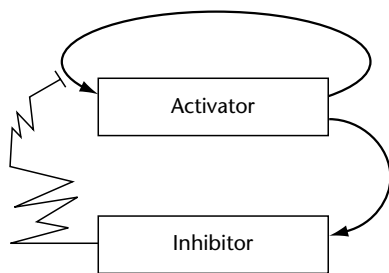


Figure 3. Reaction scheme for pattern formation by autocatalysis and long-range inhibition. The two arrows denote activation, with the activator stimulating both its own production (autocatalysis) and that of the inhibitor. The jagged line shows the effect of the inhibitor which provides negative feedback by inhibiting the effect of the activator. Adapted from: Meinhardt H (1995) *The Algorithmic Beauty of Sea Shells*. Berlin, Germany: Springer.

a two-dimensional grid or lattice. Each cell is characterized by its location on the grid and its condition (state). Cells interact with each other according to a set of simple rules which take into account their proximity to neighboring cells, their own state, and the states of their neighbors. The rules specify the transition of the cell from one state to another as the system evolves over time.

Consider the example of animal coat patterns presented above. This can be implemented as a cellular automaton model that consists of a set of cells laid out on a grid. Each cell is initially assigned a state randomly, 'on' or 'off'. Each 'on' cell is assumed to produce a specified amount of activator and a specified amount of inhibitor that diffuse at different rates across the grid. In the simulation, each 'on' cell is represented as black and each 'off' cell is represented as white. At each timestep, the program calculated the net amount of activation at each site on the grid. This is determined as the difference between the sum of all the activation from the cells in the neighborhood and the sum of all the inhibition from those cells in the neighborhood. If this total is above a prespecified threshold level, then the cell at that site is assigned the 'on' state; otherwise, it is assigned the 'off' state. In this manner, cells switch from one state to another according to a single rule. The program continually iterates the rule, causing a pattern to emerge from the initial random array of 'on' and 'off' cells, as shown in Figure 4. For one set of diffusion rules, an irregular mottled pattern develops. When the

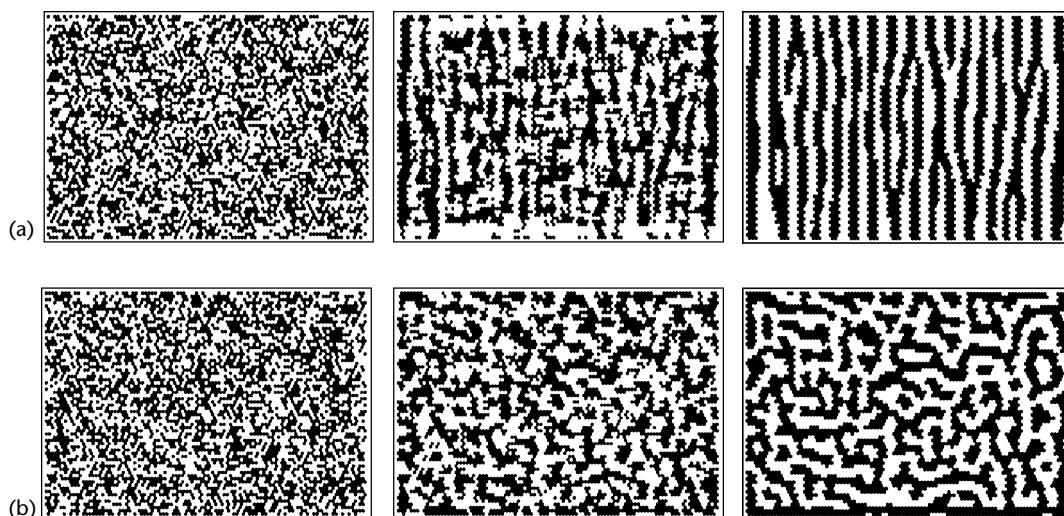


Figure 4. Cellular automaton simulations of pattern formation according to an activation-inhibition model. In each example, the first grid shows the initial random state of the system, the second grid shows an intermediate state, and the third grid shows the final stable pattern. (a) Time sequence showing a striped pattern formation, as in Figures 2(a) and 2(c). (b) Time sequence showing a mottled pattern formation, as in Figure 2(b).

conditions are changed slightly, a zebra-stripe pattern develops. The only differences between the two examples shown are that in the zebra-stripe pattern the diffusion of the activator and inhibitor is greater in one direction than the other, and that the relative strengths of the activator and inhibitor are different in the two cases.

SELF-ORGANIZATION IN THE NEURAL AND COGNITIVE SCIENCES

To understand the brain is one of the greatest challenges in biology. The brain of an insect such as a honey-bee contains relatively few neurons – approximately one million. In isolation, each neuron is essentially a simple switch. When stimulated sufficiently, an impulse is fired, and a brief electrical event called the *action potential* moves through the cell from one end to the other. Although the insect brain is miniscule, with relatively few neurons, compared with that of birds or mammals, it nonetheless coordinates very sophisticated behaviors. The honey-bee is arguably more complex than any computer. This tiny insect can navigate by the sun, fly to a food source, make decisions, communicate with other honey-bees, and perform many other complex activities.

The brain achieves this complexity largely through the connectivity of its elements and their interactions. Each neuron is connected to others through synapses, which form a vast network of dense interconnections. In ways that we are just beginning to understand, this connectivity is the basis of the brain's enormous complexity.

Neuroscientists are beginning to understand both how these connections among the neurons develop and how their interactions make cognition possible. Both of these processes rely, in large part, on self-organization. One of the great mysteries of biology is how the enormous morphogenic, physiological, behavioral, and cognitive complexity of an organism can be achieved with the limited amount of genetic information contained within the genome. It is inconceivable that the pattern of connections for each neuron in the brain could be genetically coded. Rather, there must exist special mechanisms for economizing on the amount of

information that must be coded within the genes. Self-organization is such a mechanism. For example, the pattern of ocular dominance stripes in the visual cortex of the brain (Figure 2(c)) is a characteristic morphogenic feature of neuroanatomical organization. The neural inputs from each eye to the visual cortex in the back of the brain consist of a series of alternating stripes. This architecture is believed to play an important role in how the brain organizes and interprets visual information received by the retina. This functional architecture can be seen by injecting radioactive proline into one eye, and making autoradiographs of sections of the cortex. The resulting pattern is reminiscent of the stripes seen on a zebra's coat or the ridges of a sand dune. These patterns are believed to arise through a self-organizing activation–inhibition mechanism similar to that described above.

Studies such as these suggest that through natural selection, organisms can evolve mechanisms that rely on relatively simple sets of rules – algorithms economically encoded in the genome. Through self-organizing processes these algorithms can generate the enormous complexity seen in biological systems. The result has been the evolution of complex morphological and physiological adaptations and behavioral and cognitive abilities.

Further Reading

- Camazine S, Deneubourg JL, Franks N *et al.* (2001) *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.
- Gierer A and Meinhardt H (1972) A theory of biological pattern formation. *Kybernetik* **12**: 30–39.
- Hubel DH and Wiesel TN (1977) Functional architecture of the macaque monkey visual cortex. *Proceedings of the Royal Society, Series B* **198**: 1–59.
- Meinhardt H (1995) *The Algorithmic Beauty of Sea Shells*. Berlin, Germany: Springer-Verlag.
- Miller KD, Keller JB and Stryker MP (1989) Ocular dominance column development: analysis and simulation *Science* **245**: 605–615.
- Swindale NV (1980) A model for the formation of ocular dominance stripes. *Proceedings of the Royal Society, Series B* **208**: 243–264
- Turing A (1952) The chemical basis for morphogenesis. *Philosophical Transactions of the Royal Society* **237**: 37–72.